RESEARCH ARTICLE

Comparative ecology of two specialist bees: *Dasypoda visnaga* Rossi, 1790 and *Dasypoda maura* Pérez, 1895 (Hymenoptera, Melittidae)

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Abstract

Many wild bee species are declining globally. To design efficient mitigation strategies to slow down or reverse these trends, we urgently need to better understand their basic ecological requirements. In this context, we studied two specialist species for which ecological data are scarce: *Dasypoda visnaga* and *Dasypoda maura*. We provide for the first-time detailed information on their phenologies, morphological traits, floral preferences, and nesting behaviours based on historical data and new samples from Morocco. The flight season of both species extends from late spring to late summer but *D. maura* emerges earlier than *D. visnaga*. Though the two species show different morphological traits, palynological analyses show that *D. visnaga* and *D. maura* females collect almost exclusively pollen from *Scolymus* sp. (Asteraceae). Concerning their nesting behaviour, *D. visnaga* seems to be more gregarious than *D. maura*. Both species build nests in sandy soil that can reach a depth of 80 cm. These ecological observations show that the differences between *D. visnaga* and *D. maura* are minor with regards to habitat requirements.

Keywords

Conservation, floral preferences, habitat requirements, nesting behaviour, phenology, *Scolymus*

Introduction

Worldwide declines in wild bee populations have been reported over the past two decades (Biesmeijer et al. 2006; Burkle et al. 2013; Nieto et al. 2014; Kleijn et al. 2015; Potts et al. 2016; Christmann 2019; Powney et al. 2019). To contain these declines, there is an urgent need to better understand their specific foraging and nesting requirements in order to design efficient mitigation strategies (Müller et al. 2006). Host plant and nesting resource (i.e. materials and substrates) availability 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).

Regarding their floral choices, wild bees are usually described as specialists or generalists depending on their foraging strategies. Specialist (or oligolectic) bees exhibit a high fidelity for particular 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). These diverse foraging behaviours influence the composition of bee communities (Scheper et al. 2014) and their conservation. Specialist bees are more affected than generalists by disturbances such as agricultural intensification (Williams et al. 2010) as they are not able to switch to alternative plant resources.

Bees also show a great diversity of nesting behaviours. The majority are ground nesters but some species nest above ground in various substrates such as hollow or pithy stems or abandoned cavities in dead wood or build their nests on open surfaces (Radchenko and Pesenko 1994; Danforth et al. 2019). They can also use various material to build their cells such as mud, pebbles, resin, flower petals, plant leaves, plant hairs, floral oils or secreted building materials (Radchenko 1996; Cane et al. 2007; Danforth et al. 2019). In addition, there are also parasitic (e.g. cuckoo bees) species, which exploit the nest built by their bee host and lay their eggs on the pollen provisions (Michener 2007). They can even exploit the social system of their host in the case of socially parasitic bees (Lhomme and Hines 2019). Within ground-nesting bees, species can show specific nesting site requirements (e.g. soil texture / moisture / compaction, vegetation cover, exposed bare ground) (Potts and Willmer 1997; Sardiñas and Kremen 2014) or nest architecture (e.g. variation in depth and relative position of cells). 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). Unfortunately, disturbances like habitat fragmentation, agricultural intensification, pesticide use and tillage can have a negative impact on nesting resources (Williams et al. 2010).

Among the ~20 000 described bee species, melittid bees constitute one of the smallest families (201 species; Michez et al. 2009; Danforth et al. 2013). As they are relatively rare and localised, data on their ecology are scarce. Within this bee family, the genus *Dasypoda* comprises 39 described species (Michez et al. 2004a; Radchenko 2016, 2017; Radchenko et al. 2019). Among them, nine species are recorded in Morocco (Lhomme et al. 2020). *Dasypoda* species are predominantly oligolectic, with the exception of some species such as *Dasypoda crassicornis* Friese which are known to

be polylectic. The subgenera *Dasypoda* s. str. and *Megadasypoda* forage on Asteraceae and Dipsacaceae respectively while *Heterodasypoda* and *Microdasypoda* subgenera visit mainly Cistaceae and Malvaceae (Michez et al. 2004b). Regarding their nesting behaviour, *Dasypoda* species are known to nest in the ground based on studies of three species: *D. argentata* Panzer (as *D. thoracica* Baer) (Celary 2002), *D. braccata* Eversmann (Radchenko 1988), and *D. hirtipes* Fabricius (Müller 1884; Vereecken et al. 2006; Loonstra 2010). Based on the information gathered from these species, we know that after mating, *Dasypoda* females initiate nest construction in sandy soil and then start to collect pollen. They place pollen balls in brood cells and lay an egg on the top. The larvae feed on the pollen ball and do not spin a cocoon. The nests are generally deep and can exceed more than 90 cm in depth (Celary 2002). Some species like *D. hirtipes* build their cells near the main gallery and make tripod-like structures below the pollen balls to reduce contact between the provisions and the cell wall (Müller 1884; Vereecken et al. 2006).

This paper aims to increase our knowledge concerning the ecology of the genus *Dasypoda* focusing on two species observed in Morocco, *Dasypoda maura* Pérez 1895 and *Dasypoda visnaga* Rossi 1790 (Fig. 1). The floral choices and nesting behaviour of these species are poorly documented, so this study aims to describe their phenologies, distribution, host plant preferences, and nesting ecology.

