Soil textures of nest partitions made by the mason bees Osmia lignaria and O. cornifrons (Hymenoptera: Megachilidae)

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Original article

Soil textures of nest partitions made by the mason bees *Osmia lignaria* and *O. cornifrons* (Hymenoptera: Megachilidae)

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Abstract – *Osmia lignaria* and *O. cornifrons* require mineral soil to build partitions between cells in their nests. We examined the textures of soil collected by these bees, using laser particle size analysis. For both species, soil in the nest was generally loam or sandy loam in texture, although individual partitions had wide variation in particle size. Partitions in *O. cornifrons* nests had 5.8% higher clay content than those in *O. lignaria* nests. Textural trends were similar when data from individual partitions were analyzed. For both species, we found no significant effect of nearby soil texture or the position of the partition in the nest, on the texture of individual partitions. Observations of partitions indicate that some females collect soil material from different locations to build one single partition. These results shed new light on the ecology of soil used by cavity nesting mason bees, with implications for their management as alternative pollinators.

blue orchard bee / hornfaced bee / laser particle size analysis / alternative managed bee

1. INTRODUCTION

Bees in the genus *Osmia* (Megachilidae) that nest in wood cavities commonly use a mix of plant and soil materials to build the cell partitions in their nest (Linsley 1958). Some species exclusively use mineral soil materials (Levin 1966; Cane et al. 2007), making it an essential and limiting resource for them (Krunic and Stanisavljevic 2006). These bees include *Osmia lignaria* (Say) and *O. cornifrons* (Radoszkowski), a native and introduced species in the USA, respectively (Batra 1978), used for pollination of rosaceous tree crops (Bosch and Kemp 2002; Peterson et al. 2014; Sheffield 2014).

In recent years, more attention has been given to the nesting preferences and biology of wild bees (Christmann and Aw-Hassan 2012; Sedivy and Dorn, 2014). However, for mason bees (Hymenoptera: Megachilidae: *Osmia*), most studies have focused on nesting preferences and nest management (Torchio 1982; Sampson et al. 2009; Artz et al. 2013, 2014). Little attention has been paid to understanding some other important aspects of their biology, including their use of soil for nest construction.

Although the behavior of *Osmia* species during soil collection and partition construction has

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been described in detail (Levin 1966; Raw 1972; Torchio 1989; McKinney and Park 2012), it is still unclear whether *Osmia* bees have specific preferences or requirements for the physical or chemical characteristics of soil they collect. Soil texture (percentage of clay, silt, and sand) is a factor that can influence nest site selection by ground nesting bees and wasps (Krombein 1967; Cane 1991; Scott 2016), so it is likely this will also play a role in nest construction by *Osmia* species. Anecdotal reports suggest a preference for soil with high clay content (Rau and Mo 1937; Medler 1967), but we are unaware of detailed analyses of the textural composition of *Osmia* nest soil partitions.

The lack of data on soil use by *Osmia* bees is partly due to the small size of the partitions. Standard soil analysis methods typically require > 20 g of soil, whereas the weight of individual partitions may be < 1 g. The availability of laser diffraction for measurement of soil texture (Miller and Schaetzl 2012, Fisher et al. 2017) provides an opportunity to determine the textural composition of soil used in nest partitions, because far less soil is required. Quantifying the textural composition of the soil materials these bees use will provide insights into their soil foraging ecology and thus improve our ability to maximize their propagation in agricultural landscapes. In this study, we addressed the following objectives: (1) determine the textural composition of soils used by two *Osmia* bee species to construct their nest partitions; (2) determine how nest partition composition varies between species, between nests, and within nests; and (3) determine whether soil used by *Osmia* bees is influenced by the textures of soil in the vicinity of the nest.

2. MATERIALS AND METHODS

2.1. Study area

The research was carried out at the Trevor Nichols Research Center in Fennville, Michigan (USA) (42° 35′ 38″ N, 86° 9′ 18″ W) (Figure 1). In this 63-ha station, 12 locations spanning a range of soil types and with low risk of pesticide exposure were selected for *Osmia* nests. Each location was separated by at least 45 m.

