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ORIGINAL PAPER

Ecology and population assessment of *Megachile cypricola* Mavromoustakis, 1938 (Hymenoptera, Megachilidae), a threatened bee endemic to Cyprus

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Abstract

Megachile cypricola is a solitary bee endemic to Cyprus, assessed as Critically Endangered in 2014 following IUCN criteria. Recent records suggest that the species is still occurring in a few locations, however information on its ecology and population size is required to revise its status and implement conservation measures. For this purpose, samplings were carried out in four areas during spring 2022. We evaluated: (i) the habitat of *M. cypricola*; (ii) its foraging ecology and the importance of *Onobrychis venosa* (endemic Fabaceae reported as its main host-plant) in its diet; (iii) its nesting biology; (iv) its population size. We observed *M. cypricola* in mediterranean shrublands growing on limestone. *O. venosa* represented over 95% of the female pollen loads on average, confirming its narrow oligolecty. The nests consisted of external structures made of a dried mortar of sand and secretions regurgitated. A mark-recapture study resulted in an estimate of 849.4 female individuals across three assessment locations. Overall, the study highlights the high degree of specialisation of *M. cypricola* on a single endemic plant species. It also provides evidence that the species, only known from a restricted number of localities, is relatively abundant locally.

Keywords Solitary bee · Threatened species · Conservation · Foraging ecology · Population size · Endemism

Implications for insect conservation

Although *M. cypricola* does not appear to be at imminent risk of extinction, population monitoring should be conducted as this highly specialised species may be particularly vulnerable to habitat modifications, especially those driven by tourism development in coastal areas. This study highlights sites of interest and a potential method to implement such a monitoring.

Introduction

Decline in wild bee populations has been reported over the past two decades, mainly in Europe and North America (Biesmeijer et al. 2006; Burkle et al. 2013; Nieto et al. 2014; Kleijn et al. 2015; Potts et al. 2016; Powney et al. 2019). To mitigate these declines, there is an urgent need to better understand bee ecology, including specific foraging and nesting requirements in order to design efficient conservation strategies (Müller et al. 2006; Michez et al. 2023). The availability of host-plants and nesting resources (i.e. materials and substrates) are the two principal components driving the structure of wild bee communities (Potts et al. 2003, 2005; Goulson et al. 2015; Razo-León et al. 2018).

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Regarding floral choices, wild bees are usually described as specialists or generalists depending on the taxonomic range of their host-plants. Specialist (or oligolectic) bees exhibit a high fidelity for plant taxa of the same botanical family, while generalist (or polylectic) bees forage on a wide range of plants from multiple botanical families (Rasmussen et al. 2020). Bees also show a great diversity of nesting behaviours. Most of them are ground nesters, while others nest above ground in various substrates (e.g. hollow or pithy stems, dead wood abandoned cavities) or build external structures (Radchenko and Pesenko 1994; Danforth et al. 2019). There are also parasitic species (e.g. cuckoo bees) exploiting the nest and brood cells provisions of their bee host (Michener 2007; Michez et al. 2019). Several species need additional material to build their cells (e.g. mud, pebbles, resin, plant leaves or other tissues) and ground-nesting bees can show specific nesting site requirements (e.g. soil depth and structure, soil texture, moisture and compaction, vegetation cover) (Radchenko 1996; Potts and Willmer 1997; Cane et al. 2007; Sardiñas and Kremen 2014; Danforth et al. 2019).

Nesting resource availability and soil characteristics can therefore greatly affect the composition of bee communities, and 40% of the variation in species abundance pattern can be explained by the availability of nesting resources (Potts et al. 2005). Landscape modifications, resulting in loss and fragmentation of these floral and nesting resources, are a main cause of bee decline (Nieto et al. 2014; Potts et al. 2016; LeBuhn and Luna 2021). Populations of many species are becoming smaller and more isolated, increasing the risk of local extinction (e.g. Drossart et al. 2019; Hejda et al. 2017). Indeed, small populations tend to have a lower adaptability to environmental changes, a higher inbreeding rate and are more likely to disappear due to stochastic events (Lande 1988). Facing the increasing fragmentation of resources, species able to use a wider range of pollen sources, and to forage farther from their nest are likely to be more resilient (Biesmeijer et al. 2006; Bommarco et al. 2010; Carrié et al. 2017; Török et al. 2022).

The European wild bee fauna includes 2,138 species (Ghisbain et al. 2023). While European bees are among the best-studied species in the world, there are still many knowledge gaps on their spatial distribution, population size and trends, habitat requirements, host-plants and nesting resources (Michez et al. 2019). This is particularly true in South European countries, including islands, where bee species diversity and endemism are at the highest level (Nieto et al. 2014; Reverté et al. 2023).

Endemic species in southern islands like Cyprus are of particular interest as their geographical range is small, and they might be quickly threatened. Lying at the junction between Africa, Asia, and Europe, Cyprus hosts a rich bee fauna of over 370 species including 23 endemics (Varnava et al. 2020; Reverté et al. 2023). However, several species have not or have rarely been recorded since the seminal work carried out by G. A. Mavromoustakis published between 1937 and 1957 (Varnava et al. 2020). We present here a study on *Megachile (Chalicodoma) cypricola* Mavromoustakis 1938; one of the endemic species of Cyprus.

