The habitat preference of *Meta bourneti* (Simon, 1922)(Araneae, Tetragnathidae) in the UK differ from populations in Southern Europe

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Abstract

Invasive species often expand their niche and broaden their habitat preferences when they colonise new areas. The cave orb spider *Meta bourneti* (Simon, 1922) is thought to be a relatively recent invasive species in the UK and anecdotal evidence suggests that it might be found in a broader range of habitats in the UK than in its native range in Southern Europe. In the present study I investigate these claims, by first comparing the distribution and habitat preferences of *M. bourneti* to the more common cave orb spider *Meta menardi* (Latreille, 1804) in the UK using historic data from the UK Spider Recording Scheme. Secondly, I use data obtained mainly from published studies to compare *M. bourneti* populations in the UK with those from France, Italy and Spain. The results confirm that the *M. bourneti* habitat preferences are significantly different from both *M. menardi* and from populations in Southern Europe in that the UK populations are predominantly found in non-cave dark habitats such as under manhole covers, in culverts and icehouses with only 11% of records coming from caves and mines. My results indicates that *M. bourneti* offers significant potential for further studies including citizen science projects as several observations have been made in private gardens.

Keywords: invasive species, cave spiders, niche expansion, subterranean biology, citizen science

Running title: Habitat preference in UK populations of *Meta bourneti*

Introduction

The large cave spiders in the genus *Meta* (Family Tetragnathidae) are some of the most enigmatic spiders in Europe, probably because they spend most of their lives in constant darkness in natural caves, mines and tunnels (Mammola & Isaia 2014; Hesselberg, Simonsen & Juan 2019). Two species, *M. menardi* (Latreille 1804) and *M. bourneti* (Simon 1922) are found in Europe and are both relatively common in the twilight zone within the first 20 to 30 m of caves (Lunghi 2018; Hesselberg, Simonsen & Juan 2019). Both of these species are found in the UK with the more abundant *M. menardi* thought to be native, while *M. bourneti*, which is geographically restricted to southern lowland areas of the UK, is thought to be invasive (Mammola 2017). It was first reported from the UK, when a colony of adult females, males and egg sacs from a culvert in Suffolk were positively identified in 1941 (Browning and Tams 1944). The authors speculate that the species was introduced to the UK from France by wine merchants, although it has to be noted that *M. bourneti* and *M. menardi* look similarly with the former first recognised as a separate species in 1922, so it is certainly possible that it has been present undetected in the UK for much longer (Browning and Tams 1944; Mammola 2017).

The two species have slightly different ecological preferences with *M. menardi* preferring subterranean habitats with a relative humidity above 97% and temperatures ranging from 8 °C to 12

°C, while *M. bourneti* tolerates a slightly lower relative humidity (but still above 90%) and warmer temperatures (between 10 °C to 17 °C) (Mammola & Isaia 2017). Where there is geographically overlap between the two species in central and Southern Europe, they are predominantly segregated through elevation with *M. menardi* found at higher altitudes (Mammola, Hesselberg & Lunghi 2021). Climate change, which is likely to have serious, but delayed, consequences for cave-dwelling spiders (Mammola, Goodacre & Isaia 2018), may result in an expansion of both species to more northern parts of Europe (Mammola & Isaia 2017) and the UK (Mammola 2017). The two species seemingly never appear in the same cave, and when environmental conditions favour both species, *M. bourneti* is apparently excluded (Mammola & Isaia 2014).

Interestingly, while *M. menardi* is known to also occur in smaller man-made structures (including outhouses, culverts, sheds and icehouses), in hollow trees and under boulders in scree habitat in both the UK and Central Europe (Eckert & Moritz 1992; Smithers 2005; Růžička, Ŝmilauer & Mlejnek 2013), *M. bourneti* in Southern Europe seems restricted to the darker recesses of natural caves and mines with spiders being virtually absent within the first 6 m from the entrance (Lunghi 2018). However, in the UK, *M. bourneti* are anecdotally more prevalent in non-cave habitats and it has even been suggested that while *M. menardi* prefers natural habitats, *M. bourneti* might prefer artificial habitats in the UK (Cropper 1997). The majority of published accounts relate to dark and humid aboveground habitats including a hollow lime tree in Hampshire (Halsted 2000), in telephone junction boxes in Oxfordshire (Cooke 1981), under a manhole cover outside the visitor centre in Sherwood Forest (Pendleton and Pendleton 2009), under a manhole-cover outside the John Innes Research Centre in Norwich (Collyer 2013), in an ice-house in a forest in Somerset (Cropper 1997), in cemetery vaults in London (Milner 2013), in an abandoned military hut in Devon where it, highly unusually co-existed with *M. menardi* (Prince 2018) and in a garden compost bin in Gloucestershire (Fig. 1; Twissel 2019).