Methods

Data collection

Historical data on distribution, floral choices and phenology were obtained from the database "*Banque de données fauniques Gembloux Mons*". In total, we gathered information from 839 specimens of *D. visnaga* and 101 specimens of *D. maura*. These records come from different private and institutional collections (Berg, BMNH, Catania, CUI, DWB, Erfurt, FSAGX, Genève, GRUNWALD, ICC, IRSNB, Lausanne, LINSENMA, Livory A, MCN, Mendoça Li, University of Mentouri, MNHNP, Munich, NMV, OOLL, RNHL, Schwarz, UMons, UMO, UZMC, VERHOEFF, ZMA; 86% of the data) and literature (14% of data) (Suppl. material 1: Table S1).

We also collected additional specimens in Morocco to study the floral choices and some morphological traits related to the foraging behaviour of both species. Bees were collected using insect nets. They were then killed and separated for identification, trait measurement, and pollen analysis. Specimens are conserved in the collection of the University of Mons.

Phenological, morphological and ecological analyses

Phenological data were obtained from historical records and new Moroccan samples. Initially, records from all years were grouped by month and by country and we

calculated the flight period of each species based on presence/absence of the species in each month. Then, we pooled all data for all countries to estimate the month(s) with the greatest number of observations for each species.

We considered the distance in millimetres between the two insertion points of the wings, the inter-tegular distance (ITD), as a proxy of body size (Cane 1987). We measured the length of the glossa and the prementum as a proxy of tongue length using a Facom 150 mm digital calliper (France, Morangis). These measurements were made from 31 specimens of *D. visnaga* (16 females and 15 males) and 39 specimens of *D. maura* (24 females and 15 males) from Morocco (Suppl. material 1: Table S2).

The floral utilization study of the two species of *Dasypoda* was based on floral visit observations and palynological analyses. The floral records represented 132 specimens, 87 specimens of *D. visnaga* (50 females and 37 males) and 45 specimens of *D. maura* (19 females and 26 males) (Suppl. material 1: Table S3).

Pollen analyses were based on the pollen loads removed from female scopa and the pollen balls sampled within the nest of both species. We analysed pollen from female scopa (three females of *D. maura* and seven for *D. visnaga*) and pollen balls (three pollen balls for *D. maura* and 10 for *D. visnaga*) from specimens newly collected in Morocco. We also used information from historical data presented by Michez et al. (2008), specifically 49 pollen loads of *D. visnaga* (from 34 localities) and 21 of *D. maura* (from 8 localities). Pollen was suspended in water on a microscope slide and allowed to rehydrate. The slide was then heated to evaporate the excess of water. Molten fuchsin jelly was added, and the slide was covered with a coverslip. Pollen grains were identified by light microscopy at a magnification of x400 using a reference collection of West Mediterranean plant species assembled from Iberia and North Africa (TJW *pers. colln.*). Identification to or below genus level in the family Asteraceae is highly challenging, and *Scolymus*-type pollen is characterised by typical Cichorieae shape at the tribal level, and to the group level by the diameter of the grains which measure 45–55 μm. This grain size included the related genera *Cichorium*, *Helminthotheca*, and *Sonchus*. Pollen grains representing less than 2% of the load were assumed to be contamination and neglected (Westrich and Schmidt 1986).

Foraging behaviour was evaluated by measuring visitation rate and time spent per flower (Pesenko et al. 1980; Akter et al. 2017). We examined the time of foraging on *Scolymus hispanicus* L. for the two species at the same site (45 females of *D. visnaga* and 44 females for *D. maura*). To quantify the visitation rate, we counted the number of flowers visited by each female (N = 18 females for each species) and the total time spent foraging. We then calculated the mean number of flowers visited per minute.

Investigation of the nesting architecture of both species was conducted in May (2019, 2020) and July (2019) in two locations in Rabat-Kenitra region. The nests of *D. visnaga* and *D. maura* were excavated in a site located at Douar Oulad Taleb near Maâmora forest (34.1243033°N, -6.5755842°W). The ground was sandy, bare, and exposed to the sun, with plants of *Scolymus* sp. 200 m away. A second nesting site of *D. maura* was investigated in Salé Al-Jadida (34.0226357°N, -6.7495343°W). This site

was moderately vegetated with sandy and compacted soil. The flora included mostly *Scolymus* sp. and *Carduus* sp., but no *Cichorium* sp., *Helminthotheca* sp., or *Sonchus* sp. were recorded. One nest of each species was filled with liquid plaster and left 30 min until the plaster had solidified. This method allowed us to follow the tunnels and reconstruct the nest architecture (Tschinkel 2010). The other nests were excavated to sample pollen balls and larvae. After excavation, different parameters were measured: the distance between neighbouring nests, the width and the height of the tumulus, the length of tunnels, the number of cells and the depth of each cell.

Results

Phenology and distribution

Dasypoda visnaga is distributed in the north of Mediterranean Sea from Portugal to Turkey and in Maghreb (Morocco, Algeria, and Tunisia). *Dasypoda maura* is endemic to Northern Africa (Morocco and Algeria) (Fig. 1). In Morocco, *D. maura* is more widespread than *D. visnaga*, which is found only in coastal parts of the country while *D. maura* is also found in mountainous regions (Rif, Middle and High Atlas).