M. cypricola belongs to the long-tongued bee family Megachilidae, which is characterised by a scopa positioned on the ventral part of the metasoma instead of the hind legs. It is a medium sized bee species with strong sexual dimorphism (Fig. 1). The subgenus *Chalicodoma* is part of the "dauber bees", a paraphyletic group of *Megachile* building brood cells with mud or resin in contrast to leafcutter bees which use leaf discs to line their brood cells in cavities or in the ground (Eardley 2012). Species of this subgenus often have a strong preference for Fabaceae (Müller et al. 1997; Praz 2017; Westrich 2019). *M. cypricola* has been observed from late February to May, foraging mainly on the endemic *Onobrychis venosa* (Fabaceae) (Fig. 2) and exceptionally on *Astragalus cyprius* (Fabaceae) and *Echium angustifolium* (Boraginaceae) (Mavromoustakis 1938, 1948, 1951, 1952, 1957; Varnava et al. 2020). Mavromoustakis (1938) has qualified this solitary bee as "oligotrophic" on *O. venosa*, based on his direct observations. He observed nests made of mud, fixed on stones or in shrubs of *Sanguisorba spinosa* (Rosaceae) (Mavromoustakis 1938, 1951).

The absence of any records for nearly 60 years despite sampling efforts, led Nieto et al. (2014) to classify *M. cypricola* as "Critically Endangered". It was inferred that the species was possibly extinct, or that its overall population was reduced to less than 50 individuals (Dewulf and Praz 2015). Since then, in-depth research revealed that the bee was still present in several coastal areas around Limassol (23 specimens recorded between 2015 and 2018) (Varnava et al. 2020). As explained by Dewulf and Praz (2015) and Varnava et al. (2020), an investigation was needed to assess the population size of *M. cypricola*, and to better understand its ecology. Therefore, we organised field work in Cyprus aiming to: (i) describe the habitat of *M. cypricola*; (ii) characterise its foraging ecology through quantitative palynological analyses; (iii) characterise its nesting biology; (iv) evaluate its population size through mark and recapture.

Methods

Study area and habitats

The study was carried out in the surroundings of Limassol, where most of the records of the target species originated (Mavromoustakis 1938, 1951, 1952, 1957; Varnava et al.

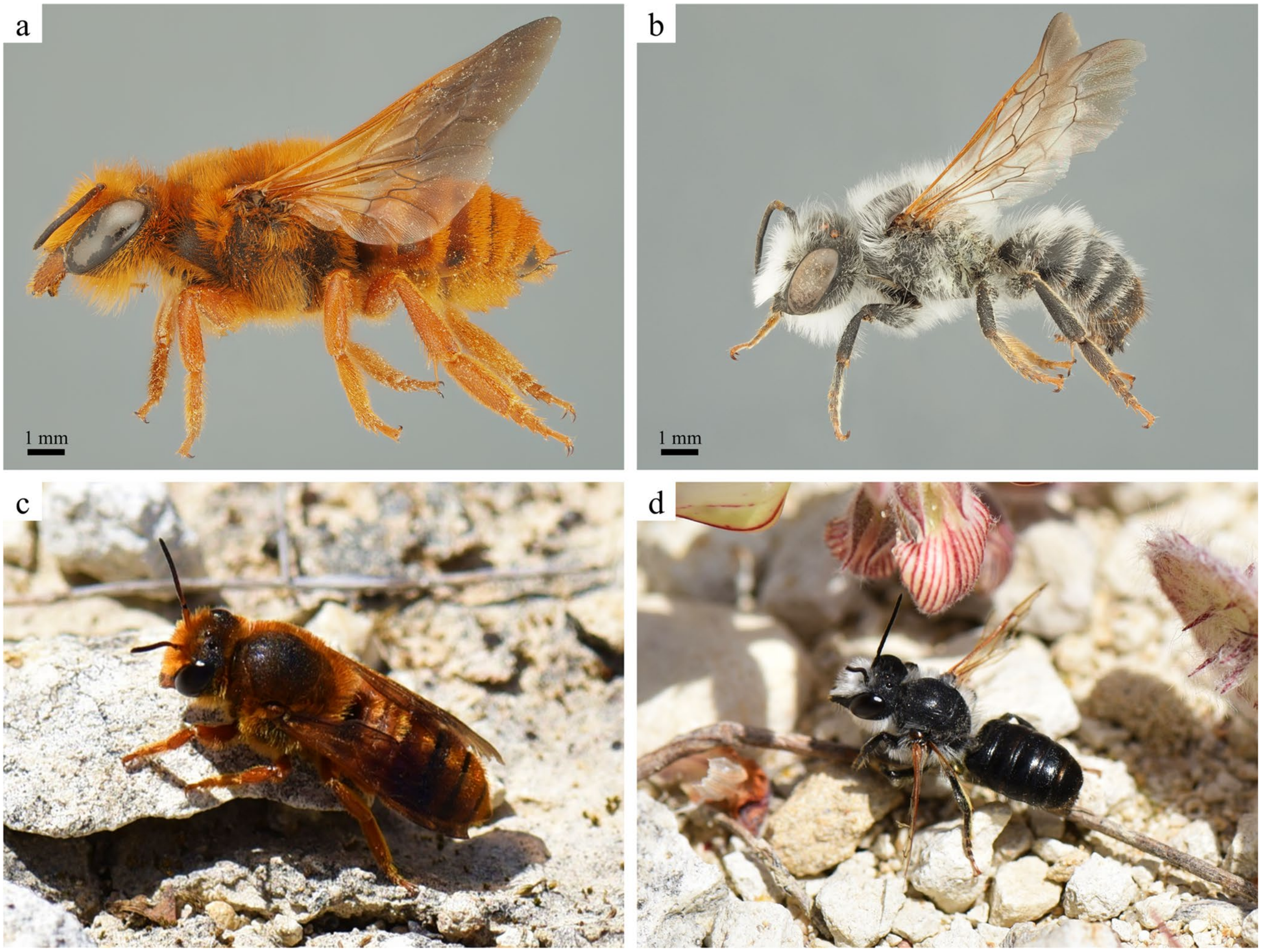

Fig. 1 Specimens of *Megachile cypricola*; **a**, **c**, females; **b**, **d**, males. Credit: Rémi Santerre (**a**, **b**), Jordan Benrezkallah (**c**, **d**)

