

Ecology and life history of *Meta bourneti* (Araneae: Tetragnathidae) from Monte Albo (Sardinia, Italy) (#29230)

1

First revision

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Ecology and life history of *Meta bourneti* (Araneae: Tetragnathidae) from Monte Albo (Sardinia, Italy)

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The orb-weaver spider *Meta bourneti* Simon, 1922 (Araneae: Tetragnathidae) is one of the most common cave predator occurring in the Mediterranean basin. Although the congeneric *M. menardi* represented the model species in several studies, our knowledge of *M. bourneti* is founded on observations performed on a handful of populations. In this study *M. bourneti* spiders were studied in caves of Monte Albo (Sardinia, Italy) over a full year. Generalized Linear Mixed Models were used to analyze spider occupancy inside cave environments, as well as spider abundance. Analyses on *M. bourneti* occupancy and abundance were repeated three times: for all individuals and for adults and juveniles separately. Generalized Linear Models, were used to weight species absence based on its detection probability. Linear Mixed Models were used to detect possible divergences in underground spatial use between adult and juvenile spiders. Although widespread on the mountain, *M. bourneti* generally showed low density and low detection probability; most of the individuals observed were juveniles. The spiders generally occupied cave sectors with high ceilings that were deep enough to show particular microclimatic features; adults tended to occupy less illuminated areas than juveniles, while the latter were more frequently found in sectors showing high humidity. The abundance of *M. bourneti* was strongly related to high humidity and the presence of two troglophile species, *Hydromantes flavus* and *Oxychilus oppressus*. The abundance of juveniles was related to sector temperature and humidity, to the presence of *H. flavus* and *O. oppressus* and to morphological sector features. However, when adults only were considered, no significant relationships were found. Adult and juvenile spiders did not differ in spatial distribution inside the caves studied, but a seasonal distribution of the species along cave walls was observed. Microclimate appears to be one of the most important features affecting both presence and abundance of *M. bourneti* in underground environments. Individuals tended to occupy a lower height during hot seasons, probably looking for more suitable microclimatic

conditions. This study added further useful information to better comprehend the ecology of these widespread cave-dwelling spiders.

Ecology and life history of *Meta bourneti* (Araneae: Tetragnathidae) from Monte Albo (Sardinia, Italy)

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14 Abstract

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37 environments. Individuals tended to occupy a lower height during hot seasons, probably looking
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INTRODUCTION

Underground environments, from shallow cracks and burrows to the deepest karst systems, are peculiar habitats showing a characteristic combination of environmental features: they generally show little or no light, high air humidity and a relatively stable temperature resembling the mean annual temperature occurring in outdoor surrounding areas (Culver & Pipan, 2009; Smithson, 1991). Underground microclimate is generally shaped by the influence of external climate which, through openings connecting underground environments with outer ones, spread in and contribute to creating different microhabitats (Badino, 2004; Badino, 2010; Campbell Grant, Lowe & Fagan, 2007; Lunghi, Manenti & Ficetola, 2015). The most evident result of such influence is the formation of three different macro-ecological zones (Culver & White, 2005). The zone adjacent to the connection with the outdoor is the most affected by external influences; indeed, the microclimate of this area generally resembles the environmental conditions occurring in surrounding outdoor areas. Then, there is the so-called twilight zone, where external influences are weaker and incoming light is generally low. Finally, there is the deep zone, where incoming light is absent and microclimatic features are the most stable.

Underground environments house a rich biodiversity of species, that display unique and peculiar adaptations to the different ecological zones (Romero, 2011). A species' degree of association to subterranean conditions represents the basis for the general ecological classification used in distinguishing between different groups of cave-dwelling organisms (Christiansen, 1962; Novak et al., 2012; Pavan, 1944; Sket, 2008); however, several other characters are used to classify cave animals (to a complete overview of this classification see Trajano & de Carvalho, 2017). The most specialized are called troglobites, species closely connected to the deep areas of subterranean environments. Troglobites often show specific

adaptations, such as depigmentation, anophthalmia, elongation of appendages, and reduction in metabolic rates (*Aspiras et al., 2012; Bilandžija et al., 2013; Biswas, 2009; Hervant, Mathieu & Durand, 2000*). In contrast, troglaphiles can exploit both epigean and hypogean environments and their adaptations to cave life are reduced or even absent (*Di Russo et al., 1999; Fenolio et al., 2006; Lunghi, Manenti & Ficetola, 2017*). Troglaxenes are epigean species accidentally found in the shallowest part of subterranean environments. However, this classification has turned out to be too strict (*Lunghi, Manenti & Ficetola, 2014; Romero, 2009*), as species usually thought to be accidental are indeed potential residents playing an important role for the entire ecosystem (*Lunghi et al., 2018a; Manenti, Lunghi & Ficetola, 2017; Manenti, Siesa & Ficetola, 2013*).