Records of both species show *D. visnaga* specimens were mainly collected in July (67%) whereas *D. maura* specimens were largely collected in May and June (90%) (Fig. 6). The beginning of the flight season of *D. visnaga* varies between countries, it starts in mid-April in Greece, in May in Morocco, Algeria, Tunisia, Spain and Portugal. It seems to start much later in France and Italy with specimens appearing in June. *Dasypoda maura* flies from April to July in Morocco and has been observed in July in Algeria (Fig. 2).

Morphological traits

Females of *D. visnaga* have the greatest ITD (3.60 ± 0.05 mm) followed by *D. maura* females (3.31 ± 0.02 mm) while the males of the two species have the smallest ITDs (*D. visnaga*: 3.18 ± 0.03 mm; *D. maura*: 3.19 ± 0.02 mm; Fig. 4A). We found a significant difference in ITD between females of both species and between males and females within and between species (Kruskal-Wallis, chi-squared = 40.55, df = 3, p = $8.122*10^{-9}$). No difference was found in ITD between males of both species (Wilcoxon rank-sum test, p = 1).

Using a model estimating the foraging range based on body size (Greenleaf et al. 2007), we estimated the foraging distance of each species. The results showed that the estimated mean of foraging distance of *D. visnaga* females is 1.67 ± 0.03 km while *D. maura* females is 1.47 ± 0.01 km.

Tongue length was significantly different between species and sex (Kruskal-Wallis, chi-squared = 36.145, df = 3, p = $6.977*10^{-8}$). *Dasypoda maura* has the longest
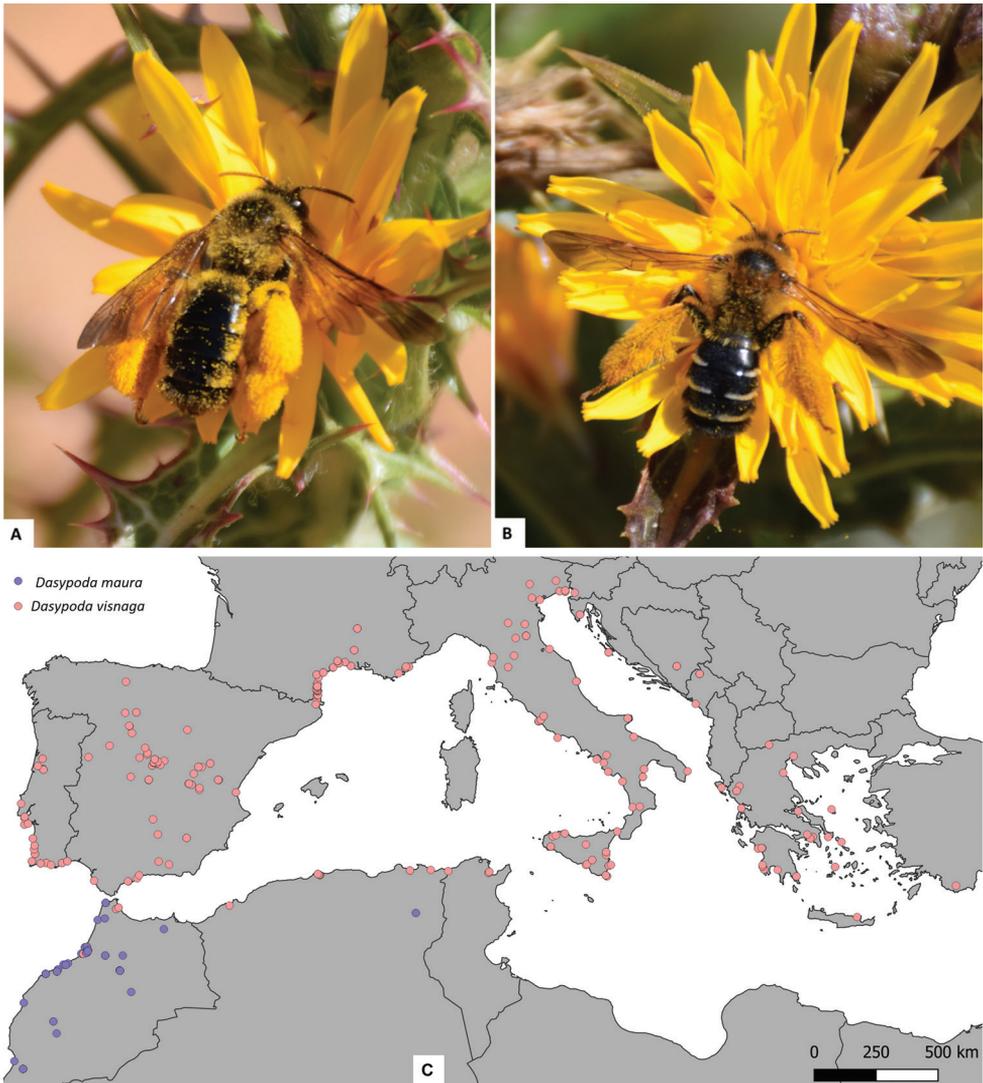
Figure 1. A *Dasypoda visnaga* female. Photo by Patrick Lhomme (2020) **B** *Dasypoda maura* female foraging on *Scolymus hispanicus*. Photo by Insafe El Abdouni (2020) **C** geographical distribution of the two species (pink circles = records of *Dasypoda visnaga*; black circles = records of *Dasypoda maura*).

proboscis (female: 4.87 ± 0.019 mm; male: 4.66 ± 0.02 mm) while that of *D. visnaga* is shorter (female: 4.61 ± 0.07 mm; male 4.47 ± 0.04 mm, Fig. 4B).