2020). After preliminary research in this area, four sites (sites A to D) were selected based (i) on recent observations of *M. cypricola*, (ii) on the presence of consistent populations of *O. venosa*, and (iii) aiming to include areas from a wide geographical range and high diversity in the sampling scheme (Fig. 3; Table 1). Attention has been paid to the presence of honeybee hives, as these have been shown to impact the surrounding wild bee communities and their foraging behaviours (Hudewenz and Klein 2013; Torné-Noguera et al. 2016; Henry and Rodet 2018; Weekers et al. 2022). Several were recorded 1.2 km away from site A, and one less than 100 m away from site D.

Sampling process

The fieldwork took place in spring 2022, during the presumed peak abundance of *M. cypricola* (Mavromoustakis 1938, 1952, 1957; Varnava et al. 2020). The complete process consisted of four standard sampling sessions in each site (different days and times), allowing to generate mark-recapture data. It was carried out at sites A, C and D from March 30th to April 4th. Site B could not be included in the complete process because of a delay in the flowering of *O. venosa* and was therefore sampled once on April 19th. Additional material was collected near to the site C on April 5th to complete the assessment of foraging ecology (see Site C' in Online Resource 1 (Table S1)).

A standard sampling session consisted of 60 min of hand netting along free transects, conducted simultaneously by two collectors. All sessions took place between 9 am and 6 pm, on clear days, with temperatures between 18 and 29 °C. All specimens of *M. cypricola* observed on the sites, and all other wild pollinators observed foraging around *O. venosa* were captured and placed in individual tubes. Because of their overabundance in certain locations, honeybees (*Apis mellifera*) foraging on *O. venosa* were not collected but counted to obtain a rough indication of their abundance in the different sites. Specimens of *M. cypricola* were placed in a cool box at 5 °C to slow them down and allow them to be handled (Zurbuchen et al. 2010a, b). Once they were

Fig. 2 *Onobrychis venosa*. Credit: Jordan Benrezkallah

numb, pollen from the scopa of females was scraped with an entomological pin and transferred in individual tubes. The bees were then marked with a unique colour code and released (Fig. 4). Acrylic paint markers Posca (Uni Mitsubishi Pencil, Tokyo, Japan) were used, as these are considered to be non-toxic and have no impact on bee survival rate (De Souza et al. 2012; Hennessy et al. 2020, 2021; Briggs et al. 2022). Other bee species were taken to the laboratory and pinned in collection.

Palynological analyses

The pollen loads of *M. cypricola* (recovered from individual tubes) and of the other species collected (scraped with an entomological pin from the specimens in collection) were each transferred to a drop of water on a microscope slide. The pollen was homogenised, left for a few minutes to rehydrate, and the slide was then gently heated to allow the remaining water to evaporate. Molten fuchsin-stained glycerine jelly (Brunel Microscopes Ltd, UK) was added, and the slide was sealed with a coverslip.

Pollen types in each load were identified to species level when possible, otherwise to genus or family level, by comparison with a reference collection of pollen grains built with samples of flowering plant from the sites studied (70 species), and with the reference collection of PalDat (www.paldat.org). The proportion of the different pollen types collected by each bee specimen was estimated by counting at least 400 grains from microscope fields of view taken randomly along transects at magnification ×400 (Montero & Tormo Molina 1990; Aleixo et al. 2013, 2017; Rocha-Filho and Garófalo 2016; Rocha-Filho et al. 2022). To better reflect the total volume of pollen in the scopae, a coefficient was attributed to each pollen type according to the relative surface occupied by a grain. As explained by Cane and Sipes (2006), using the absolute number of grains may lead to a significant bias towards the actual diet, given the variable size of pollen grains in mixed pollen loads. Pollen types representing less than 2% on the slides were considered as contaminations and were therefore neglected. Species for which less than three pollen loads were available were not included in the analyses (Müller and Kuhlmann 2008). The results of the analyses were interpreted using the approach of Müller (1996), in which a species is considered oligolectic when at least 95% of the pollen collected belongs to a same family/genus (average of all individuals).

Fig. 3 Location of the sampling sites: **A**, Avdímou Bay; **B**, Souni-Zanakia Forest; **C**, Monagroúlli, coastal cliffs; **D**, Tochni

Table 1 Information on the sites studied. SBA-SAC02: episkopi special area of conservation

Site	Location	Latitude	Longitude	Altitude	Protection status
A	Avdímou Bay	34.656750	32.773167	7 m	SBA-SAC02
B	Souni-Zanakia Forest	34.761778	32.906917	298 m	Natura 2000
C	Monagroúlli, coastal cliffs	34.706722	33.218306	17 m	-
D	Tochni	34.765278	33.326528	92 m	-

Nesting biology

The nests of *M. cypricola* at the sites were photographed, and an old nest was sampled and dissected after all specimens had emerged. The construction process of one was observed and documented with photographs over a five-day period.