Despite an increasing interest in subterranean ecological spaces and their related biodiversity that has occurred in the last decades (*Culver & Pipan, 2009; Culver & Pipan, 2014; Juan et al., 2010; Romero, 2009*), current knowledge on cave-dwelling species is still far from being considered complete. A good example is given by the troglaphile orb-weaving spider *Meta bourneti* Simon, 1922 (Araneae, Tetragnathidae). *Meta* spiders are among the most common predators in cave environments (*Mammola & Isaia, 2017b; Mammola, Piano & Isaia, 2016; Manenti, Lunghi & Ficetola, 2015; Pastorelli & Laghi, 2006*). These spiders show an interesting complex life history: during their early life stages they are phototaxic and disperse in outdoor environments, while during the adult phase they become photophobic and inhabit subterranean environments, where they reproduce (*Chiavazzo et al., 2015; Smithers, 2005b; Smithers & Smith, 1998*; but see also Fig. 6 in *Mammola & Isaia, 2014*). *Meta* spiders are at the apex of the subterranean food-chain, preying on several species using both web and active hunting (*Lunghi, Manenti & Ficetola, 2017; Mammola & Isaia, 2014; Novak et al., 2010; Pastorelli & Laghi,*

2006; Smithers, 2005a; Tercafs, 1972). However, young spiders are in turn potential prey of other cave predators (Lunghi et al., 2018b).

In Europe and the Mediterranean basin area, two species of *Meta* spiders are commonly observed: *M. menardi* and *M. bourneti* (Fernández-Pérez, Castro & Prieto, 2014; Fritzén & Koponen, 2011; Mammola & Isaia, 2014; Nentwig et al., 2018). Although the former is the subject of several studies (Ecker & Moritz, 1992; Hörweg, Blick & Zaenker, 2012; Lunghi, Manenti & Ficetola, 2017; Mammola, Piano & Isaia, 2016; Manenti, Lunghi & Ficetola, 2015), research on *M. bourneti* is very limited (Boissin, 1973; Mammola, 2017; Mammola & Isaia, 2017a). In a recent study, Mammola and Isaia (2014) studied the distribution and abundance of *M. menardi* and *M. bourneti* in six caves located in the north-west of Italy. Although they confirm the previously hypothesized similarities in habitat selection between the two cave-dwelling *Meta* spiders (Gasparo & Thaler, 1999), in this study it emerged that *M. bourneti* was present at warmer ~~temperature~~ ^{temperatures} and showed a shift in its life cycle compared to the congeneric *M. menardi*; these findings likely result from the competition between the two species (Mammola & Isaia, 2014).

The present study provides the first report of the ecology and life history of *M. bourneti* populations from Sardinia (Italy). In this area the congeneric *M. menardi* is not present and thus, no potential interspecific interactions limit habitat selection of *M. bourneti* (Mammola & Isaia, 2014; Nentwig et al., 2018). This study aims to produce information related to *i*) the effect of abiotic and biotic factors on both occupancy and abundance of *M. bourneti* in subterranean environments, *ii*) evaluate spatial distribution of these spiders within caves, *iii*) see whether differences between life stages (juveniles vs adults) occur and *iv*) gather and summarize information on the life history of the species.

108

109 MATERIALS & METHODS

110 Dataset

111 The analyzed dataset focuses on *M. bournetii* observed in caves from the Monte Albo (north-east
 112 Sardinia, Italy) (Fig.1; Table S1). Data were collected from seven different caves; however, in
 113 one of the surveyed caves the presence of the species has never been detected and thus, it will
 114 not be considered in the following analyses (N of considered caves = 6) (Fig. 1). Surveys were
 115 performed seasonally, from autumn 2015 to summer 2016, thus covering a full year. For every
 116 season, at least a pair of samplings was performed with ^{gaps}gap of 1-7 days. Inner cave environments
 117 were divided horizontally into portions of 3 m (hereafter, sectors), to collect fine-scale data on
 118 both cave morphology and microclimate, as well as on the occurrence of other cave-dwelling
 119 species (*Ficetola*, *Pennati* & *Manenti*, 2012; *Lunghi*, *Manenti* & *Ficetola*, 2017). Caves ^{were}where
 120 explored entirely or up to the point reachable without speleological equipment. Within each cave
 121 sector the following abiotic data were recorded: maximum height and width, wall irregularity,
 122 average temperature (°C), humidity (%) and illuminance (lux). Using a ^{meter tape}tape-meter, the ^{inner}cave ^{inner}inner
 123 environment was divided into sectors of 3-linear meters ^{of length}of length. At the end of each sector,
 124 using a laser meter (Anself RZE-70, accuracy 2 mm) the maximum height and width were
 125 recorded. In the same point, the average wall irregularity (i.e., presence of wall protuberance)
 126 was estimated. To perform such measurement, a string of one meter of length was placed along
 127 the cave wall, between 0.5 – 2 m of height, unrolling it vertically and following the shape of the
 128 cave wall; a ^{meter tape}tape-meter was used to measure the linear distance between the two extremities of
 129 the string (*Ficetola*, *Pennati* & *Manenti*, 2012; *Lunghi*, *Manenti* & *Ficetola*, 2014). During each
 130 survey, inner microclimatic data were recorded using a Lafayette TDP92 thermo-hygrometer

