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

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Abstract

Underground environments and related biodiversity are still relatively understudied. Even widespread cave-dwelling species show a considerable paucity of information regarding their ecology and life traits. This is the case of one of the most common cave predators occurring in Europe and in the whole Mediterranean basin: the orb-web spider *Meta bourneti*. Although the congeneric *M. menardi* represented the model species in several studies, *M. bourneti* was considered very little and available information regarding this species is founded on observations performed on a handful of populations. Therefore, further studies are required to produce a more complete species overview. In this study I analyzed data on *M. bourneti* spiders collected in caves of Monte Albo (Sardinia, Italy) throughout a full year. I used binomial Generalized Linear Mixed Models to analyze spider occupancy inside cave environments. The same data were also analyzed with Generalized Linear Models, an approach which allows weighting of species absence based on its detection probability. Generalized Linear Mixed Models were used to analyze spider abundance. Analyses on *Meta bourneti* occupancy and abundance were repeated three times: for all individuals and for adults and juveniles separately. Finally, Linear Mixed Models were used to detect possible divergences in underground spatial use between adult and juvenile spiders. Although widespread on the whole 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 and 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*); morphological sector features promoting predators' avoidance positively influenced the abundance of juveniles. However, when adults

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only were considered, no significant relationships were found. Adults 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 represents a further tile useful to better comprehend the ecology of these widespread cave-dwelling spiders.

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 & Pipan, 2009*). 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 (especially in animal species) which can show unique and peculiar adaptations to the different ecological zones (*Romero, 2011*). A species' degree of adaptation to cave life represents the base of the general classification used in distinguishing between different groups of cave-dwelling species (*Novak et al., 2012; Pavan, 1944; Sket, 2008*). The most specialized are called "troglobites", species closely connected to the deep areas of underground environments that evolved 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*).

Then there are species that optionally decide to remain stable underground but still able to exit, the so called “troglophiles”; these species can exploit different underground areas and their adaptations to cave life are reduced or even absent (*Di Russo et al., 1999; Fenolio et al., 2006; Lunghi, Manenti & Ficetola, 2017*). Finally, epigean species accidentally found in the shallowest part of underground environments are called “trogloxenes”. 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*).

Although the undeniable increase of interest in underground ecological spaces and related biodiversity which has occurred in the last decades (see as examples *Culver & Pipan, 2014; de Freitas, 2010; Fernandes, Batalha & Bichuette, 2016; Lunghi et al., 2018e; Studier et al., 1986*), current knowledge on cave-dwelling species is still far from being considered complete. A good example is given by the troglophile orb-web spider *Meta bourneti*. *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 are phototaxic and disperse in outdoor environments, while during the adult phase they become photophobic and inhabit underground environments, where they reproduce (*Chiavazzo et al., 2015; Manenti, Lunghi & Ficetola, 2015*). *Meta* spiders are at the apex of the underground 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, 2005*). 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 (*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*) provided some of the few available data on the ecology and life history of *M. bourneti*. The authors 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 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*). However, to provide more solid knowledge on *M. bourneti* spiders, further studies involving populations from different areas are needed.

Here I provide the first information related to the ecology and life history of *M. bourneti* populations from Sardinia (Italy). This study is based on data collected by *Lunghi et al.* (*unpublished*) and aims to provide new information on the occurrence and abundance of *M. bourneti* spiders, also providing information on a possible divergence in habitat use of different age classes.

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MATERIALS & METHODS

Dataset

The analyzed dataset gathers information on *Meta bourneti* and inhabited caves from the Monte Albo (north-east Sardinia, Italy) (*Lunghi et al., unpublished*). In one of the surveyed caves the presence of the species has never been detected and thus, it will not be considered in the following analyses (*N* of considered caves = 6). 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*). Surveys were performed seasonally, from autumn 2015 to summer 2016, thus covering a full year. Inner cave environments were divided horizontally into portions of 3 m (hereafter, sectors), to collect fine-scale data on both cave morphology and microclimate, as well as on the occurrence of other cave-dwelling species (*Ficetola, Pennati & Manenti, 2012; Lunghi, Manenti & Ficetola, 2017*). Within each cave sector the following abiotic data were recorded: maximum height and width, wall heterogeneity, average temperature (°C), humidity (%) and illuminance (lux). Furthermore, a standardized survey method (7.5 min/sector) was used to collect data on the presence of six cave-dwelling species: *Meta bourneti*, *Hydromantes flavus*, *Metellina merianae*, *Tegenaria* sp., *Oxychilus oppressus* and *Limonia nubeculosa* (data of the latter is integrated in the present study; Table S1). 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 ≥ 10mm) and juveniles (body size <10 mm) (*Bellmann, 2011; Mammola & Isaia, 2014; Nentwig et al., 2018*). For further information on the methodology used in data collection see (*Lunghi et al., unpublished*).