Population size models and estimates

For sites A, C, and D, mark-recapture analyses were performed using program MARK, which estimates population parameters through maximum likelihood (Cooch and White 2014). The POPAN model of the Jolly-Seber method for open population was chosen to estimate population parameters since the assumption of population closure was not met. Indeed, due to the short life cycle of solitary bees (Michener 2007), a significant number of emergences and deaths may have occurred during the 5-day sampling period. POPAN determines the gross super-population size ($\widehat{N}*$), defined as the total number of individuals that entered the sampled population between the first and last sampling occasions. Additionally, it determines the apparent survival rate (φ), the capture probability (P) and the probability of entrance (pent), which indicates the probability of an individual from the superpopulation entering the subpopulation. To assess model assumptions, the Program RELEASE GOF (goodness of fit) within MARK was employed. The most appropriate model was chosen based on the Akaike Information Criterion adjusted for small sample sizes (AICc, Burnham and Anderson 2002) and likelihood ratio test (LR Test, Cooch and White 2014), comparing the appropriateness of time-dependent (t) versus constant (.) parameters for the population. Because of the differences in their phenology and behaviour, the mark-recapture data from females and males were treated separately. Both were likely to have different capture probability and mortality rates, due respectively to their foraging patterns and to life cycle (Alcock et al. 1978; Eickwort and Ginsberg 1980; Michener 2007).

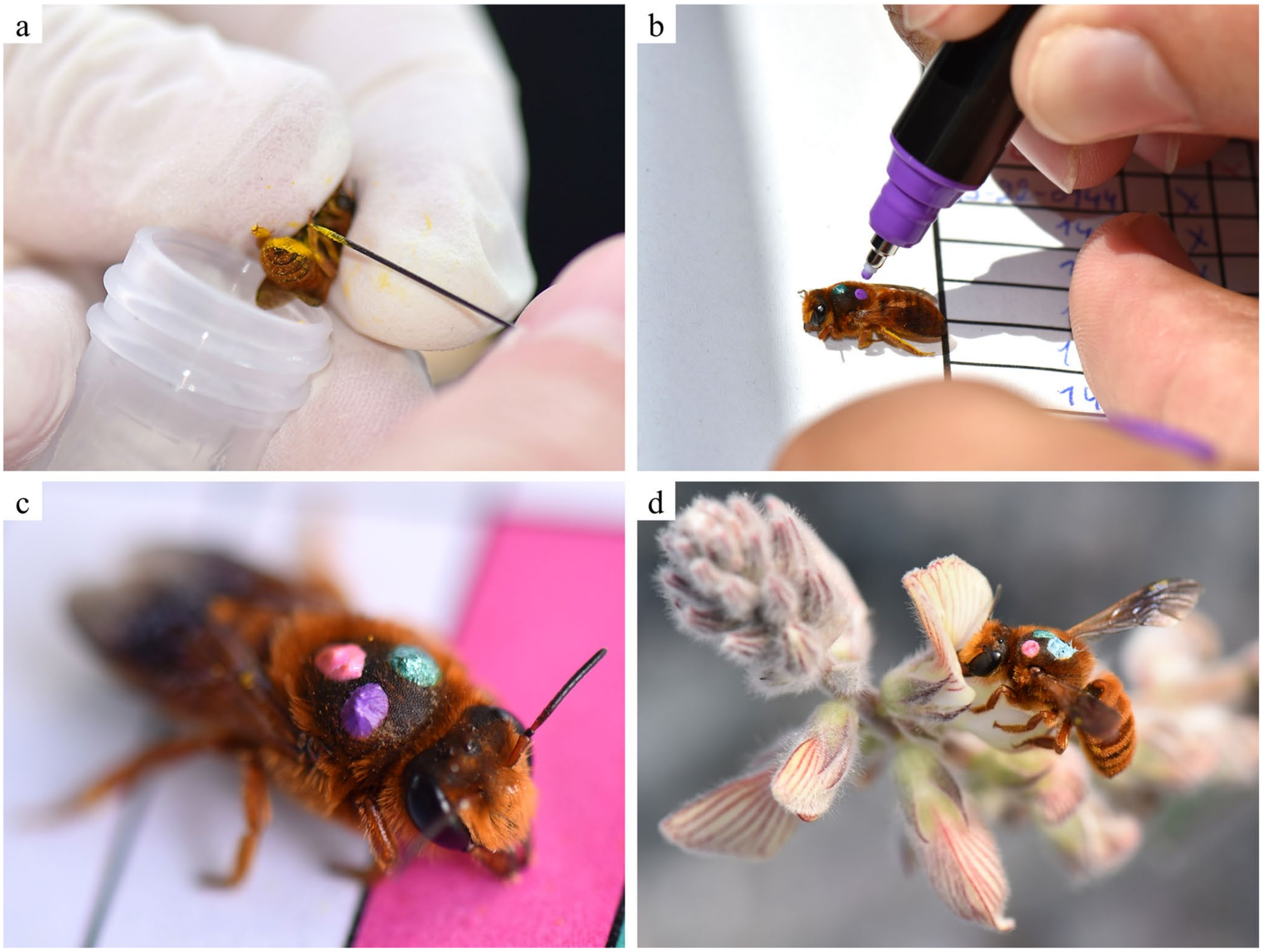

Fig. 4 Handling process of *M. cypricola* during the mark-recapture experiment. **a**, pollen collection on a living female slowed down by the cold; **b**, **c**, females marked with Posca; **d**, released female foraging on *O. venosa*. Credit: Jordan Benrezkallah (**a**, **c**, **d**), Rémi Santerre (**b**)

Results

Habitats

All of the sites investigated were composed of mediterranean shrubland growing on calcareous soil. This vegetation was generally low and sparse, with large areas of bare ground where *O. venosa* was growing (sometimes intertwined with shrubs). However, at the site B which was slightly higher in altitude (about 300 m a.s.l.), the shrubs were taller, denser and dotted with conifers, but the path there still provided an open area for *O. venosa* (Fig. 5).