(accuracy: 0.1°C and 0.1%). At the end of each cave sector, the average air temperature and humidity were estimated by merging data recorded in two different points: at ground level and at 2.5 m of height (or at the ceiling if sector height was lower). Microclimatic data were recorded paying attention to limit operator influence (*Lopes Ferreira et al., 2015*). At the end of each cave sector, the maximum and minimum incident light using a Velleman DVM1300 light meter (minimum recordable light: 0.1 lux) was also measured. A standardized survey method (7.5 min/sector) was used to collect data on the presence of six cave-dwelling species: *M. bourneti*, *Hydromantes flavus*, *Metellina merianae*, *Tegenaria* sp., *Oxychilus oppressus* and *Limonia nubeculosa*. These species likely interact with *Meta* spiders, as they represent both potential prey and predators (*Lunghi et al., 2018b*; *Manenti, Lunghi & Ficetola, 2015*; *Novak et al., 2010*). *Meta* spiders were also counted and ascribed to two different categories on the basis of body size (prosoma + opisthosoma): adults with fully developed pedipalps (body size ≥ 10 mm) and juveniles (body size <10 mm) (*Bellmann, 2011*; *Mammola & Isaia, 2014*; *Nentwig et al., 2018*). Furthermore, the number of observed cocoon^s was also recorded.

Data analyses

The following analyses were performed in R (*R Core Team, 2016*). Analyses on detection probability, species-habitat association and abundance were performed three times, one for each group studied (all individuals, adults only and juveniles only). Data for modeling species occurrence and abundance, is only related to surveys in which microclimatic features were recorded (cave surveys = 31, *N* of spiders = 110).

Detection probability

Cave spiders are among the species showing imperfect detection: a species is present when it is observed, but a lack of observation does not mean its true absence (MacKenzie *et al.*, 2006). The detection probability of *M. bourneti* was estimated on the basis of twenty-seven pairs of cave surveys (i.e., 624 pairs of cave sectors) performed during each season with a gap ≤ 7 days (package unmarked; Fiske & Chandler, 2011), a prerequisite for population closure (i.e., no immigration or emigration occurs; MacKenzie *et al.*, 2006). Three possible covariates influencing spider detection were considered: the depth of the cave sector (hereafter, depth), the season and the wall irregularity. Four models were built (one for each covariate and one with none) and then ranked following the Akaike's Information Criterion (AIC); the one with the lowest AIC value was used to estimate detection probability (Burnham & Anderson, 2002; Burnham, Anderson & Huyvaert, 2011).

Analyses on species occurrence

Binomial Generalized Linear Mixed Models (GLMM) (packages lme4, lmerTest, MASS, MuMIn; Barton, 2016; Douglas *et al.*, 2015; Kuznetsova, Brockhoff & Christensen, 2016; Venables & Ripley, 2002) were used to assess the relationship between *Meta* spiders and the abiotic features characterizing the cave environments. The presence/absence of the spiders was used as dependent variable, while sector's morphological (height, width and wall irregularity) and microclimatic (temperature, humidity and illuminance) features were used as independent variables. To evaluate whether spiders' preferences change through the year, the interaction between season and each of the considered microclimatic features was also included as a further

independent variable. Sector and cave identity were used as random factors. For each studied group, GLMMs ~~models~~ were built using all possible combinations of independent variables; such models were then ranked following the Akaike's Information Criterion corrected for small sample size (AICc) (Fang, 2011). The model showing the ~~lower~~ ^{lowest} AICc value was considered the best model. Following the recommendations of Richards, Whittingham and Stephens (2011), models representing more complicated versions of those with a lower AIC value and nested models were not considered as candidate models. The likelihood ratio test was used to assess the significance of variables included in the best AICc models. Before analyses, humidity was angular-transformed and illuminance log-transformed, to improve linearity.

Considering a potential variation in species-habitat association over time (Lunghi, Manenti & Ficetola, 2015; Lunghi, Manenti & Ficetola, 2017) and an overall low detection probability estimated for these spiders (see Results), I tested the robustness of the previous analyses using a method that allows weighting the species absence on the basis of its detection probability: the General Linear Models (GLM) (Gómez-Rodríguez *et al.*, 2012). Unfortunately, adding random factors to this analysis is impossible, hence the cave identity was included as a fixed factor. Following the same procedure described above, for each species all possible GLMs ~~models~~ were built and ranked following AICc. The significance of variables included in the best AICc model was tested using the likelihood ratio test (Bolker *et al.*, 2008).

Given that for some of the groups studied the best AICc model estimating detection probability included sector depth (see *Detection probability of M. bournetii*), I repeated the GLM analysis for each group including depth as a further independent variable.