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Data analyses

The following analyses were performed in R (*R Core Team*, *2016*) using the packages lme4, lmerTest, MuMIn, MASS, nlme, and unmarked (*Bartoń, 2016; Douglas et al., 2015; Fiske & Chandler, 2011; Kuznetsova, Brockhoff & Christensen, 2016; Pinheiro et al., 2016; Venables & Ripley, 2002*). 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). To model species occurrence and abundance, I considered data only from 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*). I estimated the detection probability of *Meta bourneti* on the basis of twenty-seven pairs of surveys performed in all caves and in each season with a gap < 7 days (*Lunghi et al., unpublished*), a prerequisite for population closure (i.e., no immigration or emigration occurs; *MacKenzie et al., 2006*). I considered two possible covariates influencing spider detection: the depth of the cave sector (hereafter, depth) and the season. I built three models (one for each covariate and one with none) and then ranked them following the Akaike’s Information Criterion (AIC); the one with the lowest AIC value was used to estimate detection probability (*Burnham & Anderson, 2002*).

Analyses on species occurrence

I used binomial Generalized Linear Mixed Models (GLMM) 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 heterogeneity) 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 considered 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 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. If necessary, variables were logarithmic or square-root transformed to better fit the normal distribution (*Lunghi et al., unpublished*).

Considering a potential variation in species-habitat association over time (*Lunghi, Manenti & Ficetola, 2015; Lunghi, Manenti & Ficetola, 2017*) and an overall low detection probability observed 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 Meta bourneti*), I repeated the GLM analysis for each group including depth as a further independent variable.

Analyses of species abundance

I used GLMM to assess whether abundance of *Meta bourneti* was related to both microclimatic and biotic recorded parameters. The observed abundance of spiders was used as a dependent variable, as it represents an index of true abundance (*Barke et al., 2017*). Season, along with both microclimatic (average temperature, humidity and illuminance) and biotic (presence/absence of the five considered species) features, were used as independent variables, while sector and cave identity as random factors. The significance of variables was tested with a Likelihood ratio test.

Analyses on spatial distribution

To test whether adult and juvenile *M. bourneti* show divergences in the spatial use of underground environments, I used two Linear Mixed Models (LMM) with age class (adult/juveniles) and season as independent factors, and both sector and cave identity as random factors. The two dependent variables were the distance from the cave entrance and the height above cave floor respectively. The dataset used in this analysis is shown in Table S2.

RESULTS

Overall, a total of 182 observations of *Meta bourneti* (64 adults and 118 juveniles) were performed within the caves studied (average ± SE = 30.33 ± 16.49 per cave). Observations of 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. 1). Of 1,538 cave surveys, spiders were observed only on 153 occasions, in most of which just one spider occupied the cave sector (129) (Table S2). Occupied cave sectors showed the following microclimatic conditions: average temperature = 14.46 ± 0.16 °C (min-max; 11.25-19.45); average humidity = 91.23 ± 0.3 % (80.6-94.3); average illuminance = 2.52 ± 1.78 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 (Fig. 2A); during winter, spiderlings abandoned the cocoon (Fig. 2B). No further information on the second cocoon is available.

Detection probability of Meta bourneti

In species analysis, the model including depth as covariate was the best model (AICc = 747.93) compared to the other two (model including season, AICc = 751.36; model without covariates, AICc = 751.45); *Meta bourneti* showed an overall low detection probability (0.232). Considering adults only, the model without covariates was the best (AICc = 385.86) compared to the other two (model including depth, AICc = 385.94; model including season, AICc = 389.37); adults showed higher detection probability (0.4). Finally, for juveniles the model including season as covariate was the best (AICc = 557.36) compared to the other two (model including depth, AICc = 558.25; model without covariates, AICc = 559.14); detection probability of juvenile *M. bourneti* was the lowest (0.173).