Floral choices and foraging behaviour

Floral records of *D. visnaga* (50 females and 37 males) and *D. maura* (19 females and 26 males) obtained from historical data and new observations indicate that the most
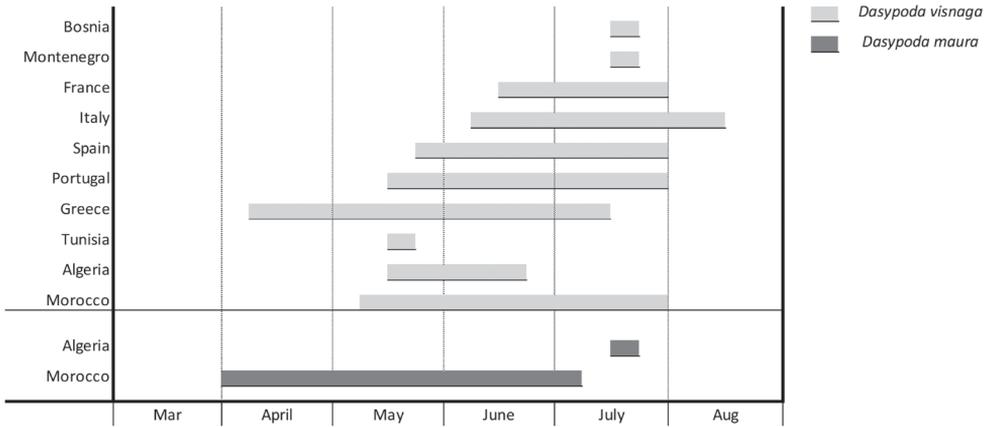
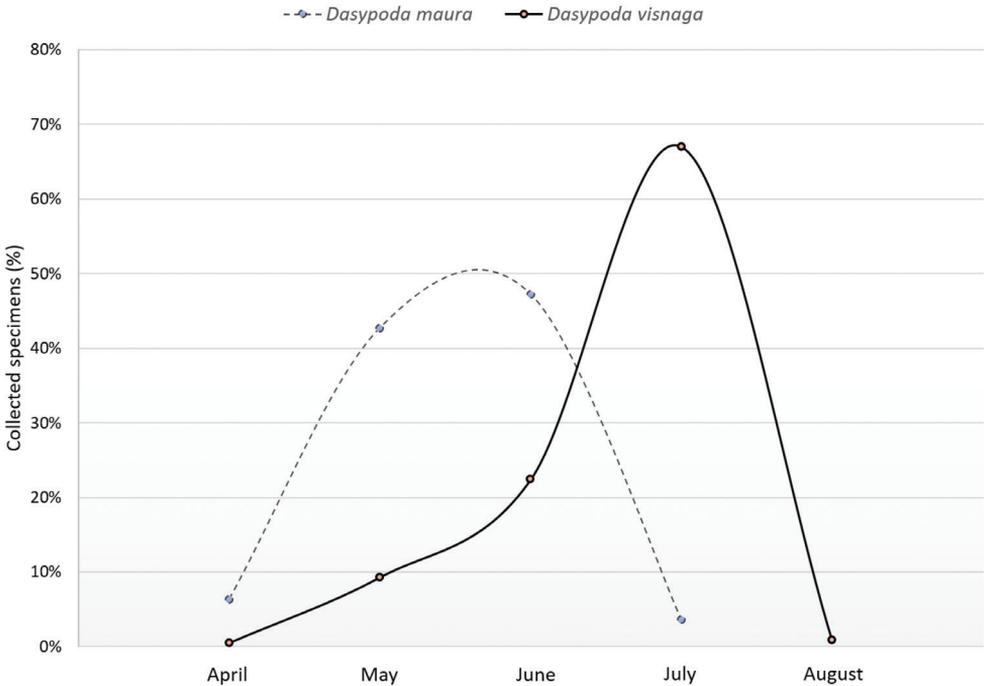**Figure 2.** Temporal records of *Dasypoda visnaga* (light grey) and *Dasypoda maura* (dark grey).

Figure 3. Percentage of collected specimens per month for *Dasypoda maura* (dashed line, N = 110) and *Dasypoda visnaga* (solid line, N = 603) including data from all countries.