Foraging ecology

M. cypricola was observed foraging only on *O. venosa*. It was the main pollen type in the 35 loads analysed and represented 95.8% in average. Of these samples, 18/35 were pure *O. venosa* and 32/35 contained more than 90%. Other Fabaceae represented 2.8% and were composed of *Astragalus cyprius* (endemic), *Lotus* sp., and a few other minor pollen types. The average Fabaceae content of the loads was therefore 98.6%, with 20/35 loads being pure Fabaceae and 34/35 containing more than 90% Fabaceae. Only Lamiaceae (*Prasium majus*) and Boraginaceae (*Lithodora hispidula* and *Echium angustifolium*) were also present in some samples, but never more than 10% and 7% respectively, for an average of less than 1% each overall (Table 2).

While *M. cypricola* appeared to be the most frequent visitor of *O. venosa* (60% of the visits observed), six other species were recorded foraging on this plant. First, an undescribed species of *Anthophora* (P. Rasmont *unpublished data*) whose pollen loads were composed of grains from various plant families, with 12.5% of *O. venosa* in average. Then, four *Osmia* species: *O. ferruginea*, *O. saxicola*, *O. viridina* (subsp. *nicosiana*) and *O. submicans*. While no specimen of the latter species was carrying pollen, the loads of the first three were mainly composed of Fabaceae, with

Fig. 5 Landscapes of the sampling sites. **a**, Avdímou Bay (site A); **b**, Souni-Zanakia Forest (site B); **c**, Monagroúlli (site C); **d**, Tochni (site D). Credit: Jordan Benrezkallah

81.1%, 87.8% and 84.5% of *O. venosa* respectively. Finally, *Andrena laevicorpus* for which no pollen load was available (Table 2). Honeybees (*Apis mellifera*) were very abundant overall, but their visits on *O. venosa* were very uneven between the different sites. Hundreds of these were foraging on this plant in site C and D (counted: 314 and 432 respectively), while no such visits were observed in site A despite their abundance on other flowers.

Nesting biology

We observed a total of eight nests, three fixed on rocks and five in the branches of shrubs (Figs. 6 and 7). These were made of a mixture of mineral components and of secretions regurgitated by the females, forming a hard and waterproof mortar protecting the brood cells. This mineral material was collected on the ground in the vicinity of nesting site. An empty nest was dissected, providing information on the sandy-loam texture of the mortar. It contained 13 brood cells lined with the old larval cocoons. However, the different sizes and shapes of nest observed suggested a highly variable number of cells.

The construction of a nest fixed on a rock could be observed for a five-day period in Monagroúlli (site C) (Fig. 7): The female was stacking slices of mortar to form cylindrical cells, which were then supplied with a viscous liquid mixture of pollen and nectar. Once these larval provisions had been built up, each cell was sealed with a similar mortar. Over the five-day observation period, five brood cells were built (one per day).

Population size

At the sites A, C and D, a total of 191 specimens were captures and marked: 66 females and 4 males at the site A, 98 females and 3 males at the site C, and 15 females and 5 males at site D (Online Resource 1 (Table S2), Online Resource 2 (Table S3)). The female populations were

Table 2 Wild pollinators observed on *O. venosa* and results of the palynological analyses. *Obs.*, number of direct observations on *O. venosa* (recaptured specimens are not taken in account); *n*, total number of pollen loads used for the palynological analysis; *N*, number of locations from which these loads originated, *BOR* Boraginaceae, *BRA* brassicaceae, *CIS* cistaceae, *FAB* Fabaceae, *LAM* lamiaceae. Detailed information on the specimens mentioned in this table can be found in Online Resource 1 (Table S1)

Species	Obs.	Results of the analysis of pollen (%)	*n*	*N*
Andrena laevicorpus Wood, 2023	3	-	-	-
Anthophora sp. (undescribed)	31	FAB 26.5 (*O. venosa* 12.5, other 14.0), CIS 23.6, BRA 19.1, LAM 17.9, BOR 12.8	15	4
Megachile cypricola Mavromoustakis, 1938	104	FAB 98.6 (*O. venosa* 95.8, other 2.8), LAM 0.8, BOR 0.5	35	4
Osmia ferruginea Latreille, 1811	18	FAB 100 (*O. venosa* 81.1, other 18.9)	11	3
Osmia saxicola Ducke, 1899	8	FAB 93.1 (*O. venosa* 87.8, other 4.9), BOR 6.9	8	1
Osmia submicans Morawitz, 1870	4	-	-	-
Osmia viridana nicosiana Mavromoustakis, 1939	5	FAB 100 (*O. venosa* 84.5, other 15.5)	4	1

estimated to be 138.1, 693.7 and 17.6 in these respective sites, for a total of 849.4 (Table 3). Survival estimates (φ) ranged from 0.6 to 1, while capture probabilities (P) varied between 0.35 and 0.66 (Online Resource 2 (Table S4)). The number of males captured in each of these sites was too low to compute population estimates. In addition to the above populations, 22 females were captured in site B during the single sampling sessions that were carried out there (Online Resource 1 (Table S1)).

Discussion

By exploring both the ecological needs of *M. cypricola* and the status of several of its current populations, this study provides critical elements for understanding the conservation issues associated to this hitherto little-known species. Its pollen diet was accurately established throughout quantitative palynology, and its habitat and nesting biology was described and illustrated. Population sizes were estimated in three different locations using repeated mark-recapture, providing another example of how these non-lethal methods can be used to monitor species of particular interest (e.g. Hennessy et al. 2020, 2021).