Spider occurrence

Results of the two analyses (GLMM and GLM) were consistent, thus showing a substantial similarity in the identification of significant variables (Tables 1 and 2). The occurrence of *M. bourneti* was positively related to sector height and humidity; the best GLMM model also included the interaction between season and illuminance (Tables 1 and 2). The occurrence of adult spiders was negatively related to illuminance; the best GLM model also detected a positive relationship to sector height (Tables 1 and 2). The occurrence of juvenile spiders was positively related to sector height and humidity; a significant relationship with season was included in the best model of both analyses. The best GLMM model also included a significant relationship between season and illuminance (Tables 1 and 2).

Results of GLM including sector depth as a further independent variable were identical to those of the previous GLM analyses (Table S3).

Spider abundance

The abundance of *Meta bourneti* was related to sector humidity ($F_{1,481.38}$ = 6.61, P = 0.01) season ($F_{3,518.3}$ = 3.36, P = 0.018) and the presence of *Hydromantes flavus* ($F_{1,645.19}$ = 21.91, $P < 0.001$) and *Oxychilus oppressus* ($F_{1,645.1}$ = 24.01, $P < 0.001$). Spiders were more abundant in cave sectors with high humidity and where *H. flavus* and *O. oppressus* were present. The abundance of adults showed no significant correlation with the variables considered. The abundance of juveniles showed a relationship to sector temperature ($F_{1,223.76} = 4.15$, $P = 0.043$), humidity ($F_{1,524.87} = 7.41$, $P = 0.007$), season ($F_{3,548.94} = 4.22$, $P = 0.006$) and the presence of bot *H. flavus* ($F_{1,645.47} = 25.06$, $P < 0.001$) and *O. oppressus* ($F_{1,645.38} = 31.33$, $P < 0.001$); 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 by age classes ($F_{1,122} = 0.26$, $P = 0.608$) (Fig. 3A) 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 by age classes ($F_{1,113} = 0.85$, $P = 0.358$) (Fig. 3B) but a significant effect of season was detected ($F_{3,113} = 6.20$, $P < 0.001$); spiders were generally at a lower height during spring and summer.

DISCUSSION

Meta bourneti spiders represent one of the top predators commonly occurring in Monte Albo caves; indeed, spiders were usually present in all underground environments considered. The only cave of the dataset in which *M. bourneti* was never observed was located at an elevation exceeding 1000 m a.s.l. (*Lunghi et al., unpublished*); there, unsuitable environmental conditions for the species likely occur there (*Lunghi et al., 2018d; Mammola & Isaia, 2014*). The 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. bourneti* differed slightly from what was observed in north-western Italian populations (*Mammola &*

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Isaia, 2014); in September, cocoons were already spun, and spiderlings started to emigrate in January. This variation in breeding phenology probably occurred because the two study areas are characterized by different climatic conditions (*Hijmans et al., 2005*). Indeed, it was recently shown that climatic conditions occurring at the surface can significantly influence the underground 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 was due to a change in local climate or to an annual fluctuation of climatic conditions.

Occurrence of *M. bourneti* was generally related to cave sectors showing high humidity; this variable was observed to have the same effect on 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 areas far from the connection to 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 reasons. 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, *Meta bourneti* showed the highest abundance. Furthermore, the presence of two 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., in press*), trophic interactions between *M. bourneti* and these two species may explain this particular association (*Lunghi et al., 2018b; Mammola & Isaia, 2014*). However, results from spider abundance analyses must be carefully interpreted. The majority of observations were related to juveniles (~73%) 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.

Distribution of spiders in underground environments did not differ by age class: all individuals showed the same horizontal and vertical distribution (Fig. 3). 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 (*Lunghi et al., unpublished*), further studies are needed to better comprehend the behavior of *Meta 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; 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 more a suitable microclimatic condition (*Lunghi, Manenti & Ficetola, 2017*).

CONCLUSION

This study represents the first analysis performed on island populations of *Meta bourneti*, 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 underground 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. bourneti* in underground environments; morphological cave features promoting predators avoidance were also important for juvenile spiders. During their underground phase, spiders showed the same tendency to avoid the shallowest part of the caves, areas which likely have unsuitable microclimatic conditions. Surely enough, the vertical movement of spiders suggests a specific behavior of individuals aiming to limit exposure to unsuitable microclimatic conditions. However, further studies on populations from different geographical areas may help in providing a better overview of the ecology of these widespread cave-dwelling species.

References

Aspiras AC, Prasad R, Fong DW, Carlini DB, and Angelini DR. 2012. Parallel reduction in expression of the eye development gene hedgehog in separately derived cave populations of the amphipod *Gammarus minus*. *Journal of Evolutionary Biology* 25:995-1001. 10.1111/j.1420-9101.2012.02481.x

Badino G. 2004. Cave temperatures and global climatic change. *International Journal of Speleology* 33:103-114.