On May 3, 2016, one nest shelter with 50 bamboo stems for nesting by *Osmia* bees was installed at each location; each stem was approximately 15 cm long with an inside diameter of 7–10 mm and with a node at the rear of each stem. Inside each shelter, we placed an emergence box containing female and male loose cocoons of both species. Female cocoons were 73% *O. lignaria* and 27% *O. cornifrons*, while male cocoons were 88% *O. lignaria* and 12% *O. cornifrons*. Cocoons were gathered from trap nests located at Michigan State University (MSU) campus in September 2015.

2.2. Soil sampling

We collected soil samples from the surrounding area, based on the assumed foraging range of *O. lignaria* and *O. cornifrons* (Figure 1). To that end, we delineated a 250-m radius around each nesting shelter, exceeding the 150-m foraging range reported for these bees (Monzón et al. 2004; Matsumoto et al. 2009; Biddinger et al. 2013). Using the USDA Soil Survey website (https://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx), a map of surface mineral soil textures was generated. To confirm the textures reported in the map, a total of 62 soil samples (Figure 1) were taken from the various soil units shown as different soil textures in the USDA map. At each location, five subsamples were taken from the upper 10-cm layer in a 2-m radius. Subsamples from each location were mixed, resulting in approximately 500 g of soil from each location.

To obtain soil samples from the bee nests, the bamboo was collected in early June, after the nesting period. Nests were kept at outside ambient temperatures until September 2016, when bees had finished their development into adults. To confirm the species that built each nest, one cocoon per nest was opened and the bee inside was identified using the key of Arduser (2009). Two groups of soil samples were collected, each from a different set of nests. In the composite nest samples, 24 *O. cornifrons* and 22 *O. lignaria* nests were opened and all partitions present were collected. Partitions recovered from the same nest were homogenized. Of these nests, 13 *O. cornifrons* and four *O. lignaria* nests came