[INSERT FIGURE 1]

A broader diet or use of habitats, also referred to as niche expansion and niche shifts respectively (Zhang et al 2020), often occurs when species colonise new areas with fewer predators and competitors, such as for example the colonization of newly emerged oceanic islands (Whittaker & Fernández-Palacios 2007). Examples include use of new habitats further away from water in the American Mink after colonising a remote predator-free island in Chile (Crego, Jiménez & Rozzi 2018), a general niche expansion through most successional stages of bird communities on Corsica (Blondel, Chessel & Frochot 1988) and, interestingly, a niche shift (away from water into more open habitats) and more varied web-building in the endemic *Wendilgarda galapagensis* (Keyserling, 1886)(family Theridiosomatidae) on Islas de Cocos in the Pacific compared to closely related species from the mainland (Eberhard 1989). Similar patterns of niche expansion and niche shifts have been reported in many invasive species (Fernández and Hamilton 2015), although the pattern is far from uniform with other species showing strong niche conservation, at least in terms of climatic variables (Liu et al. 2020). Examples include populations of the common ragweed adapting their cold tolerance at an invasion front in the French Alps (Gallien *et al.* 2016), the common waxbill utilizing habitats with denser vegetation, higher temperatures and more rainfall in Brazil compared to its native range in Africa (da Silva *et al.* 2018) and increased cold tolerance in the wasp spider (*Argiope bruennichi* (Scopoli, 1772), family Araneidae) in the Northern European invasive populations (Krehenwinkel, Rödder & Tautz 2015). Thus, if *Meta bourneti*, as hypothesised (Mammola 2017), is an invasive species in the UK, this might lead to niche shift or expansion in British populations compared to populations in its native range in Southern Europe.

Here I use data collected by the UK Spider Recording Scheme to compare the observed habitat preferences of *M. bourneti* and *M. menardi* in the UK, and use similarly collected data on *Meta* *bourneti* from France, Italy and Spain to confirm if the habitat preference of the UK populations is broader than those in their native range in Southern Europe.

Methods

Data collection and categorisation

Observations of occurrence of *M. bourneti* and *M. menardi* in the United Kingdom were obtained from the UK Spider Recording Scheme (http://srs.britishspiders.org.uk/) on 20 February 2020, while data on the distribution of *M. bourneti* in Spain was obtained from the Iberian Spider Catalogue (http://sea-entomologia.org/gia/map/index.html) on 18 April 2020. Data from *M. bourneti* in France and Italy was extracted from the underlying database of the paper by Mammola and Isaia (2017), which was last updated in January 2015.

All raw data was cleaned by removing multiple records of individual spiders from the same location on the same date. From notes or location data associated with the records, the records were sorted into one of the following habitat categories: (1) Caves – any observations within the twilight and dark zones of natural caves. (2) Mines – any observations within the twilight and dark zones of mines, tunnels and other man-made caves. (3) Artificial habitats – observations from small artificial dark chambers including bunkers, culverts, icehouses, manhole covers, compost bins, drains etc. (4) Buildings – observations from cellars, churches and other non-disclosed locations within buildings (5). Woods – observations from tree cavities or other non-disclosed locations within woodland; and (6) Unknown – any observations that had no specific location data associated with them.

Statistical analysis

The distribution of *M. bourneti* and *M. menardi* across habitat types were analysed with a Chi-square contingency test as less than 20% of the expected frequencies were below 5 (only the expected number of records of *M. bourneti* in woods was below 5 at 3.8). However, in the comparison between habitat preferences of *M. bourneti* in the UK and in France, Italy and Spain, the assumptions of the Chi-square contingency test were not met. Instead, a Fisher's Exact test for contingency tables were carried out (Mehta and Patel 1986). All statistical tests were carried out in R version 3.5.1 (R Core Team 2018) with a significance level of 5%.