197 *Analyses of species abundance*

198 The relationship between abundance of *M. bournetii* and both microclimatic and biotic recorded
 199 parameters was examined using ~~GLMM~~^{GLMMs}. The observed abundance of spiders was used as a
 200 dependent variable, as it represents an index of true abundance (*Barke et al., 2017*). Season,
 201 along with both microclimatic (average temperature, humidity and illuminance) and biotic
 202 (presence/absence of the five considered species) features, were used as independent variables,
 203 while sector and cave identity as random factors. The significance of variables was tested with a
 204 Likelihood ratio test.

205

206 *Analyses on spatial distribution*

207 Two Linear Mixed Models (LMM) (package nlme; *Pinheiro et al., 2016*) were used to test
 208 whether adult and juvenile *M. bournetii* show divergences in the spatial use of subterranean
 209 environments; spiders' age class (adult/juveniles) and season were used as independent factors,
 210 and both sector and cave identity as random factors. The two dependent variables were the
 211 distance from the cave entrance and the height above cave floor respectively. The dataset used in
 212 this analysis is shown in Table S2.

213

214 **RESULTS**

215 Overall, a total of 182 ~~observations of *Meta bournetii*~~^{observed} (64 adults and 118 juveniles) were
 216 ~~performed within the caves studied~~^{performed within the caves studied} (average \pm SE = 30.33 ± 16.49 per cave). Observations of
 217 spiders were ~~the~~ highest in spring (3.17 spiders/visit), followed by winter (2.92 spiders/visit),

summer (2.67 spiders/visit) and autumn (1.92 spiders/visit) (Fig. 2). Of 1,958 cave surveys, spiders were observed only on 155 occasions, ~~in most of which~~ ^{with generally} just one spider ^{occupying} ~~occupied~~ the cave sector (132) (Table S2). Occupied cave sectors showed the following microclimatic conditions: average temperature = 14.47 ± 0.16 °C (min-max; 11.25-19.45); average humidity = 91.20 ± 0.3 % (80.6-94.3); average illuminance = 2.55 ± 1.8 lux (0-156.05). In only two cases two adults shared the same cave sector, while juveniles did this more frequently (4 times with an adult and 19 with other juveniles). Two cocoons were observed during autumn, each in a different cave. One of these was observed lying on the ground, already with numerous recently hatched spiders; during winter, spiderlings abandoned the cocoon. No further information on the second cocoon was available.

Detection probability of M. bourneti

In species analysis, the model including depth as covariate was the best model (AICc = 753.38) compared to the other three (model including season, AICc = 755.72; model including wall irregularity, AICc = 756.02; model without covariates, AICc = 756.24); *M. bourneti* showed an overall low detection probability (0.225). Considering adults only, the model including depth as covariate was the best (AICc = 383.72) compared to the other three (model including season, AICc = 389.71; model including wall irregularity, AICc = 389.71; model without covariates, AICc = 387.74); adults showed a very low detection probability (0.108). Finally, for juveniles the model including wall irregularity as covariate was the best (AICc = 559.02) compared to the other three (model including depth, AICc = 561.78; model including season, AICc = 559.98; model without covariates, AICc = 562.26); detection probability of juvenile *M. bourneti* was 0.164.

241

242 *Spider occurrence*

243 Results of the two analyses (GLMM and GLM) were consistent, thus showing a
244 substantial similarity in the identification of significant variables (Tables 1 and 2). The
245 occurrence of *M. bourneti* was positively related to sector height and humidity; the best GLMM
246 model also included the season and the interaction between season and illuminance, while in the
247 best GLM the site was also included (Tables 1 and 2). The occurrence of adult spiders was
248 negatively related to illuminance (Tables 1 and 2). The occurrence of juvenile spiders was
249 positively related to sector height and humidity; a significant relationship with season was
250 included in the best model of both analyses. The best GLMM also included a significant
251 relationship between season and illuminance, while in the best GLM the site was also included
252 (Tables 1 and 2).

253 Results of GLM including sector depth as a further independent variable were consistent
254 with those of the previous GLM analyses (Tables S3 and S4).

255

256 *Spider abundance*

257 The abundance of *M. bourneti* was related to sector humidity ($F_{1,543.59} = 6.7, P = 0.01$)
258 season ($F_{3,566.23} = 3.41, P = 0.017$) and the presence of *Hydromantes flavus* ($F_{1,672.34} = 21.91, P <$
259 0.001) and *Oxychilus oppressus* ($F_{1,673.13} = 22.55, P < 0.001$). Spiders were more abundant in
260 cave sectors with high humidity and where *H. flavus* and *O. oppressus* were present. The
261 abundance of adults showed no significant correlation with the variables considered. The
262 abundance of juveniles was related to sector temperature ($F_{1,267.93} = 4.22, P = 0.041$), humidity

($F_{1,561.55} = 7.65$, $P = 0.006$), season ($F_{3,580.85} = 4.27$, $P = 0.005$) and the presence of both *H. flavus* ($F_{1,673.15} = 25.65$, $P < 0.001$) and *O. oppressus* ($F_{1,673.59} = 29.73$, $P < 0.001$); juvenile spiders were generally more abundant in warm cave sectors showing high humidity and where *H. flavus* and *O. oppressus* were present.

