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SHORT COMMUNICATION

Observations on nesting preferences and success in two species of *Anthophora* (Hymenoptera: Apidae)

Michael C. Orr[1] & Hauke Koch[2]

Abstract

The drivers influencing how bees nest, either in horizontal or vertical faces, remain unclear. Here, we discuss two new examples of bees that typically prefer vertical faces, nesting horizontally when under cover.

Keywords: anthropogenic, Apoidea, behavior, natural history, life history.

Zusammenfassung

Die treibenden Faktoren, die beeinflussen, wie Bienen nisten, ob in horizontalen oder vertikalen Flächen, bleiben unklar. Hier werden beispielhaft zwei Bienenarten neu diskutiert, die normalerweise vertikale Flächen bevorzugen, aber horizontal nisten, wenn sie geschützt sind.

The persistence of a bee species in any environment is contingent upon the resources it requires. Among such resources, nesting substrates are of central but understudied importance (Linsley 1958; Harmon-Threatt 2020; Orr et al. 2022; Portman et al. 2022). For example, cavity-nesting bees require logs with beetle holes, pithy-stemmed woody plants, etc., while ground nesters may require specific substrates and other local parameters that meet their requirements (Linsley 1958; Michener et al. 1958). Although the type of substrate used is of immediately obvious importance and has been the subject of many studies (e.g., Harmon-Threatt 2020; Orr et al. 2022), substrate orientation may also prove important, as it influences exposure to sun, precipitation, debris, predators, and more.

The species *Anthophora plumipes* (Pallas, 1772) and *Anthophora villosula* (Pallas, 1772), both of the subgenus *Anthophora* Latreille, are exceedingly common species found across much of Europe and Asia, respectively. Recently proven as separate species (Černá et al. 2017), they perform well in anthropogenic environments (Banaszak-Cibicka et al. 2018) and could prove useful as managed pollinators, as both will readily nest in vertical cobb or soil boxes (Stone 1994; Batra 1994; Bond & Kirby 1999) and can be important pollinators of crops like broad bean (Bond & Kirby 1999), blueberry (Stubbs & Drummond 1999), and strawberry (Adhikari & Miyanaga 2016). Both species primarily nest in vertical soil, with few exceptions (Černá et al. 2013; Adhikari 2016; S. Droege, pers. comm.). By documenting several more such exceptions here, we endeavor to better understand why they might choose to nest in vertical or horizontal orientation.

Study sites and observations

Site A. Olympic Park, Beijing, China (*Anthophora villosula*): First visited in spring 2018, this site was found directly under a large (~8 m wide) pedestrian bridge in Chaoyang District's Olympic Park (Fig. 1A; approximately 40.014555, 116.382278). There, a subset of the area beneath the bridge was partially fenced off, with the silty loam substrate gradually and irregularly sloping down from the higher western edge of the bridge toward the buttress separating the bridge from the street that it traverses. The substrate was exceptionally dry due to the dry climate and bridge overhead. Nests were most concentrated toward the lower end of the slope in an area of ~7.5x3m where intermixed small vegetation provided more structure and perhaps stability to the soil, with nests in both essentially flat and vertical orientation depending on the crenulated structure of the slope there (oriented primarily NE). This contrasts with purely vertical nesting, usually under overhangs, observed under most natural conditions such as in Songshan, Beijing (Fig. 1B), although at that location they also nested partially horizontally (flat) beneath an old gazebo in similarly dry silt loam/silty clay loam, exposed to the S–SE. At site A, the highest density observed entailed entrances spaced only a few cm apart, and a conservative estimate of nest entrances for the site is 100, although likely fewer nests were active at any given time, given the generally higher than usual (among other bees) tendency for reuse across generations in the genus (Orr et al. 2016). The nests themselves were relatively shallow, nearly all under 6 cm in length based on 10 nests, generally in agreement with prior works. The nests and related debris remained visible throughout the year—a testament to the shelter provided by the bridge above.