visited plant is almost exclusively *Scolymus* sp., except for males of *D. maura* who visit a greater diversity of host plants (Fig. 5). Males of *D. maura* visit a greater diversity of plants than males of *D. visnaga*. The alternative plants visited are *Onopordum* sp. (Asteraceae), *Marrubium vulgare* L. (Lamiaceae), *Echinops spinosus* L. (Asteraceae), and *Scabiosa atropurpurea* L. (Caprifoliaceae).
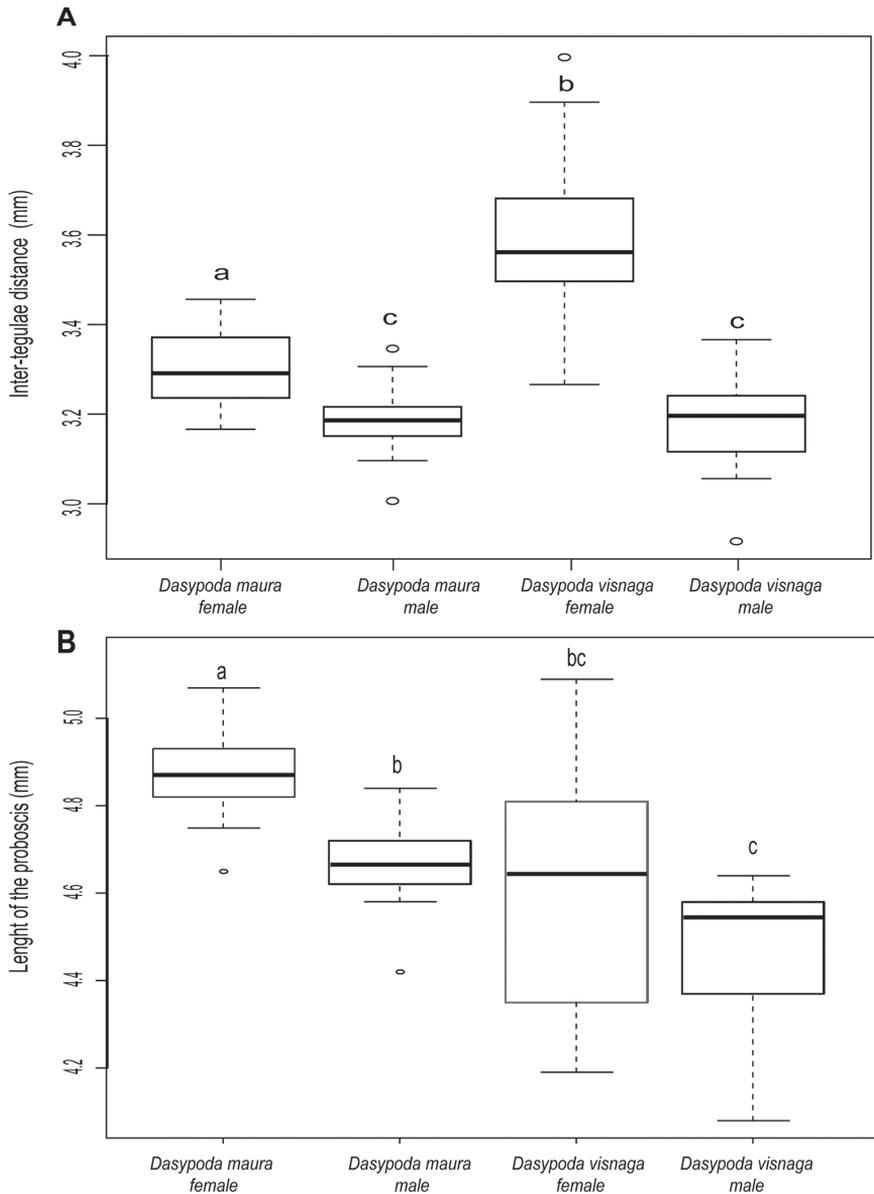
Figure 4. Morphological traits and estimated foraging distance of *Dasypoda visnaga* and *D. maura* **A** inter-tegulae distances **B** lengths of the proboscis. Box plots show the median and 25–75% percentiles. Whiskers show all data excluding outliers. Outliers (circles) are values being more than 1.5 times box length from upper and lower edge of respective box. The different letters indicate significant differences between treatments within experiments (Pairwise comparisons using Wilcoxon rank-sum test, $p < 0.05$).

Palynological analyses revealed that pollen loads of *D. maura* contain only pollen of *Scolymus*-type. while 98% of loads from females of *D. visnaga* did the same. This result was confirmed by pollen analysis of pollen balls found in the nest in Morocco as all pollen balls analysed consisted of *Scolymus*-type pollen. Given the absence of related
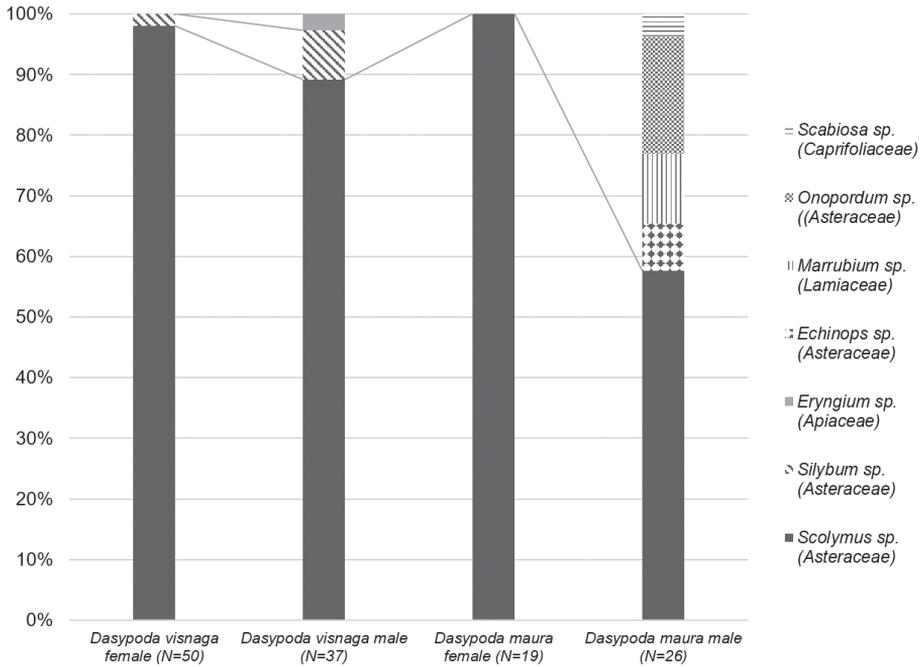
Figure 5. Floral choices of *Dasypoda visnaga* and *D. maura* based on historical and new Moroccan records. N is the number of records for each species and sex..
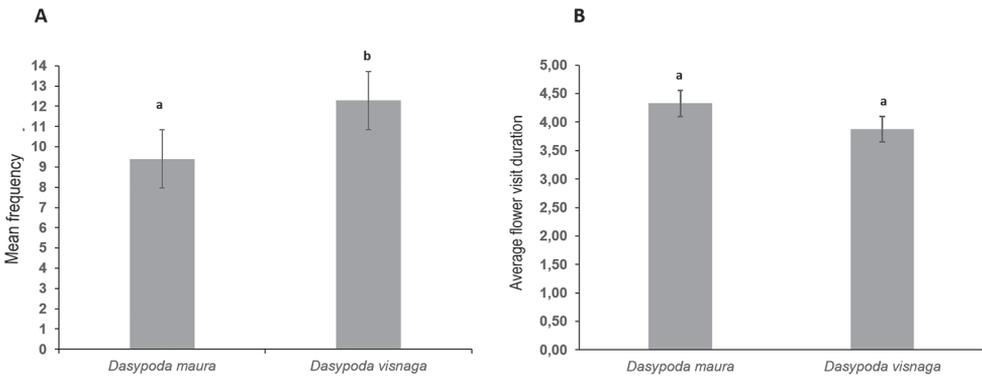