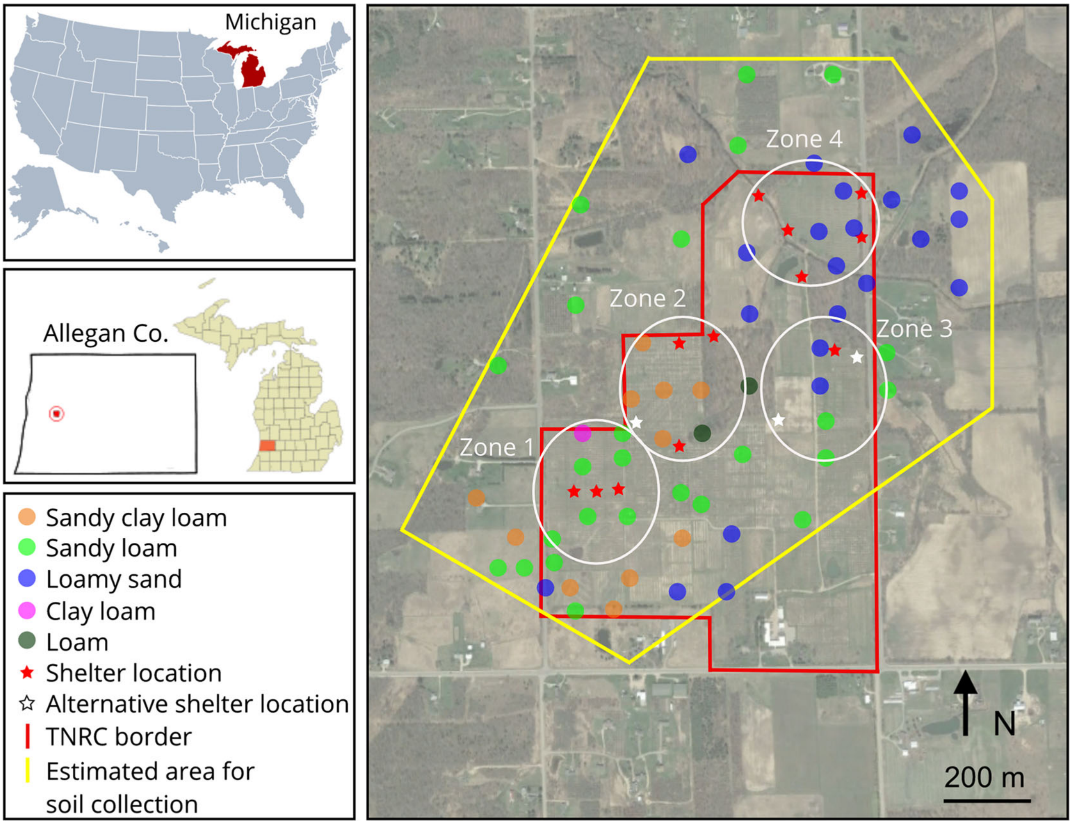

Figure 1. Map of the Trevor Nichols Research Center near Fennville, MI, showing the textures of surface samples (0–10 cm). The estimated area available for bee foraging (yellow line) was based on a 250-m foraging range from each shelter location. Alternative locations correspond to *Osmia* shelters in the station installed for other experiments, from where nests were recovered and analyzed, to increase the number of samples.

from alternative nesting shelters placed at the research station, to increase the sample size (Figure 1). In addition to these composite nest samples, we also analyzed the textures of individual nest partitions from a separate group of nests. For this, an additional set of tubes were opened to collect partitions from eight *O. cornifrons* nests (totaling 67 partitions) and six *O. lignaria* nests (44 partitions). Each partition was kept separate and their relative order in the nests was noted. Nest caps were not sampled because they were usually lost during the process of opening the tubes.

2.3. Soil texture analysis

Soil samples from the plots on the research station were analyzed at the Soil and Plant Nutrient Laboratory at the Department of Plant, Soil and Microbial Sciences of MSU. To prepare the samples for analysis, 100 g of soil per sample was oven dried, and then 100 ml of a 5% sodium metaphosphate (NaO_3P) solution was added as a dispersant. Samples were shaken overnight, and the percentages of clay (< 2-µm particles), silt (3–50-µm particles), and sand (51–2000-µm particles) were determined using the standard hydrometer methodology (Foth 1990).

Textural analysis of the composite soil samples from nests and the individual partitions was performed using a Malvern Mastersizer 2000E laser particle size analyzer (Malvern Instruments Ltd., Worcestershire, UK). Results with this method are generally comparable to those obtained by hydrometer (Fisher et al. 2017). Each sample was gently ground and dispersed by adding 2 ml of a 5% sodium hexametaphosphate ($(NaPO_3)_{13}Na_2O$) solution, followed by oscillation shaking for 10 min. Samples were then analyzed to determine the percentage of clay, silt, and sand. To classify samples, we used the USDA soil texture classes (USDA Soil science division staff 2017).

To further characterize the composition of the soil in the partitions, those with distinctive color patterns were photographed using a Leica S8AP0 microscope with a MC120 HD camera attachment. Images were stacked using Zerene Stacker version 1.04 to create composite images.

2.4. Data analysis

A generalized linear mixed model (GLMM) with beta distribution and logit link function in PROC GLIMMIX in SAS version 9.4 (SAS Institute 2016) was used to examine how the percentages of sand, silt, and clay in the composite nest and individual partition samples varied between species and among nest locations, and their interactions (fixed effects). Nest tube was included as a random effect. For the analysis of individual partitions, their position in the nest (counting from the deepest section of the nest where bees start their nest construction) and the interactions with the other factors were also included as fixed effects.

3. RESULTS

3.1. Texture of soil near nests

Soil from the estimated available foraging area was generally sandy, with most samples being sandy loam (39%), loamy sand (37%), or sandy clay loam (19%). Other textures present in the area were loam (3%) and clay loam (2%) (Figure 1). Using these data, the *Osmia* shelters were classified into four zones, based on the predominant soil texture nearby (Figure 1). Zone 1 contained mainly sandy loam soil, zone 2 mainly sandy clay loam, zone 3 mainly sandy loam and loamy sand, and zone 4 mainly loamy sand. In zone 2, *O. lignaria* was not included in the partition analysis because there were not enough completed nests.