Bee activity was confirmed in 2018, 2019, 2021, and 2022, in both the last week of March and first week of April, minimally. Temperatures ranged generally from 10–20 °C (visits were made on sunny days averaging 15 °C to ensure activity). Males were almost entirely absent from nest sites, instead patrolling nearby *Forsythia* and other plants, but at peak activity there were up to five females at the site at any given time, suggesting a considerable population. There were no evident signs of population size change across years, despite the presence of *Melecta chinensis* Cockerell, 1931 actively invading nests each year at relatively high densities (up to three females visible at any given time Fig. 1C; note that at times they were most obvious while sunning on the bridge above, when colder). Around the periphery, especially slightly above and southwest, *Osmia cornifrons* (Radoszkowski, 1887) was found reusing old *Anthophora* nest tunnels (at least three individuals; Fig. 1D; separately seen bringing in pollen). Interestingly, soil nest reuse was previously undocumented in this species.

Site B. Royal Botanic Gardens, Kew, Richmond, UK (*Anthophora plumipes*): Visited by the authors on March 15th 2018, the site is located in a small courtyard of the Sir Joseph Banks Building within Kew (coordinates: 51.48464, -0.29292). The nests were located beneath a 1.3 m overhang, which provided shade for much of the day, spaced 60 cm from the wall in a relatively narrow band stretching for 6.5 m in parallel to the building, where the sandy loam soil was flat and relatively drier than the surrounding area, intermixed with various small rocks and debris (Fig. 2A). The nests were exposed to sun from the south-southwest. Most nests were shallow, roughly 5 cm deep, and many of the entrances were located beneath small rocks.

Numerous females were seen at the site concurrently in 2018, with a conservatively estimated total population of 20 nesting females. Again, males were more often seeking females at flowers such as *Pulmonaria* spp. and *Lamium purpureum*, where the females commonly collected pollen. From all appearances, the site was healthy. Visits to the site in March and April 2019 showed similar activity of nesting females as in 2018. In 2022, however, only one female was observed nesting at the site during a 30-minute period on May 5th in sunny weather with scattered clouds at 19 °C (following earlier observations that year when they were either not active or present), although many females were still visiting a bed of *Pulmonaria* nearby. Many nest cells were also exposed in May, and approximately 100 such nest cells were observed; among them, five had fungal growth and spoilt pollen remnants. It is possible that the cells were exposed via human activity or possibly inundation, as *Anthophora* cells are waterproofed via Dufour's gland secretions and would be more resistant than the surrounding soil matrix. Later examination of the site near the end of the flight season in late May revealed no contemporary nests (Fig. 2B), although two additional nest cells were found with larvae from prior years that had failed to develop. Notably, a rodent burrow was also noticed nearby, but predation seems unlikely because debris from eaten larvae was non-evident and it seems likely that larvae which failed to develop would also have been eaten. Similar to Site A, *Melecta albifrons* (Forster, 1771) was visiting the nests at Site B; it is possible that their cleptoparasitic behavior could dissuade bees from re-nesting, but they were relatively uncommon. Fungal growth seen in nest cells could also have played a role, though relatively few cells were so afflicted, instead with many empty cells suggesting abandonment rather than mortality-driven extirpation.

Specimens were identified with reference material at the respective author institutions, where they were also deposited.