Figure 6. A frequency of floral visits **B** average flower visit duration between *Dasypoda maura* and *Dasypoda visnaga*. The different letters indicate significant differences between species (**A** student t-test, p < 0.05 **B** Wilcoxon rank-sum test, p > 0.05).

plant genera that produce this pollen type at this study site (see Methods), *Scolymus* plants are highly likely to be the sole pollen source at this locality.

The mean time spent on a flower of *Scolymus hispanicus* L. by *D. visnaga* (4.17 s) and *D. maura* (3.83 s) were similar (Wilcoxon rank-sum test, p = 0.25) (Fig. 6B). However, *D. visnaga* visited a higher number of flowers per minute (13 flower/min) than *D. maura* (9 flowers/min) (Fig. 6A).

Nest architecture

Females of *D. visnaga* construct their nests in sandy and non-compacted soil making a heap of sand above the nest entrance called a tumulus (Fig. 7B). This tumulus is built from soil displaced by the female during nest excavation. The diameter of the tumulus
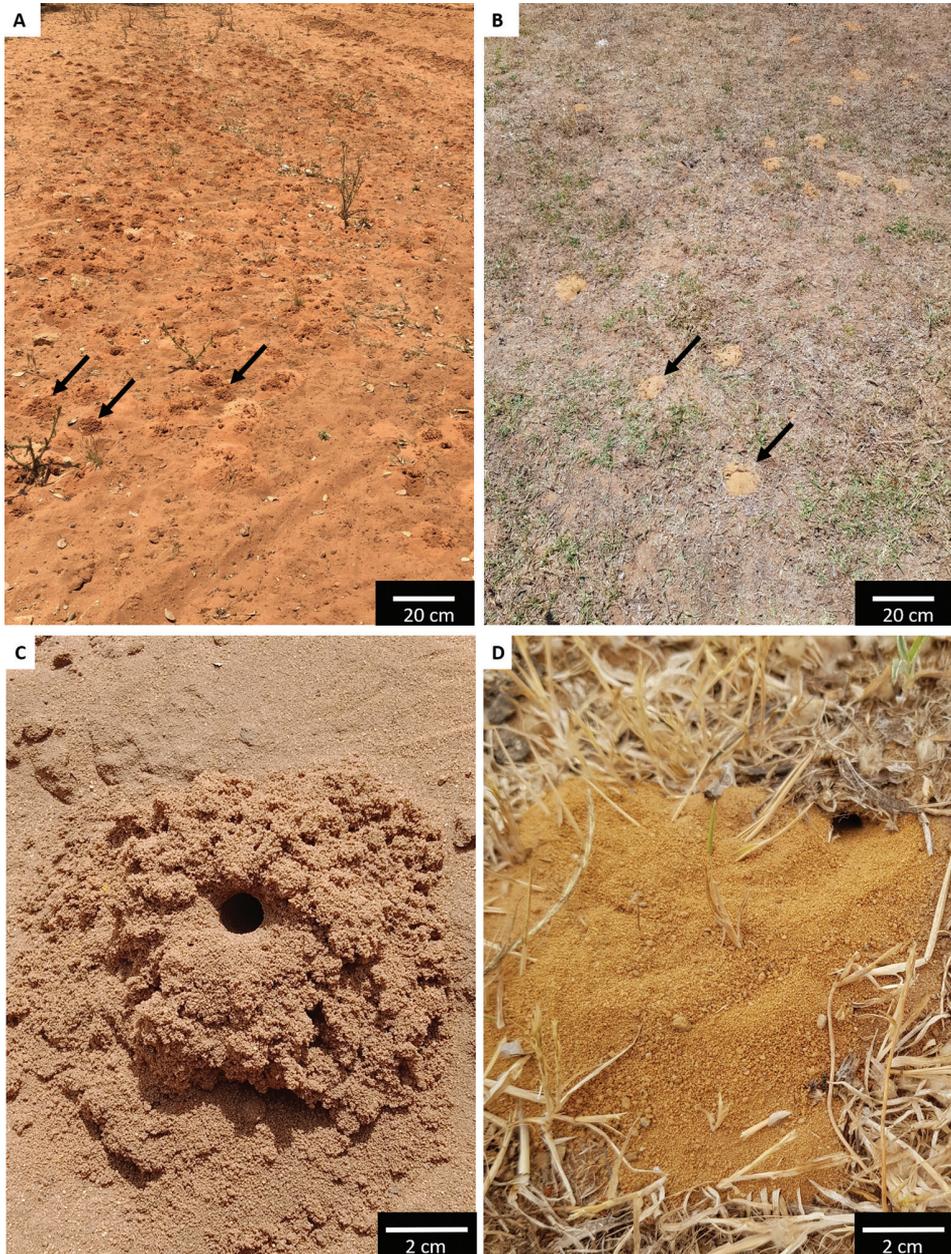