Spider distribution

Distance from cave entrance did not differ ^{between} ~~by~~ age classes ($F_{1,122} = 0.26$, $P = 0.608$) nor between seasons ($F_{3,122} = 0.58$, $P = 0.626$). Vertical distribution of spiders (i.e., height from the cave floor) did not differ ^{between} ~~by~~ age classes ($F_{1,113} = 0.85$, $P = 0.358$) but a significant effect of season was detected ($F_{3,113} = 6.20$, $P < 0.001$); *Meta* spiders were generally at a lower height during spring and summer (Fig. 3).

DISCUSSION

M. bournetii spiders represent one of the top predators commonly occurring in Monte Albo caves; indeed, spiders were present in most of the subterranean environments sampled. The only cave of the dataset in which *M. bournetii* was never observed was located at an elevation exceeding 1000 m a.s.l.; unsuitable environmental conditions for the species likely occur ^{at these higher elevations} (Lunghi et al., 2018d; Mammola & Isaia, 2014). The ^{largest} ~~highest~~ number of spiders observed occurred in spring, a season in which invertebrates are generally more active (Bale & Hayward, 2010). In the populations studied, the life cycle of *M. bournetii* seems to differ slightly from what was observed in north-western Italian populations (Mammola & Isaia, 2014); in September, the cocoon was already spun, and spiderlings started to emigrate in January. This possible variation in breeding

phenology probably occurred because the two study areas are characterized by different climatic conditions (data derived from *Hijmans et al., 2005*). Indeed, it was recently shown that climatic conditions occurring at the surface can significantly influence the subterranean breeding activity of troglophile species (*Lunghi et al., 2018c*). However, the two data collections on *M. bourneti* were performed in different periods (2012-2013 in north-west Italy and 2015-2016 in Sardinia), it is therefore still unclear whether such a divergence may be due to a change in local climate or to an annual fluctuation of climatic conditions. In the future, an improvement ⁱⁿ of the number of cocoon^s observed, as well as repeated survey^s over different years, will help in understanding whether populations of *M. bourneti* show divergences in their life cycle.

Detection probability of *M. bourneti* was very low within cave sectors. Although the possibility to show a more secretive behavior if compared to the congeneric *M. menardi*, some other environmental factors may have had a strong influence on the availability of individuals to be detected (*Nichols, Thomas & Conn, 2008; Pollock et al., 2002*). For example, the average ceiling height was usually too high for an exhaustive survey (average height (\pm SD) = 3.19 ± 2.28 m). A potential vertical movement of individuals could have put them in a position where they become ^{difficult to} hardly detectable, ^{resulting in a} with a consequently negative effect on species detection (*Nichols, Thomas & Conn, 2008*). Another possibility is that the wall irregularity sheltered spiders (especially smaller ^{individulas} ~~one~~ ^{being observed} from ~~observer view~~). Despite the general low detection probability ^{allows for avoiding} ~~estimated for studied spiders~~ ~~allowed to avoid~~, the adopted methodology of data analysis ^S allowed to avoid potential biases due to such estimation^s, and highlighted a high consistency of results obtained by both GLMM^s and GLM^s (Tables 1 and 2). Occurrence of *M. bourneti* was generally related to cave sectors showing high humidity. Sector humidity also positively affected the presence of juvenile spiders, while adults showed a high occurrence in cave sectors with low light (Table 2).

These particular microclimatic conditions (high humidity and low illuminance) usually occur in cave areas far from the surface, where external influences are weaker and the microclimate is more stable (Culver & Pipan, 2009; Lunghi, Manenti & Ficetola, 2015). As was pointed out for both *M. bourneti* and *M. menardi*, these spiders occupy cave areas deep enough to show suitable microclimatic conditions, but still in the proximity of sites with elevated prey abundance (Lunghi, Manenti & Ficetola, 2017; Mammola & Isaia, 2014; Manenti, Lunghi & Ficetola, 2015). However, the tendency of *M. bourneti* to occupy cave sectors with high ceilings is just the opposite of what was observed for *M. menardi* (Lunghi, Manenti & Ficetola, 2017). Considering that these two species show similar hunting strategies (Mammola & Isaia, 2014), the different preferences of cave sector morphology may be driven by some other ecological factors. For example, in cave sectors with high ceilings, spiders may have more surface (i.e., cave wall) to escape from potential predators present in the same cave sectors (e.g., *Hydromantes* salamanders; Lunghi et al., 2018b). Indeed, sector height was particularly significant for juveniles, while for adults this variable was not included in the best AICc model (Tables 1 and 2).