Habitat

The type of habitat observed was relatively similar in all the sites investigated, despite a higher and denser vegetation in site B. Considering all known records of *M. cypricola* (Fig. 8), it appears that most are distributed in areas dominated by mediterranean shrubland growing on calcium-rich soil, thus similar to what was observed in the framework of this study. However, two historic records are located in the south-eastern part of the island (Mavromoustakis 1948), where landscape and soil biochemistry differ substantially (Delipetrou et al. 2008; Cohen et al. 2012). Further work is therefore needed to better understand its overall distribution and the range of habitat in which it can be found.

Relationship with host-plants

Our analyses based on 35 specimens from four localities revealed that the pollen diet of *M. cypricola* consists of over 95% *O. venosa* on average, and about 3% other Fabaceae. When present in the loads, Lamiaceae and Boraginaceae pollen represented generally less than 5% and never more than 10%, for an average of less than 1% overall. Such proportions are considered by some authors as contaminations (e.g. <5% in Kleijn and Raemakers 2008; Scheper et al. 2014; <10% in Sedivy et al. 2008; Müller and Kuhlmann 2008). It is therefore likely that these plant families were visited for nectar rather than for pollen harvest. These results provide quantitative evidence about the oligolecty of *M. cypricola*, in line with what was suggested by Mavromoustakis (1938). More specifically, its diet was composed almost exclusively of *O. venosa*, bringing it close to the outdated concept of “monolecty”. Therefore, *M. cypricola* can be qualified at least as narrowly oligolectic (Müller 1996; Sipes and Tepedino 2005; Cane and Sipes 2006; Cane 2021). Specialisation on Fabaceae is common in the subgenus *Chalicodoma* (Praz 2017). For example, *M. pyrenaica and M. parietina* are polylectic with a preference for Fabaceae, the latter feeding its larvae primarily with pollen of *Onobrychis viciifolia* and *Lotus corniculatus* in central Europe (Müller et al. 1997; Westrich 2019), and with that of *Hedysarum coronarium* in central Italy (Monterastelli et al. 2024). In Israel, *M. sicula* has been observed collecting pollen and nectar almost exclusively from *Lotus creticus* (Willmer 1986).

Two other endemic species, *Andrena laevicorpus* and the undescribed *Anthophora* (Wood 2023; P. Rasmont pers. comm. 2024), were foraging on *O. venosa* alongside *M. cypricola*. These represented together 80% of the floral visits by wild species, suggesting strong endemic interactions, similar to those reported from other islands (Olesen et al. 2002; Valido et al. 2002).

Fig. 6 **a**, **c**, **d**, **e**, **f**, nests observed in Souni-Zanakia Forest; **b**, first brood-cell of a nest observed in Avdímou; **g**, female *M. cypricola* collecting sand and loam; **h**, **i**, dissected nest. Credit: Jordan Benrezkallah (**a**, **b**, **c**, **d**, **e**, **f**, **h**, **i**), Androulla I. Varnava (**g**)

In terms of pollination, *M. cypricola* probably plays a key role for *O. venosa*. Indeed, among the wild pollinators observed, it was the most abundant on the plant and, on average, carried the purest pollen loads. The latter parameter can prevent pollination failure related to contact with heterospecific pollen (Wilcock and Neiland 2002). Moreover, *M. cypricola* also presents morphological traits known to be associated with high pollen transfer: a relatively large body size (about 12–13 mm), and a ventral scopa particularly adapted to the sternotribe stamens and pistil of Fabaceae (e.g. Sahli and Conner 2007; Woulsa et al. 2019).