Figure 7. A, B nesting sites **C, D** nest entrances **E, F** nest architecture showing main galleries, hypothetical cells, and pollen balls **G, H** larva with pollen balls. Right side: *Dasypoda maura*, left side: *Dasypoda visnaga*.
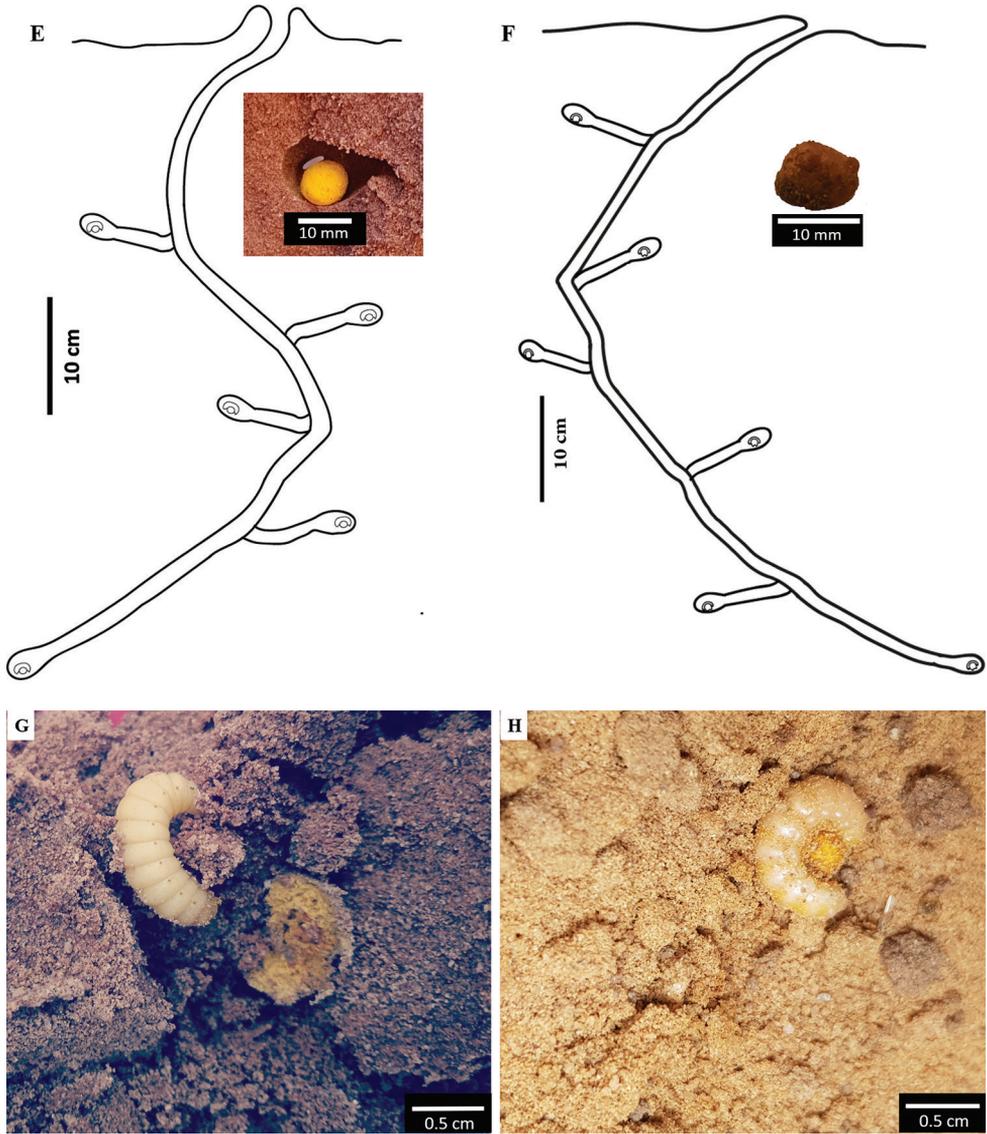
Figure 7. Continued.

ranges from 7 to 10 cm (8.6 ± 1.07 cm) and the height ranges from 1 to 4 cm (2.89 ± 1.34 cm). The main burrow has a diameter of 10 mm, it is oblique on 25 cm and at an angle of 45° then it becomes vertical. The main burrow reaches 80 cm in length (Fig. 7E). The female constructs the brood cells connected to the main burrow by lateral burrows located at different depths. Cells were filled with a spherical pollen ball (without a tripod) with the egg placed on the top (Fig. 7E). After laying the egg, the female closes the cell with an earthen plug and tightly fills the lateral burrow with soil.