Analyses of spider abundance identified both environmental and biological features as potential determinants. In cave areas with high humidity, *M. bourneti* showed the highest abundance. Furthermore, the presence of two ^{other} ~~of the~~ species considered (*Hydromantes flavus* and *Oxychilus oppressus*) had a strong influence on spider abundance. While it is possible that *M. bourneti* shares the same microhabitat preference with these species (Ficetola et al., 2018), trophic interactions between *M. bourneti* and these two species may also explain this particular association (Curry & Yeung, 2013; Lunghi et al., 2018b; Mammola & Isaia, 2014). However, compared to *H. flavus*, very limited ecological information on *M. bourneti* and *O. oppressus* are

available and thus, future studies are needed to shed light on this particular relationship. Overall, results from spider abundance analyses must be carefully interpreted. The majority of observations were related to juveniles (~66%) and this may have biased the analysis performed at species level. Indeed, results from the two analyses (all spiders and juveniles only) were basically the same, while when only adults were considered, no significant variables were detected.

~~No significant differences were found in the horizontal or vertical distributions between age classes.~~

~~Distribution of spiders in subterranean environments did not differ by age class: all individuals showed the same horizontal and vertical distribution.~~ Two or more spiders were rarely observed inside the same cave sector, and these circumstances generally involved juveniles (Table S2). Information relating to the behavior of this species is virtually absent; hence it is possible that individuals may be territorial, at least in some populations. Considering the limited sample size analyzed here (Table S1), further studies are needed to better comprehend the behavior of *M. bourneti* spiders. Seasonality did not affect *Meta* spider distribution along the horizontal development of the cave, but it strongly affected the vertical distribution of all individuals (Fig. 3); during hot seasons, spiders were found closer to the cave floor. Air circulation in cave environments is characterized by two main air layers, where the lowest has a cooler temperature (*Badino, 2010*). Therefore, it may be that during hot seasons the temperature of the upper layer becomes too high and spiders move toward the ground floor looking for a more suitable microclimatic condition (*Lunghi, Manenti & Ficetola, 2017*).

CONCLUSION

This study represents the first analysis performed on island populations of *Meta bournetii*, with the aim of adopting a more complete approach to the study of different ecological aspects of these cave-dwelling spiders. *Meta* spiders were found to be widespread in subterranean environments of Monte Albo, but with low densities. The species' life cycle, as well as the distribution of individuals inside caves, appears to be strongly dependent by local climatic conditions, showing some divergences from mainland Italian populations. Microclimate was one of the main features affecting both presence and abundance of *M. bournetii* in subterranean environments. Morphological cave features may help *Meta* spiders in ~~escape~~^{escaping} unsuitable microclimatic conditions and ~~avoid~~^{avoiding} potential predators. During their subterranean phase, spiders showed the same tendency to avoid the shallowest part of the caves (only one out of 182 observed individuals was found within the first six meters), areas which likely have unsuitable microclimatic conditions. ~~Surely enough, the~~^{The} vertical movement of spiders ~~suggests a specific~~^{during different seasons also} behavior of individuals aiming to limit exposure to unsuitable microclimatic conditions. However, further studies on populations from different geographical ~~areas~~^{regions} may help in providing a better overview of the ecology of this widespread cave-dwelling species.

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Table 1 (on next page)

The best five AICc models relating the presence of *Meta bournetii*.

(*Meta* spiders, Adults and Juveniles)
In both GLMM and GLM analyses, the presence of the respective group (~~a-f~~) was used as a dependent variable. Independent variables were: Height, Width and wall irregularity (Het) of sectors, Season of the survey, average Temperature (Temp), Humidity (Hum) and Illuminance (Lux) recorded inside each sector. Interactions (*) between season and microclimatic features (temperature, humidity, illuminance) were added as further independent variables. In GLMM analyses both sector and cave identity were used as random factors; in ^{GLMs}~~GLM~~, cave identity was included as an additional independent variable. The ^{"X"}~~X~~ indicates the presence of the variable in the respective AICc model; ~~-~~ indicate that the variable was not used in the analyses.