Badino G. 2010. Underground meteorology - "what's the weather underground?". *Acta Carsologica* 39:427-448.

Bale JS, and Hayward SAL. 2010. Insect overwintering in a changing climate. *The Journal of Experimental Biology* 213:980-994. 10.1242/jeb.037911

Barke RJ, Schofield MR, Link WA, and Sauer JR. 2017. On the reliability of N-mixture models for count data. *Biometrics*:1-9. 10.1111/biom.12734

Bartoń K. 2016. MuMIn: Multi-Model Inference. *R package version 1156*. https://CRAN.R-project.org/package=MuMIn

Bellmann H. 2011. *Guida ai ragni d'Europa*. Roma: Franco Muzzio Editore.

Bilandžija H, Ma L, Parkhurst A, and Jeffery WR. 2013. A potential benefit of albinism in *Astyanax* cavefish: downregulation of the oca2 gene increases tyrosine and catecholamine levels as an alternative to melanin synthesis. *PLoS ONE* 8:e80823. 10.1371/journal.pone.0080823

Biswas J. 2009. Kotumsar Cave biodiversity: a review of cavernicoles and their troglobiotic traits. *Biodiversity and Conservation* 19:275-289. DOI 10.1007/s10531-009-9710-7

Boissin L. 1973. Étude ultrastructurale de la spermiogenèse de *Meta bourneti* Simon (Arachnides, Aranéides, Metinae). *Comptes Rendus deuxième de la Réunion Arachnologique d'Expression Française* 7:22.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, and White J-SS. 2008. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24:127-135. 10.1016/j.tree.2008.10.008

Burnham KP, and Anderson DR. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. New York, NY: Springer.

Campbell Grant EH, Lowe WH, and Fagan WF. 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters* 10:165-175. 10.1111/j.1461-0248.2006.01007.x

Chiavazzo E, Isaia M, Mammola S, Lepore E, Ventola L, Asinari P, and Pugno NM. 2015. Cave spiders choose optimal environmental factors with respect to the generated entropy when laying their cocoon. *Scientific Reports* 5:7611. 10.1038/srep07611

Culver DC, and Pipan T. 2009. The biology of caves and other subterranean habitats. New York: Oxford University Press. p 254.

Culver DC, and Pipan T. 2014. *Shallow Subterranean Habitats: Ecology, Evolution, and Conservation*. New York, U.S.A.: Oxford University Press.

de Freitas CR. 2010. The role and importance of cave microclimate in the sustainable use and management of show caves. *Acta Carsologica* 39:477-489.

Di Russo C, Carchini G, Rampini M, Lucarelli M, and Sbordoni V. 1999. Long term stability of a terrestrial cave community. *International Journal of Speleology* 26:75-88.

Douglas B, Maechler M, Bolker B, and Walker S. 2015. Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software* 67:1-48. 10.18637/jss.v067.i01

Fang Y. 2011. Asymptotic equivalence between cross-validations and Akaike Information Criteria in Mixed-Effects Models. *Journal of Data Science* 9:15-21.

Fenolio DB, Graening GO, Collier BA, and Stout JF. 2006. Coprophagy in a cave-adapted salamander; the importance of bat guano examined through nutritional and stable isotope analyses. *Proceedings of the Royal Society B* 273:439-443. 10.1098/rspb.2005.3341

Fernandes CS, Batalha MA, and Bichuette ME. 2016. Does the cave environment reduce functional diversity? *PLoS ONE* 11:e0151958. 10.1371/journal.pone.0151958

Fernández-Pérez J, Castro A, and Prieto CE. 2014. Arañas cavernícolas (araneae) de la región vasco-cantábrica: nuevos registros y actualizacion del conocimiento. *Revista Ibérica de Aracnología* 25:77-91.

Ficetola GF, Lunghi E, Canedoli C, Padoa-Schioppa E, Pennati R, and Manenti R. in press. Differences between microhabitat and broad-scale patterns of niche evolution in terrestrial salamanders. *Scientific Reports*.

Ficetola GF, Pennati R, and Manenti R. 2012. Do cave salamanders occur randomly in cavities? An analysis with *Hydromantes strinatii*. *Amphibia-Reptilia* 33:251-259.