Results

The cleaned database of observations held by the UK Spider Recording Scheme (as of February 2020) of both cave species, confirms that *M. bourneti* is far less widespread than *M. menardi* with most observations from the South West and the South East of the United Kingdom (Fig. 2). The two northern most outliers on the map include four records from Sherwood Forest in Nottinghamshire between 1978 and 2006, and two records from Puffin Island, Anglesey, Wales both from 1962. The former species was also encountered less than the latter, as the database only holds 75 unique records of *M. bourneti*, but 497 of *M. menardi*. Interestingly, it also appears from figure 2 that *M. menardi* is rarely found in in the central and south easter regions of the UK (i.e. Bedfordshire Buckinghamshire, Cambridgeshire, , Essex, Herfordshire, Norfolk and Suffolk), where *M. bourneti* is most frequently observed.

[INSERT FIGURE 2]

[INSERT FIGURE 3]

Similarly, when comparing the habitat preferences of the two species in the UK, there was a significant difference in that *M. bourneti* was predominantly found in buildings and artificial habitats, while *M. menardi* was predominantly encountered in natural caves (Fig 3A, $\chi^2 = 53.76$, df = 6, $P < 0.0001$). The most common artificial habitats in which *M. bourneti* was encountered included manhole covers (N=9, 12%), culverts, sewers and drains (N = 6, 8%), icehouses (N = 6, 8%) and bunkers and air raid shelters (N = 3, 4%). There was also one unspecific record from the grounds of Shuttleworth College in Bedfordshire from 1994, one from a disused septic tank in Essex from 2019 and one from a compost bin in a garden in Gloucestershire from 2019. Interestingly, only 8 records (10.7%) of *M. bourneti* were from caves and mines, whereas 42.7% of all records of *M. menardi* in the UK were from these habitats (Fig. 3A). However, it is also worth noting that, while rare, *M. menardi* was also observed under manhole covers (1.6%), culverts etc. (3.8%), icehouses (2.6%) and bunkers etc. (2.4%). In addition, there was one record of this species from a compost bin in a garden in Yorkshire from 2014 and one from a dark, narrow and humid gap between two garden sheds in Pembrokeshire, Wales from 2014.

The habitat preferences of *M. bourneti* in the UK is significantly different from those of France, Italy and Spain, where this species was strongly associated with natural caves (Fig 3B, Fisher's Exact test $P < 0.0001$). As mentioned above, only 11% of records of *M. bourneti* in the UK were associated with caves and mines, while this was 92%, 99% and 93% for France, Italy and Spain respectively. Interestingly, only 0-2% of records were associated with artificial small dark habitats and buildings in France, Italy and Spain compared to 63% of records in the UK (Fig. 3B).

Discussion

The results of this study confirms that *Meta bourneti* in the UK, unlike *M. menardi*, is more often found in smaller dark artificial habitats, such as under manhole covers, in culverts, drains and icehouses than in natural caves and mines. This is markedly different to its habitat preferences in its native range in Southern Europe, where almost all observations were from inside caves and mines. Given that invasive species are known to broaden their niches when colonising new areas (Fernandez & Hamilton 2015; Eberhard 1989), the findings from this study supports the claim that *M. bourneti* must be considered an invasive species in the UK (Browning and Tams 1944; Mammola 2017). Interestingly, *M. bourneti* appears to be moving northwards, possibly as a consequence of climate change, both in the UK (Mammola 2017) and in Europe (Mammola & Isaia 2017), so data on habitat preferences from other countries on the invasive front in Central Europe could be used to confirm if the trend in the UK is a sign of a general strategy in this species when encountering new habitats, possibly because of indirect competition from *M. menardi* (Mammola & Isaia 2014), or if it is unique to the UK. The situation in the central and south eastern regions of the UK is interesting as it appears from the distribution of records (Fig. 2) that *M. bourneti* is dominant in this area with only very few *M. menardi* observed. However, whether this is a direct consequence of competition or it is due to fewer suitable cave habitats for *M. menardi* in this area is not currently clear.