Independent variables included into the model											df	AICc	Δ-AICc	Weight		
	Height	Width	Het	Season	Cave	Temp	Hum	Lux	Temp*S	Hum*S	Lux*S					
GLMM											GLMM					
Meta spiders	a) Meta spiders															
	X			X	—		X	X			X	12	456.9	0	0.254	
	X		X	X	—		X	X			X	13	457.3	0.41	0.207	
	X			X	—		X	X		X	X	15	457.8	0.91	0.161	
	X	X		X	—		X	X		X	X	13	458.2	1.34	0.130	
Adults	X		X	X	—		X	X		X	X	16	458.3	1.42	0.125	
	b) Adults															
			X		—			X				5	220	0	0.220	
			X		—		X	X				6	220.2	0.17	0.202	
	X				—			X				5	220.6	0.56	0.166	
Juveniles					—			X				4	220.9	0.89	0.141	
	X		X		—			X				6	220.9	0.95	0.137	
	e)															
	X			X	—	X	X	X			X	13	344.4	0	0.246	
	X			X	—		X	X		X	X	15	345.1	0.74	0.171	
	X			X	—		X	X			X	12	345.2	0.81	0.164	
	X			X	—	X	X			X		12	345.4	0.96	0.153	
	X			X	—		X			X		11	345.4	0.98	0.151	
	GLM											GLM				
	Meta spiders	d) Meta spiders														
X				X	X		X					11	149.3	0	0.357	
X			X	X	X		X					12	150.9	1.53	0.166	
X		X		X	X		X					12	151	1.66	0.156	
X				X	X		X	X				12	151.3	2.02	0.130	
Adults	X			X	X	X	X					12	151.5	2.17	0.121	
	e) Adults															
	X			X	X			X				11	77.3	0	0.233	
			X	X	X			X				11	77.5	0.22	0.209	
	X		X	X	X			X				12	77.7	0.45	0.186	
Juveniles				X	X			X				10	79.2	0.95	0.145	
	X			X	X			X				12	78.5	1.15	0.131	
	f) Juveniles															
	X			X	X		X					11	102.5	0	0.315	
	X			X	X	X	X					12	103.1	0.56	0.238	
	X			X	X		X	X				12	104.4	1.93	0.120	
	X	X		X	X		X					12	104.5	1.96	0.118	
	X		X	X	X		X					12	105	1.99	0.117	

Table 2 (on next page)

Parameters related to the presence of *Meta bourneti* spiders.

(*Meta* spiders, Adults and Juveniles) the

For each group (a-c) are shown significance of variables included in the relative best AICc model of the respective analysis. Shaded variables are those included in the best model of both GLMM and GLM analyses.

Factor	GLMM			GLM		
	β	χ^2	P	β	χ^2	P
Meta spiders a) Meta-bourneti						
Season		10.33	0.016		4.99	0.173
Cave					12.08	0.034
Height	0.28	16.12	<0.001	0.27	17.51	<0.001
Humidity	13.29	13.87	<0.001	11.23	9.64	0.002
Illuminance	-1.71	0.01	0.917			
Illuminance*Season		14.57	0.002			
Adults b) adults						
Season					0.86	0.834
Cave					5.65	0.342
Height				0.24	3.75	0.053
Wall_Irreg	5.18	2.92	0.087			
Illuminance	-2.58	7.52	0.006	-3.03	10.06	0.001
Juveniles c) juveniles						
Season		18.7	<0.001		8.9	0.031
Cave					14.14	0.015
Height	0.29	14.65	<0.001	0.28	13.73	<0.001
Temperature	0.34	2.89	0.089			
Humidity	17.14	16.25	<0.001	13	8.19	0.004
Illuminance	-1.5	0.08	0.779			
Illuminance*Season		10.57	0.014			

Figure 1

Map of the surveyed area.

The map shows the surveyed caves in Monte Albo (Sardinia, Italy).