Fiske I, and Chandler R. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43:1-23. http://www.jstatsoft.org/v43/i10/

Fritzén NR, and Koponen S. 2011. The cave spider *Meta menardi* (Araneae, Tetragnathidae) – occurrence in Finland and notes on its biology. *Memoranda Soc Fauna Flora Fennica* 87:80-86.

Gasparo F, and Thaler K. 1999. I ragni cavernicoli della Venezia Giulia (Italia nord-orientale) (Arachnida, Araneae). *Atti e Memorie della Commissione Grotte "E Boegan"* 37:17-55.

Gómez-Rodríguez C, Bustamante J, Díaz-Paniagua C, and Guisan A. 2012. Integrating detection probabilities in species distribution models of amphibians breeding in Mediterranean temporary ponds. *Diversity and Distributions* 18:260-272. 10.1111/j.1472-4642.2011.00837.x

Hervant F, Mathieu J, and Durand JP. 2000. Metabolism and circadian rhythms of the European blind cave salamander *Proteus anguinus* and a facultative cave dweller, the Pyrenean newt (*Euproctus asper*). *Canadian Journal of Zoology* 78.

Hijmans RJ, Cameron SE, Parra JL, Jonesc PG, and Jarvisc A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal Of Climatology* 25:1965-1978. 10.1002/joc.1276

Hörweg C, Blick T, and Zaenker S. 2012. The large cave spider, *Meta menardi* (Araneae: Tetragnathidae), spider of the year 2012. *Arachnologische Mitteilungen* 42:62-64. 10.5431/aramit4214

Kuznetsova A, Brockhoff B, and Christensen HB. 2016. lmerTest: Tests in Linear Mixed Effects Models. R package version 20-29.

Lunghi E, Bruni G, Ficetola GF, and Manenti R. 2018a. Is the Italian stream frog (*Rana italica* Dubois, 1987) an opportunistic exploiter of cave twilight zone? *Subterranean Biology* 25:49-60. 10.3897/subtbiol.25.23803

Lunghi E, Cianferoni F, Ceccolini F, Mulargia M, Cogoni R, Barzaghi B, Cornago L, Avitabile D, Veith M, Manenti R, Ficetola GF, and Corti C. 2018b. Field-recorded data on the diet of six species of European *Hydromantes* cave salamanders. *Scientific Data* 5:180083. 10.1038/sdata.2018.83

Lunghi E, Corti C, Manenti R, Barzaghi B, Buschettu S, Canedoli C, Cogoni R, De Falco G, Fais F, Manca A, Mirimin V, Mulargia M, Mulas C, Muraro M, Murgia R, Veith M, and Ficetola GF. 2018c. Comparative reproductive biology of European cave salamanders (genus *Hydromantes*): nesting selection and multiple annual breeding. *Salamandra* 54:101-108.

Lunghi E, Corti C, Mulargia M, Manenti R, Ficetola GF, and Veith M. unpublished. Cave morphology, microclimate and abundance of five cave predators from the Monte Albo (Sardinia, Italy). *Scientific Data*.

Lunghi E, Ficetola GF, Mulargia M, Cogoni R, Veith M, Corti C, and Manenti R. 2018d. *Batracobdella* leeches, environmental features and *Hydromantes* salamanders. *International Journal for Parasitology: Parasites and Wildlife* 7:48-53. https://doi.org/10.1016/j.ijppaw.2018.01.003

Lunghi E, Manenti R, and Ficetola GF. 2014. Do cave features affect underground habitat exploitation by non-troglobite species? *Acta Oecologica* 55:29-35. http://dx.doi.org/10.1016/j.actao.2013.11.003

Lunghi E, Manenti R, and Ficetola GF. 2015. Seasonal variation in microhabitat of salamanders: environmental variation or shift of habitat selection? *PeerJ* 3:e1122. 10.7717/peerj.1122

Lunghi E, Manenti R, and Ficetola GF. 2017. Cave features, seasonality and subterranean distribution of non-obligate cave dwellers. *PeerJ* 5:e3169. 10.7717/peerj.3169

Lunghi E, Manenti R, Mulargia M, Veith M, Corti C, and Ficetola GF. 2018e. Environmental suitability models predict population density, performance and body condition for microendemic salamanders. *Scientific Reports* 8:7527. 10.1038/s41598-018-25704-1

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, and Hines JE. 2006. *Occupancy estimation and modeling. Inferring patterns and dynamics of species occurrence*. San Diego, California, U.S.A.: Academic Press.