One area where the situation in the UK is potentially unique, is the large number of amateur natural historians in the country (Alberti 2001). Most of the records to the spider recording scheme is done by amateur recorders (Spider Recording Scheme 2021), whereas the data used from Italy, Spain and France is likely to be mainly collected by professional entomologists and arachnologists (Mammola & Isaia 2017). This difference might to some extent explain why *M. bourneti* in the UK is observed near people's houses rather than in caves, although it is unlikely to explain the drastic differences in habitat preference between UK and Southern European populations. Especially, given that the same Spider Recording Scheme data-set for *M. menardi* has significantly more records from caves. However, we cannot with the present data completely rule out that the observed broader habitat preferences of UK populations could be due to underreporting from non-cave habitats in its native range. To fully answer this, we would need a more systematic and comparative survey of non-cave habitats in the different countries. However, some support for a general broader habitat preferences in *Meta* spider comes from recent observations of the related *Meta dolloff* (Levi 1980) from California, US. This species is very restricted in its distribution and was previously only known from a handful of caves with its stronghold in the Empire Cave system near the University of California in Santa Cruz (Graham 1967). However, recently this species has been found to be very abundant in a disused rail tunnel (Cotoras et al., in preparation) and has been reported from small covered human-dug pits in woodland (Krohn & Jones 2020). *Meta bourneti* could also be closer to the habitat preferences of another tetragnathid orb spider, *Metellina merianae* (Scopoli 1763), which while common and widespread in in caves, is also found in other dark and humid habitats, including in woodland and under overhang along river banks (Novak *et al.* 2010; Hesselberg & Simonsen 2019). Clearly much more research on the distribution and habitat preferences of *M. bourneti* is needed from the UK, from other possible invasive fronts in for example Germany and from its native range in Southern Europe.

Conclusion and Future research

The findings in this study strongly suggests that *M. bourneti* populations in the UK show a broader habitat preference than both *M. menardi* in the UK and *M. bourneti* populations in Southern Europe with the UK populations being much more frequently reported from small dark and mainly human-made non-cave habitats. Thus, the results provide some support to the notion that *M. bourneti* is an invasive species in the UK (Mammola 2017) as invasive species often broaden their niches and habitat preferences when colonising new territories (Eberhard 1989; Fernandez & Hamilton 2015).

However, the study also highlights the need for much more research on this fascinating, but often overlooked, species. In the following, I outline some potential fruitful future directions of research including a detailed suggestion for a citizen science project.

Adaptations in web-building behaviour and foraging

Cave orb spiders in the genus *Meta*, but not *Metellina* (Hesselberg & Simonsen 2019), are known to show a range of potential behavioural adaptations to subterranean habitats, with the most obvious adaptation being a drastic reduction in the number of frame threads in their webs (Hesselberg, Simonsen & Juan 2019). This results in the radii attaching directly to the cave walls and is thought to be an adaptation to hunting walking prey that impacts on the radii and alerts the spider to their

presence (Simonsen & Hesselberg 2021). This would be beneficial as cave habitats generally have low species richness and abundance with flying insects being especially few and far between (Gibert & Deharveng 2002; Mammola 2019). However, this form of off-web hunting has not been properly documented and even the changes to web geometry has only really been documented in *M. menardi* (Simonsen and Hesselberg 2021), *M. japonica* (Yoshida & Shinkai 1993) and *M. dolloff* (Cotoras et al., In preparation). Thus, studies on the web geometry and hunting behaviour of *M. bourneti* from a range of different habitats in the UK will be important not only to fill gaps in our understanding of this species and comparing to Southern European cave populations (Mammola & Isaia 2014; Lunghi 2018), but also to answer questions in relation to behavioural flexibility of cave spiders in response to different micro-habitats and to the degree to which the niche expansion observed in this study also extends to more varied foraging and web-building behaviour.
Aboveground orb spiders (from both the families Araneidae and Tetragnathidae) are well known for displaying high behavioural flexibility in response to a large number of environmental variables including spatial constraints (Heiling & Herberstein 2000; Barrantes & Eberhard 2012; Hesselberg 2013, 2015) and there is also evidence that the endemic orb spider *Wendilgarda galapagensis* (family Theridiosomatidae), which colonised and evolved on the remote Cocos Island off the coast of Costa Rica, show more varied web-building behaviour than other species of *Wendilgarda* on the mainland (Eberhard 1989).