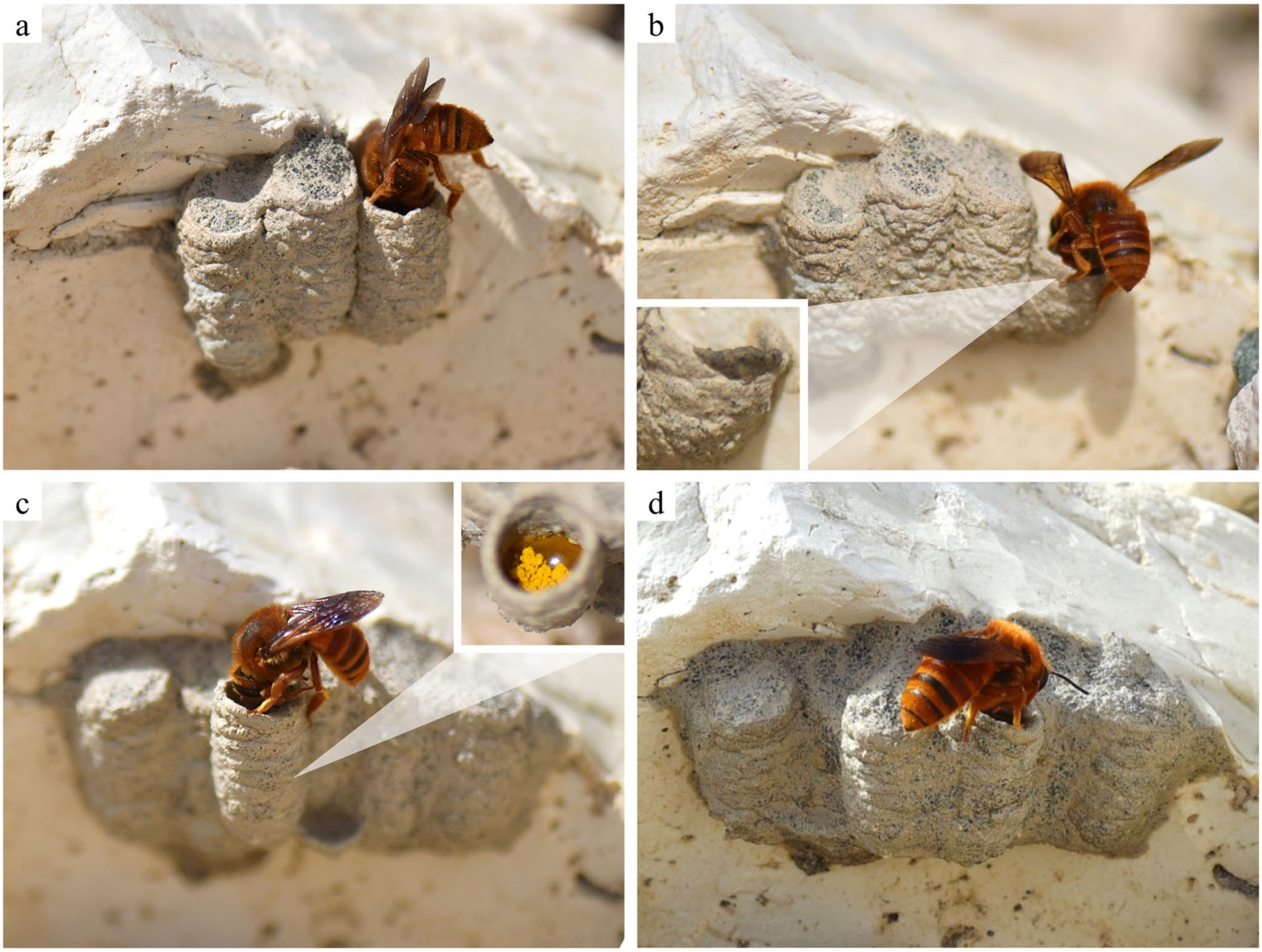

Fig. 7 Progression of the construction of a *M. cypricola* nest in Monagroúlli (site C). **a**, April 1st; **b**, April 2nd, focus on a piece of mortar freshly laid; **c**, April 4th, focus on the dry pollen freshly deposited at the surface of the nectar; **d**, April 5th. Credit: Jordan Benrezkallah

Table 3 Gross mark-recapture population estimates of females for each site, calculated with the program MARK and the models detailed in Online Resource 2 (Table S5). No estimates were made for the male population because of the insufficient data

Site	Total caught	Total marked	Total recapture	Gross population	Standard Error
A	109	66	43	138.1	25.66
C	119	98	21	693.7	157.30
D	26	15	11	17.6	2.68

A last point concerns the abundance of *Apis mellifera* on *O. venosa* in the sites C and D, with over 300 and 400 interactions counted respectively. Although these numbers could be biased by multiple counting of same specimens, they provide a rough indication on the exploitation of *O. venosa* by this managed species in some locations. Several studies demonstrated that competition with the honeybee can have a detrimental effect on wild bee communities (e.g. Dupont et al. 2004; Hudewenz and Klein 2013; Torné-Noguera et al. 2016; Henry and Rodet 2018; Weekers et al. 2022). Further research is therefore required to better understand the impact of this competition on the foraging behaviour of *M. cypricola*.

Nesting biology

Eight nests were observed and photographed (three fixed on rocks, five in shrubs), one which was dissected and one whose construction process was monitored over a period of five days. This allowed to provide a first detailed description of the nest architecture and construction behaviour, completing the observations reported by Mavromoustakis (1938, 1951).

The nesting biology of *M. cypricola* is in line with what is generally observed in the subgenus *Chalicodoma*: the nests are made of a mortar consisting of mineral matter mixed with secretions from labial glands, which forms a hard, hydrophobic substrate once dry (Kronenberg and

Fig. 8 Overall known distribution of *M. cypricola*. Map based on this study, published records (Mavromoustakis 1938, 1948, 1951, 1952, 1957; Varnava et al. 2020) and additional unpublished records provided by the authors (details available in Online Resource 1 (Table S1)). Old records (before 1960) are represented by the orange dots, and the recent records (after 2015) are represented by the green dots

Hefetz 1984; Praz 2017). Among the species for which nesting biology was described in detail, it seems particularly close to *M. sicula* which also builds both on rocks and twigs (Kronenberg and Hefetz 1984; Vereecken et al. 2010). In contrast, *M. parietina*, which can display gregarious and anthropophilic nesting behaviour (Monterastelli et al. 2024), seems to choose rocks more often and is known to include small pebbles to the construction, while *M. pyrenaica* tends to construct nests in existing cavities (Müller et al. 1997; Westrich 2019).

The speed of brood cell construction was also similar to that described for *M. sicula* (Willmer 1986), while *M. parietina* needs two to four days to build a brood cell under favourable conditions (Westrich 2019). Although behavioural sequences during foraging trips were not accurately recorded, our observations suggest a pattern similar to that of *M. parietina* (Westrich 2019), with nectar delivered first and dry pollen deposited immediately afterwards (Fig. 7).

No brood cell parasite was observed. However, Mavromoustakis (1948) recorded *Dioxys cincta* as a visitor of *O. venosa*, including in Agia Fyla, the *Locus typicus* of *M. cypricola*. As this species is known to parasitize *M. parietina* and *M. pyrenaica* (Müller et al. 1997; Westrich 2019), it can be considered as a potential parasite of *M. cypricola*.

Population size

The mark-recapture experiment carried out in the sites A, C and D resulted in female population estimates of 138.1, 693.7 and 17.6 respectively, for a total of 849.4 in the three sites. Moreover, other populations whose size was not estimated in this study are still occurring in Souni-Zanakia Forest (site B) and several other localities (Varnava et al. 2020) (Fig. 8). The population size of *M. cypricola* was therefore underestimated by Dewulf and Praz (2015) who assumed that there were probably less than 50 mature individuals remaining in Cyprus, given the absence of records for decades.