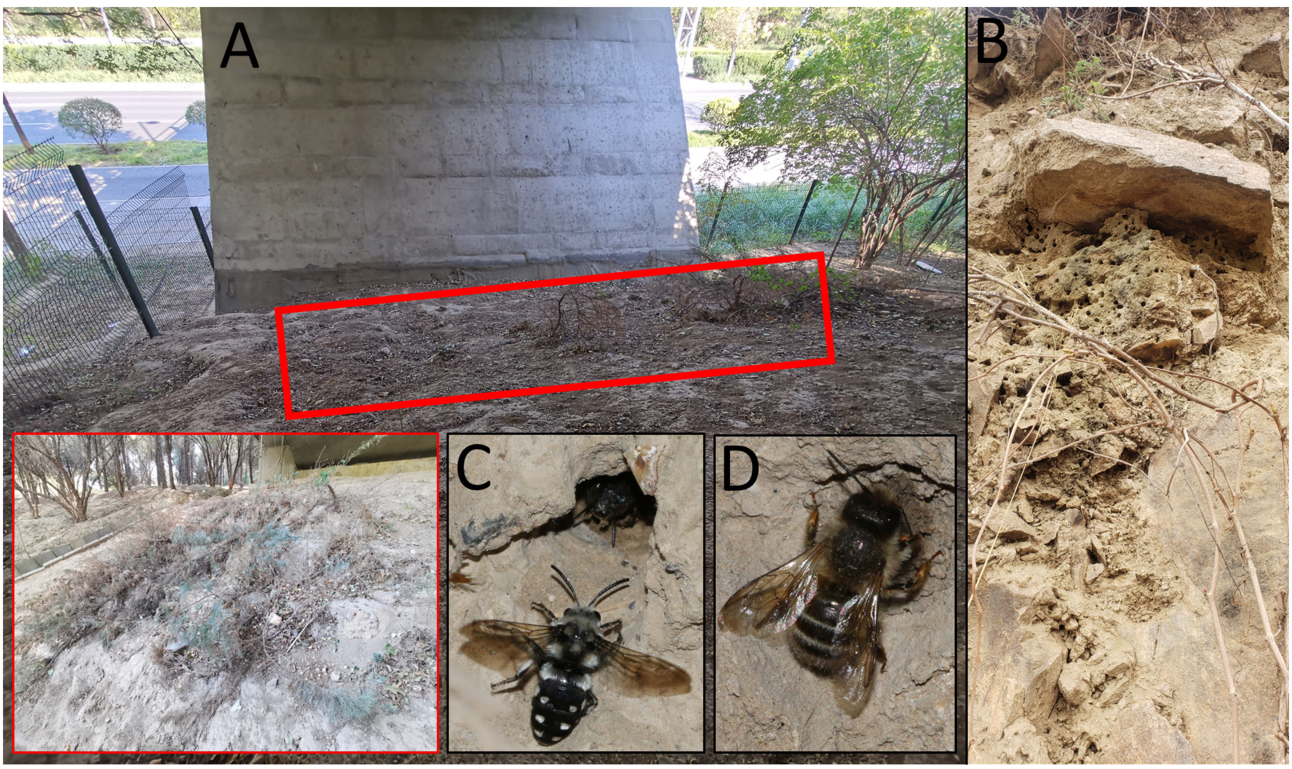

Fig. 1. Site A, Olympic Park, Beijing. **A**. Overall site, with the visible area used for nesting outlined in red. **B**. One of many natural *Anthophora villosula* nest sites in Songshan, Beijing, in dry silty loam facing south. **C**. *Melecta chinensis* attempting to invade an occupied nest. **D**. *Osmia cornifrons* using an abandoned *Anthophora* nest.

Fig. 2. Site B, Kew Gardens, London, UK. **A**. Overall site, with the visible area used for nesting outlined in red. **B**. Empty nest cells from previous years.

Discussion

Although experimental manipulations would be necessary to be sure, the available evidence suggests that precipitation, known to be detrimental in excess (Fellendorf et al. 2004), is a driving factor in nest site choice, as hypothesized previously by Černá et al. (2013). This means that, for some species, the choice to nest in vertical or horizontal (flat) surfaces may be primarily to avoid exposure to precipitation. Especially interesting is the case at Site B, where the population has virtually disappeared. Nest abandonment is not rare in *A. plumipes* (Černá et al. 2013), but the unusually cold temperature and wetness of spring 2021 (second wettest May on record since 1836, 2018 and 2019 more typical; Kendon et al. 2022) may have impacted these populations.

The new examples given here are from the same subgenus of bees, making them a limited sampling of the breadth of bee biodiversity, so the generalization of this reasoning is somewhat limited. However, high plasticity in nest orientation is not uncommon under sheltered conditions (and sometimes without shelter) in other bees such as cavity-nesting megachilids, e.g., *Megachile willughbiella* (Kirby, 1802), and many others (F. D. Parker, pers. comm.; H. Koch, pers. obs.). Additional species may nest in both horizontal and vertical faces, including *Panurgus calcaratus* (Scopoli, 1763) (Rozen 1967) and *Lasioglossum morio* (Fabricius, 1793) (Westrich 2022), but our knowledge is limited by few natural history accounts for all but the best-known species (Harmon-Threatt 2020); since most studies used one site, environment-dependent variation may be entirely unaccounted for in most species, and our knowledge is further limited primarily to higher-income countries (Orr et al. 2020). With further study of the natural history of these and other urban-adapted species (Orr et al. 2022; Portman et al. 2022), it may also be possible to better understand their nest site preferences and design cities better equipped for bees.

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