Dispersal behaviour and gene flow

Invasive species often show adaptations for active or passive long-distance dispersal (Sakai et al. 2001). There is evidence of this in *M. bourneti* due to its relatively rapid northward spread in the UK. It is likely that *M. bourneti*, like many others spiders, uses passive ballooning for long-distance dispersal (Bell *et al.* 2005) given that it is thought to have a juvenile stage spend above ground (Smithers 2005; Mammola & Isaia 2014). However, whether all juveniles disperse from their natal caves in *Meta* spiders, and if so whether they use ballooning for dispersal, have not been conclusively demonstrated in any of these species (Hesselberg, Simonsen & Juan 2019), although a preliminary ex-situ study found that *M. menardi* spiders showed positive phototaxis and moved towards the entrance of a small artificial cave in the laboratory (Smithers & Smith 1998). Thus, there is both scope for behavioural studies in the laboratory, perhaps measuring ballooning propensity in response to electric fields (Morley & Robert 2018) and for population genetics studies. The latter, especially if in comparison with *M. menardi*, would allow us to measure gene flow between different populations as an estimate for dispersal (Slatkin 1987; Hesselberg, Simonsen & Juan 2019), as well as investigating if small populations in isolated artificial dark chambers differ in whether they are source or sunk populations in the two species. Finally, genetic comparisons between *M. bourneti* populations in the UK and Southern Europe may also shed light on whether the difference in habitat preferences indicated by this study has a genetic basis or is part of their natural behavioural flexibility.

A potential role for amateur arachnologists and citizen scientists

The fact that *M. bourneti* has been found in and around our houses and gardens, including in cellars and garden compost bins (Twissell 2019) suggest that citizen science could potentially be a fruitful approach to answer questions on the occurrence of *M. bourneti* in non-cave habitats and if these are distributed within certain distances of tunnels, mines and natural caves. The citizen science approach has proved successful in obtaining valid scientific data on the distribution and spread of specific species (Dickinson, Zuckerberg & Bonter 2010), although the approach has still only to a limited extent resulted in scientific papers (Burgess *et al.* 2017). While the most successful citizen science projects have been on birds (Tulloch *et al.* 2013; Newson *et al.* 2016; Gorta *et al.* 2019), there have also been a number of successful projects on insects, including ladybirds (Gardiner *et al.* 2012), butterflies (Dennis *et al.* 2018),ant swarms (Hart *et al.* 2018a) and spiders (Wang *et al.* 2018).

There has even been a citizen science project on house spiders in the UK, which, based on 10,000 records from UK homes, found unsurprisingly that most sightings of house spiders were of males and in the early autumn, while there were no differences in number of sightings between rooms (Hart, Nesbit & Goodenough 2018b). An international citizen project – SpiderSpotter (https://www.spiderspotter.com/en/) – which look at spiders, their webs and their distribution has also recently been launched, and include a very interesting specific project – Spin-City (https://www.spiderspotter.com/en/info/for-scientists), which aims to investigate adaptation in webs and colouration to urban ecosystem in the garden cross spider *Araneus diadematus* (Clerck 1758) across Europe.

Thus, in recent years we are seeing a growing interest in spider related citizen science projects. The findings from this study that *M. bourneti* can potentially be found near homes and gardens in outbuildings, drains and compost bins suggest a significant potential of using citizen science to further explore questions on habitat preferences. It might be fruitful to develop a project asking participants (citizen scientists) to survey their gardens for both adult *Meta* spiders (in compost bins, outhouses, garden sheds and under manhole covers for example) in all four seasons and juvenile *Meta* spiders in the garden in early spring, when juvenile spiders are mainly thought to leave caves (Mammola & Isaia 2014), which despite their small size are relatively easy to identify due to their characteristic white and black colouration (Hesselberg, Simonsen & Juan 2019). This could be supplemented, for especially enthusiastic participants such as amateur arachnologists, with construction of standardised dark bins or boxes that are placed in gardens, to measure invasion/occupancy in relation to distances to known natural sources (such as caves and mines). Information obtained from such a citizen science project would be useful not only to determine the distribution (which could potentially be used to confirm a north-moving invasive front) and habitat preferences in the UK (Mammola 2017), but as discussed above, could also fill gaps in our understanding of web-building behaviour in cave spiders (through simple web measurements using an app similar to the SpiderSpotter project mentioned above). Data on overall web design, especially in relation to the number of frame threads, from *M. bourneti* (and *M. menardi*) building webs in smaller confined spaces, such as compost bins, could confirm if these spiders show similar abilities to adapt their web design to constrained spaces as aboveground spiders (Vollrath, Downes & Krackow 1997; Barrantes & Eberhard 2012; Hesselberg 2013).