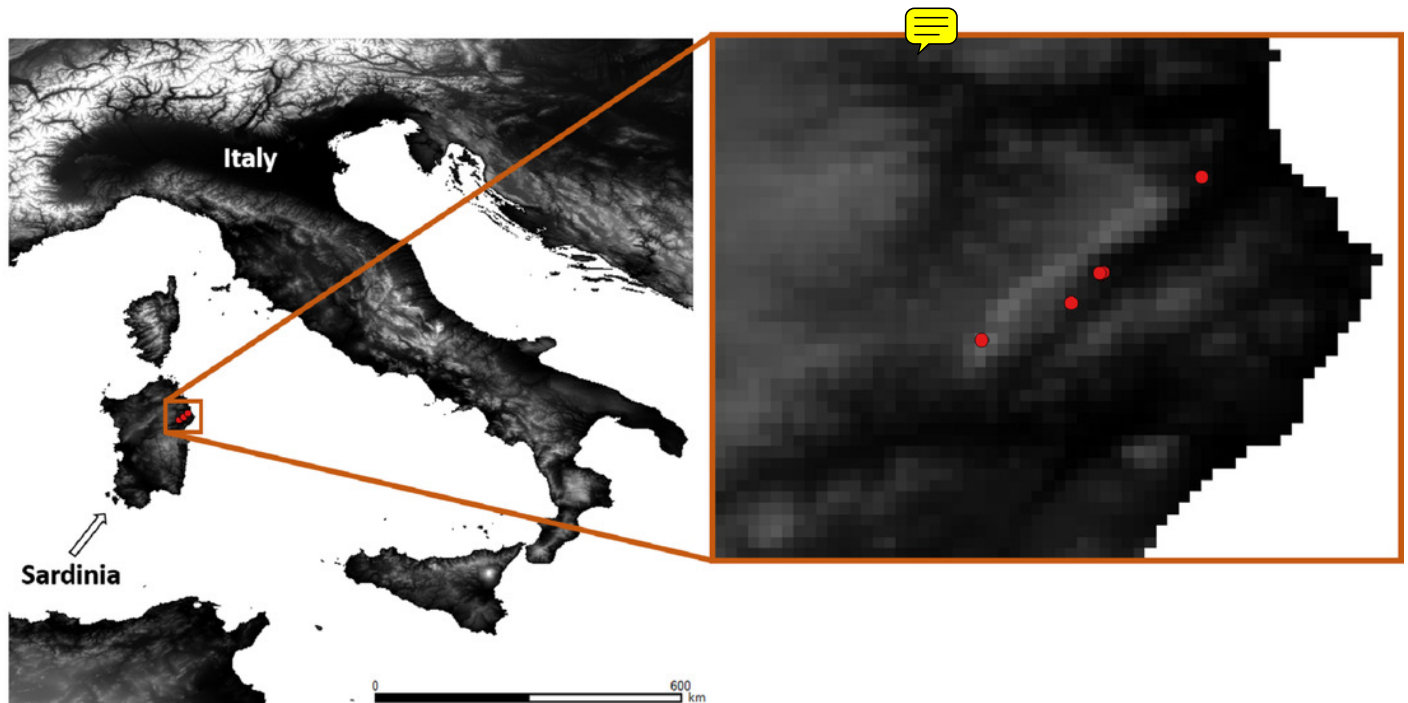


Figure 2

~~Abundance~~
~~Observation~~ of *Meta bourneti* spiders performed in Monte Albo's caves.

Seasonal number of observed spiders is given separating adults (dark grey) and juveniles (light grey) from autumn 2015 to summer 2016.

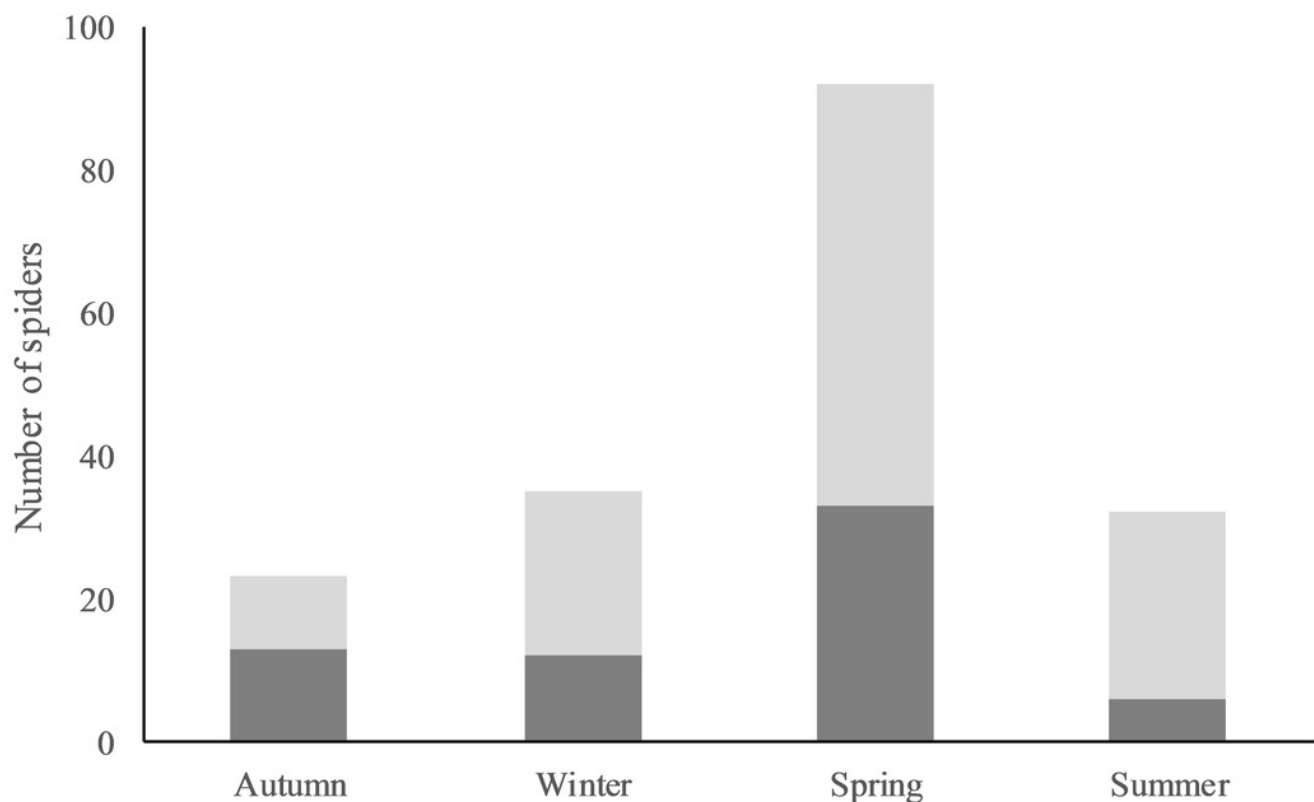


Figure 3

Boxplots indicating the vertical distribution of *Meta bourneti* along caves walls.

Differences in vertical distribution of spiders (average height above the ground floor) among seasons. Horizontal bar inside the box represents the median.