Nest entrances of *D. maura* (Fig. 7A) were difficult to find because they do not possess conspicuous tumuli like those of *D. visnaga* (Fig. 7D) and were usually found below

vegetation cover. The diameter of the flat nest tumuli ranges from 12 to 16 cm (13.5 ± 1.17 cm). The distance between nests within an aggregation ranges from 32 cm to 170 cm. The females build their nests also in sandy soil with a low proportion of clay. The main burrow has a diameter of 8 mm and a length of 80 cm. The brood cells are also connected to the main burrow by lateral ones located at different depths and each cell contains a pollen ball with a basal tripod (Fig. 7F). The egg was also laid on the top of the pollen ball.

Discussion

The present study revealed that the two studied *Dasypoda* species have similar ecological requirements with slight differences. *Dasypoda visnaga* is found in most Mediterranean countries, especially in coastal areas. This distribution is probably related to the type of soil as *D. visnaga* nests in non-compacted sand, and its main host plant *Scolymus hispanicus* is often found in coastal areas. *Dasypoda maura* is additionally found inland in Morocco. The soil where *D. maura* nests can be much more compact than the soil where nests of *D. visnaga* were observed. Phenological records in Morocco and other countries showed that *D. visnaga* and *D. maura* are mainly active during late spring and summer (April-August). This period coincides with the flowering of *Scolymus* plants. This suggests the presence of one generation per year like others species of *Dasypoda* (Radchenko and Pesenko 1989; Vereecken et al. 2006).

Morphological data showed that the females of *D. visnaga* have a larger body size than *D. maura*. Following Greenleaf et al. (2007) model, the estimated foraging distance for both species should be large. This distance is close to other large species like *Bombus terrestris* Linnaeus (1500 m) (Osborne et al. 2008) or *Hoplitis adunca* Panzer (1400 m) (Zurbuchen et al. 2010). Consequently, *Dasypoda* species could be less sensitive to disturbances like habitat destruction (De Palma et al. 2015). A slight trend for small species to be more sensitive to land disturbance has been found (Bartomeus et al. 2017), but other studies have shown a positive correlation between body size and sensitivity to agricultural land use (Bartomeus et al. 2013).

Females of the two species have a different tongue length but the same foraging duration on flowers of *Scolymus*. The time spent per flower for *D. visnaga* and *D. maura* (4.2 s and 3.8 s respectively) is higher than for *D. hirtipes* (0.7 s) (Levermann et al. 2000). According to Klumpers et al. (2019), the interaction between the length of a proboscis and the depth of corolla affects the handling time. Insects with a proboscis shorter than nectar tubes spend more time foraging per flower on these flowers and are consequently a less efficient. In this study, the two bee species forage on the same plant species so the time spent foraging does not seem to be affected by tongue length. However we used a different metric and did not investigate the handling time as described by Klumpers et al. (2019) which is the time that an insect takes to extend its proboscis and extract the nectar. Records from historical data and our observations show that *D. visnaga* and *D. maura* have similar floral preferences. They forage mostly on Asteraceae family confirming the position of Michez et al. (2008). Pollen analyses revealed that both species are strict oligoleges of Asteraceae,

and though it cannot be proved definitively with light microscopy, females are highly likely to provision their offspring with pollen of *Scolymus* plants exclusively, thus making them narrow oligoleges. The comparison between male and female choices shows the presence of large differences in floral choices that are known to exist between different bee sexes (Roswell et al. 2019).

Dasypoda maura and *D. visnaga* seem to have nesting behaviour and nest architecture similar to the other *Dasypoda* nests described so far. After emergence and mating, females of *D. visnaga* start to build their nests in sandy soil, similar observations were made for *Dasypoda hirtipes* (Vereecken et al. 2006) and *Dasypoda argentata* (Celary 2002) whereas, *Dasypoda braccata* prefers soil with a high clay content (Radchenko 1988). Females first excavate an oblique burrow for about 25–30 cm. Then, the burrow changes direction and females start to construct cells where they put pollen balls. Pollen balls made by *D. visnaga* do not possess any tripod and were put directly on the soil at the bottom of the cells, which do not have the additional lining that characteristic of many other ground-nesting bees (Fig. 7E) while *D. maura* pollen possess tripods (Fig. 7F), like *D. hirtipes*, another species from the same subgenus (Müller 1884; Vereecken et al. 2006).

Conclusion

This study is the first to compare ecological aspects of two species of *Dasypoda* bees. Both studied species are oligolectic and share many ecological traits. They have very restricted floral preferences and nesting requirements. Future surveys should be performed to better understand their ecology and assess if conservation strategies are needed. The two species were found in agricultural landscape, so these strategies should consider the role of farmers. They should be informed and trained to recognise the bee nests and their host plant to protect them in local areas.

Acknowledgements

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Supplementary material I

Tables S1–S3

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Data type: Occurences, morphological traits, floral preferences

Explanation note: **Table S1:** distribution data of Dasypoda visnaga and Dasypoda maura; **Table S2:** morphological trait and forging distance measurement; **Table S3:** floral preferences of Dasypoda visnaga and Dasypoda maura.

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