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Figure 1. *Meta bourneti* in a compost bin in Gloucestershire. (A). The compost bin with the lid removed. The scale bar is 10 cm long. (B). An adult female *Meta bourneti* inside the compost bin. Photographed taken by, and used with permission from, Colin Twissel.

Figure 2. Recorded locations of *Meta bourneti* (left panel, 75 observations) and *Meta bourneti* (right panel, 497 observations) in the United Kingdom. Based on data from the UK Spider Recording Scheme and created with the R packages *ggplot2* (Wickham 2016) and *mapdata* (Brownrigg 2018).

Figure 3. Habitat use by cave spiders. (A) A Comparison of habitat use of *Meta bourneti* (75 records) and *Meta menardi* (497 records) in the UK as proportion of total records (B) The habitat use of *Meta bourneti* in the U.K. (75 records), France (52 records), Italy (83 records) and Spain (142 records) as a proportion of total records.

Figure 1

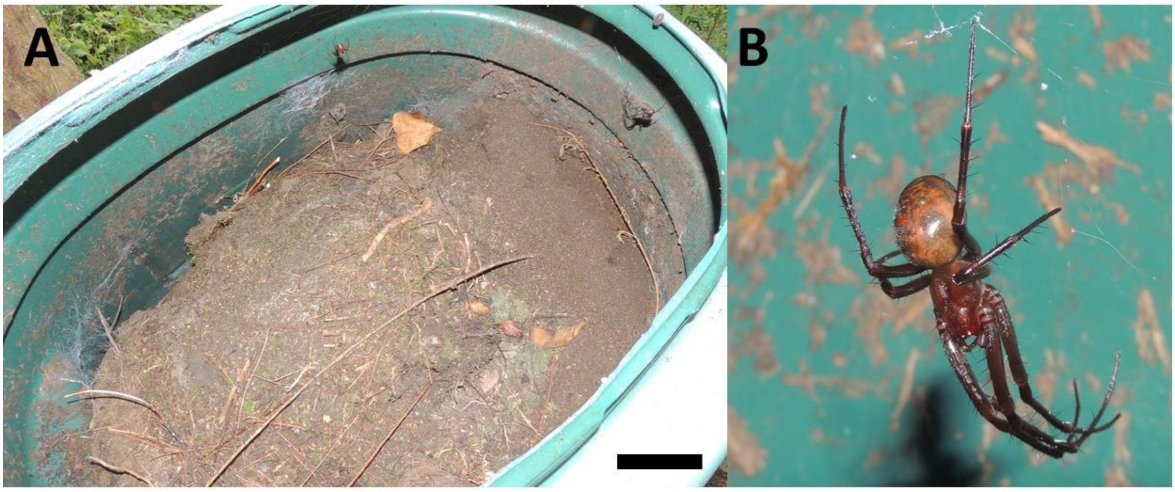


Figure 2

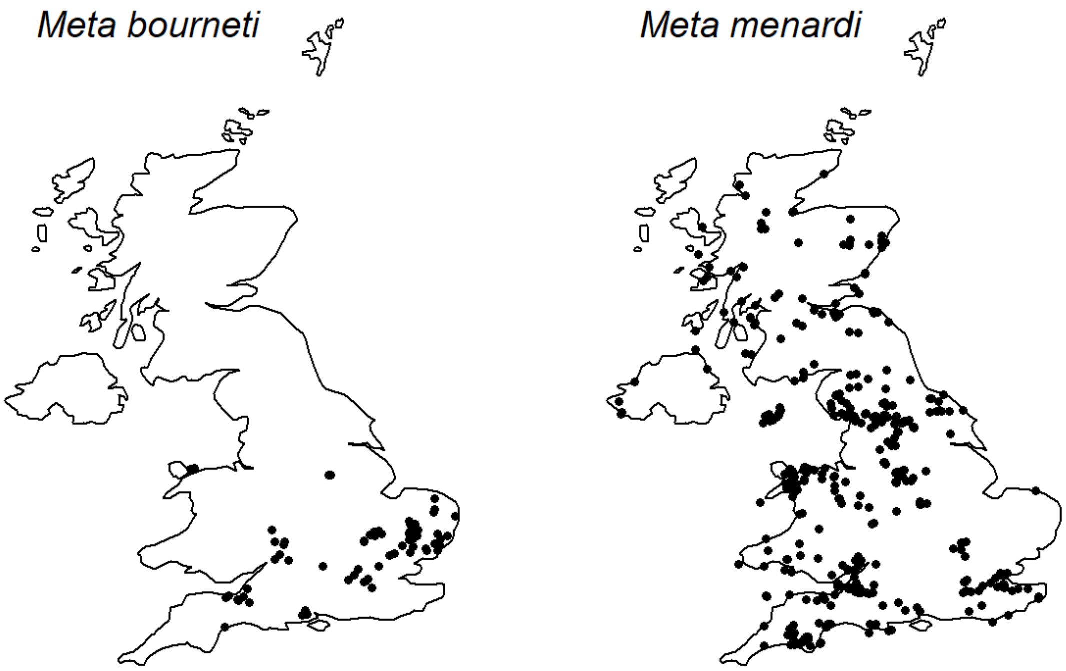
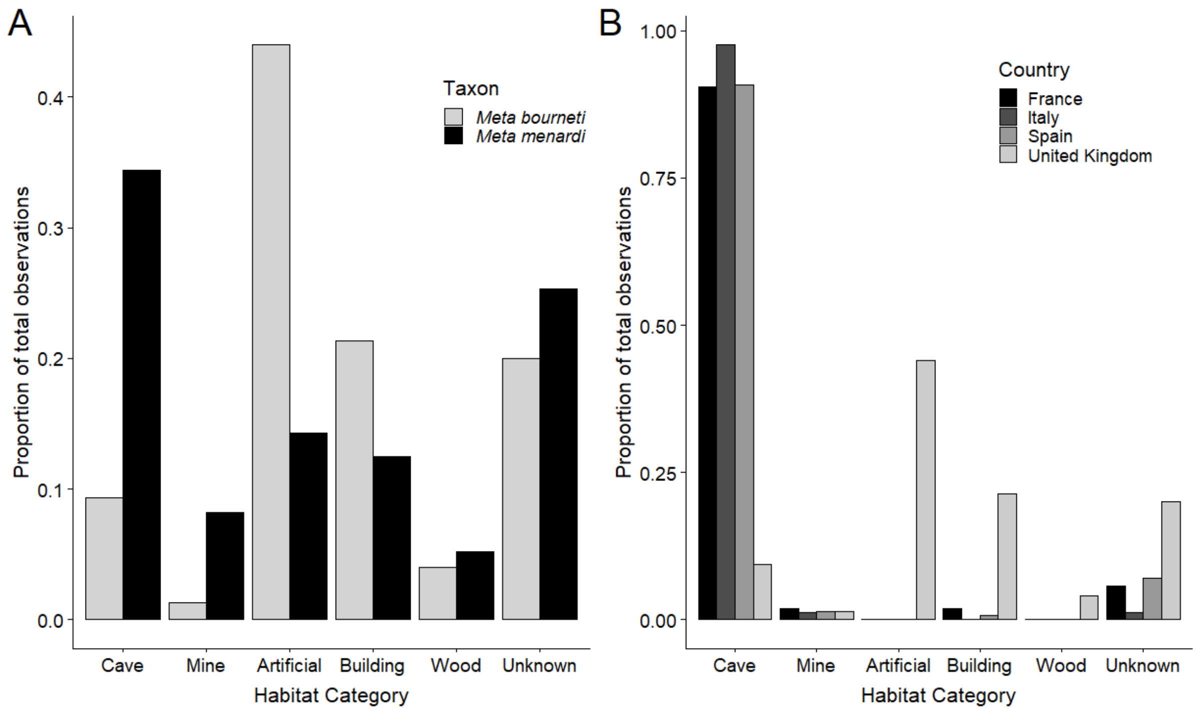


Figure 3



A
Taxon
Meta bourneti
Meta menardi
Proportion of total observations
0.0
0.1
0.2
0.3
0.4
Cave
Mine
Artificial
Building
Wood
Unknown
Habitat Category
B
Country
France
Italy
Spain
United Kingdom
Proportion of total observations
0.00
0.25
0.50
0.75
1.00
Cave
Mine
Artificial
Building
Wood
Unknown
Habitat Category