The male population estimates could not be run because of the very scarce data. This low number of males captured in comparison of females can be explained by several factors. A first element is the phenology: the sampling was probably carried out after the peak abundance of males, as they emerge and start to fade earlier than females in most solitary species (Alcock et al. 1978; Eickwort and Ginsberg 1980). Secondly, *M. cypricola* may have an unbalanced sex ratio with a predominance of females, like several other *Megachile* species (e.g. dos Santos et al. 2020; Riaño-Jiménez et al. 2023), although this ratio may vary with external factors (Peterson and Roitberg 2006). Furthermore, the capture probabilities of males and females are expected be unequal for morphological and behavioural reasons: females *M. cypricola* are visually easier to detect due to their bright red colour (Fig. 1), and they spend more time on flowers as they need to collect pollen and additional nectar to provision the brood cells, while males generally patrol in search of females to mate with (Alcock et al. 1978; Eickwort and Ginsberg 1980; Michener 2007).

The populations appeared to be very uneven between the three sites, with estimates in the sites A and C respectively 8 and 39 times higher than in the site D. The unequal abundance and density of *O. venosa* can probably explain partly this phenomenon, as the population size of a specialist species and of its host-plant can be strongly correlated (Larsson and Franzén 2007). This latter study also highlights the role of competitions with other flower visitors in the availability of pollen resources. Therefore, the impact of honeybee hives proximity on *M. cypricola* populations should be investigated in the future, as the presence of hives is known to affect the wild bee communities around (Hudewenz and Klein 2013; Torné-Noguera et al. 2016; Henry and Rodet 2018). In the specific case of this study, the site with the smallest *M. cypricola* population (site D) was located less than 100 m away from a hive, and it was there that the most interactions between *Apis mellifera* and *O. venosa* were observed.

Overall, the estimates resulting from these analyses are comparable in magnitude with those obtained by Hennessy et al. (2020, 2021) for *Eucera longicornis* (from 25 to 440 females) and *Anthophora retusa* (up to 167 males), by Bischoff (2003) for *Andrena vaga* (from 140 to 2080) or by Larsson and Franzén (2008) for *Andrena hattorfiana* (from 9 to 637). The estimated *M. cypricola* populations in site A (138 females) and C (694 females) fall in the range of these studies, suggesting sustainable populations, while the particularly low estimate obtained for site D (17 females) makes its long-term stability more questionable.

Conservation perspectives and strategies

This study provides evidence that the situation for *M. cypricola* is not as critical as stated in the European Red List of Bees (Nieto et al. 2014; Dewulf and Praz 2015). In the light of the current knowledge, the species does not match anymore the IUCN criteria for the ‘Critically Endangered’ category (IUCN Species Survival Commission 2012). The fact that the species remained unrecorded until the in-depth prospection by Varnava et al. (2020) is symptomatic of the lack of sampling in Cyprus in the last few decades, and more generally of the inadequacy of the data in southern Europe (Nieto et al. 2014).

However, *M. cypricola* appears to occur in restricted locations, sparsely distributed through its range, although being relatively abundant in some of these. Most of these locations are located close to the seacoast (Fig. 8) and are therefore threatened by the urban development in these areas, especially for tourism purposes (Mavris 2011). Moreover, *M. cypricola* tends to show a high dependency to a single plant species for pollen resources. This high degree of specialization is generally associated with low adaptability to environmental change, and oligolectic species are known to suffer a steeper decline than polylectics overall (Pekkarinen 1997; Biesmeijer et al. 2006; Burkle et al. 2013). Although this species should be transferred to a lower IUCN threat category in future assessments, it is important to remain cautious in view of the elements outlined above.

As conservation requires a multi-faceted approach, we suggest a three-axes strategy to help preserve *M. cypricola*: First, it is necessary to develop further research on population size, dynamics and mobility, as well as on aspects mentioned previously (i.e. distribution, habitat, impact of honeybees). It would also be important to survey habitat changes where the bee occurs, and to set up annual population monitoring at several control sites to provide first insights about population trends and fluctuations. Secondly, it is important to raise public awareness of the importance of wild bees (especially endemic ones), through community workshops and by installing educational signs about *M. cypricola* in locations where it is known to occur, especially in coastal areas visited by tourists (all known locations are available in Online Resource 1 (Table S1). These would include illustrations and tips to recognise this conspicuous species, information on its ecology and related conservation issues, and would encourage the report potential observations to a contact address. Finally, public policies supporting habitat preservation and restoration are required. Therefore, the Republic of Cyprus should propose the addition of *M. cypricola* to the annexes of the European Habitats Directive (Council Directive 92/43/EEC), or to a list of protected species in a national law. This would make it possible to designate areas with large populations of the bee and its host-plant as special areas of conservation (e.g. the site C, where the largest known population occurs, does not benefit from any protection status so far).

By providing detailed information on the ecological requirements of this endemic species, and by highlighting certain sites hosting significant populations, this study paves the way towards the design and implementation of a mitigation plan to protect this fragment of the natural heritage of Cyprus.

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Author contributions JB and RS designed the study under supervision of MS and DM. JB and RS carried out the fieldwork, with the support and advises of AV. Additional specimen records were provided by AV and RS. Data analyses were carried out by JB and RS with contributions from MS. RS drafted the manuscript with contributions from JB, and under the supervision of DM. All authors reviewed the manuscript and gave final approval for publication.

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Data availability Data is provided within the manuscript or supplementary information files.

Declarations

Ethical approval Not applicable as the animals studied are unregulated invertebrate species. In addition, most of the data related to the threatened *Megachile cyrpicola* was collected using a non-lethal protocol.

Competing interests The authors declare no competing interests.

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