Mammola S. 2017. Modelling the future spread of native and alien congeneric species in subterranean habitats — the case of *Meta* cave-dwelling spiders in Great Britain. *International Journal of Speleology* 46:427-437. https://doi.org/10.5038/1827-806X.46.3.2134

Mammola S, and Isaia M. 2014. Niche differentiation in *Meta bourneti* and *M. menardi* (Araneae, Tetragnathidae) with notes on the life history. *International Journal of Speleology* 43:343-353. http://dx.doi.org/10.5038/1827-806X.43.3.11

Mammola S, and Isaia M. 2017a. Rapid poleward distributional shifts in the European cave-dwelling *Meta* spiders under the influence of competition dynamics. *Journal of Biogeography* 44:2789–2797. 10.1111/jbi.13087

Mammola S, and Isaia M. 2017b. Spiders in cave. *Proceedings of the Royal Society B* 284:20170193. http://dx.doi.org/10.1098/rspb.2017.0193

Mammola S, Piano E, and Isaia M. 2016. Step back! Niche dynamics in cave-dwelling predators. *Acta Oecologica* 75:35-42. http://dx.doi.org/10.1016/j.actao.2016.06.011

Manenti R, Lunghi E, and Ficetola GF. 2015. Distribution of spiders in cave twilight zone depends on microclimatic features and trophic supply. *Invertebrate Biology* 134:242-251. 10.1111/ivb.12092

Manenti R, Lunghi E, and Ficetola GF. 2017. Cave exploitation by an usual epigean species: a review on the current knowledge on fire salamander breeding in cave. *Biogeographia* 32:31-46. 10.21426/B632136017

Manenti R, Siesa ME, and Ficetola GF. 2013. Odonata occurrence in caves: active or accidentals? A new case study. *Journal of Cave and Karst Studies* 75:205-209. 10.4311/2012LSC0281

Nentwig W, Blick T, Gloor D, Hänggi A, and Kropf C. 2018. Spiders of Europe. *Available at https://araneae.nmbe.ch/* (accessed Version of 14/05/2018).

Novak T, Perc M, Lipovšek S, and Janžekovič F. 2012. Duality of terrestrial subterranean fauna. *International Journal of Speleology* 41:181-188. http://dx.doi.org/10.5038/1827-806X.41.2.5

Novak T, Tkavc T, Kuntner M, Arnett AE, Lipovšek Delakorda S, Perc M, and Janžekovič F. 2010. Niche partitioning in orbweaving spiders *Meta menardi* and *Metellina merianae* (Tetragnathidae). *Acta Oecologica* 36:522-529. 10.1016/j.actao.2010.07.005

Pastorelli C, and Laghi P. 2006. Predation of *Speleomantes italicus* (Amphibia: Caudata: Plethodontidae) by *Meta menardi* (Arachnida: Araneae: Metidae). *Atti del 6° Congresso Nazionale della Societas Herpetologica Italica (Roma, 27IX-1X2006)*. Roma, 45-48.

Pavan M. 1944. Appunti di biospeleologia I. Considerazioni sui concetti di Troglobio, Troglofilo e Troglosseno. *Le Grotte d'Italia* 5:33-41.

Pinheiro J, Bates D, DebRoy S, Sarkar D, and Team RC. 2016. nlme: Linear and Nonlinear Mixed Effects Models. *R package version 31-128*. http://CRAN.R-project.org/package=nlme

R Core Team. 2016. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Richards SA, Whittingham MJ, and Stephens PA. 2011. Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology* 65:77-89. 10.1007/s00265-010-1035-8

Romero A. 2009. *Cave Biology*. Cambridge, UK: Cambridge University Press.

Romero A. 2011. The Evolution of Cave Life. *American Scientist* 99:144-151.

Sket B. 2008. Can we agree on an ecological classification of subterranean animals? *Journal of Natural History* 42:1549-1563. 10.1080/00222930801995762

Smithers P. 2005. The diet of the cave spider *Meta menardi* (Latreille 1804) (Araneae, Tetragnathidae). *Journal of Arachnology* 33:243-246.

Smithson PA. 1991. Inter-relationships between cave and outside air temperatures. *Theoretical and Applied Climatology* 44:65-73.

Studier EH, Lavoie KH, Wares II WD, and Linn JA-M. 1986. Bioenergetics of the cave cricket, *Hadenoecus Subterraneus*. *Comparative Biochemistry and Physiology* 84A:431-436.

Venables WN, and Ripley BD. 2002. *Modern Applied Statistics with S. Fourth Edition*. New Yourk: Springer.