Textures of composite nest samples

Silt and sand content of composite nest samples from both species were similar (Table I), with no significant difference between species or among nest locations ($P > 0.05$). However, samples from *O. cornifrons* nests had, on average, 5.8% more clay than samples from *O. lignaria* nests ($F_{(1, 38)} = 12.77$, $P < 0.001$) (Table I), without significant variation among the locations of the nests ($F_{(3, 38)} = 1.94$, $P = 0.14$) or any significant interaction between factors ($F_{(3, 38)} = 1.04$, $P = 0.39$). Clay content in *O. cornifrons* nests had a slightly wider range than did samples from *O. lignaria* nests, and consequently, there was an opposite pattern for the silt and sand content, for which *O. lignaria* showed a wider range than *O. cornifrons* (Table I). Most of the composite samples were loam (58.3% for *O. cornifrons* and 50.0% for *O. lignaria*) or sandy loam (41.7 and 43.5%) (Figure 2a).

3.2. Texture of individual partitions

The particle size composition of individual partitions was similar for both species (clay: $F_{(1, 88)} = 0.15$, $P = 0.69$; silt: $F_{(1, 88)} = 0.51$, $P = 0.48$; sand: $F_{(1, 88)} = 0.10$, $P = 0.75$). The textures of the soil that bees collected were not different among locations (clay: $F_{(3, 88)} = 0.46$, $P = 0.71$; silt: $F_{(3, 88)} = 1.30$, $P = 0.28$; sand: $F_{(3, 88)} = 1.42$, $P = 0.24$). Additionally, the textures of the partitions were similar among the different cell positions within the nest, with no evidence of the composition varying based on the order of construction (clay: $F_{(1, 88)} = 0.14$, $P = 0.71$; silt: $F_{(1, 88)} = 0.02$, $P = 0.89$; sand: $F_{(1, 88)} = 0.24$, $P = 0.62$). We did not find any two-way or three-way interactions between factors (all $P > 0.05$) on particle size composition.

The ranges of all three soil particle components were wider for individual partitions than for composite nest samples (Table I, Figure 2b). The clay content range was wider for *O. cornifrons*, whereas the silt and sand content ranges were wider for *O. lignaria* (Table I). Most partitions were of loam (41.8% for *O. cornifrons* and 27.3% for *O. lignaria*) and sandy loam (40.3% for *O. cornifrons* and 47.7% for *O. lignaria*) texture. Due to the higher variation, other partitions were

Table I. Percentage of soil separates (range and average ± SE) for composite nest and individual partition samples collected by *O. cornifrons* and *O. lignaria*

	n	Range			Average*		
		Clay (%)	Silt (%)	Sand (%)	Clay (%)	Silt (%)	Sand (%)
Composite nest samples							
O. cornifrons	24	6–21	23–45	37–70	14 ± 1a	34 ± 1a	52 ± 2a
O. lignaria	22	2–15	15–49	40–82	8 ± 1b	37 ± 2a	54 ± 2a
Individual partition samples							
O. cornifrons	67	2–34	20–76	4–78	12 ± 1a	39 ± 1a	48 ± 2a
O. lignaria	44	1–28	20–86	0–79	9 ± 1a	46 ± 3a	45 ± 2a

*For each particle size category (clay, silt, sand) in each type of sample, means with different letters are significantly different ($P < 0.05$)

of loamy sand, silt loam, and silty clay loam texture (Figure 2b).

When considering partitions from the same nest, most were within the same texture class, but in a minority of the nests, the partitions were much more variable (Figure 3). Visual inspection of the nest partitions showed that approximately 8% of the partitions for both species (data not shown) exhibited noticeable color patterns, indicating the use of variable soil types/textures for a single partition. These patterns ranged from spirals and circular arrangements (Figure 4b–d) to spotted color arrangements (Figure 4e). Some partitions also showed different colors in each face (Figure 4f), suggesting a switch from one soil type to another during construction.

4. DISCUSSION

Even with the increasing interest in mason bees as commercial pollinators (Peterson et al. 2014), little is known about the soil that bees utilize to build the partitions in their nests. In this study, we report on detailed soil composition data from nests made by two of the most promising *Osmia* species, revealing differences between a native and a

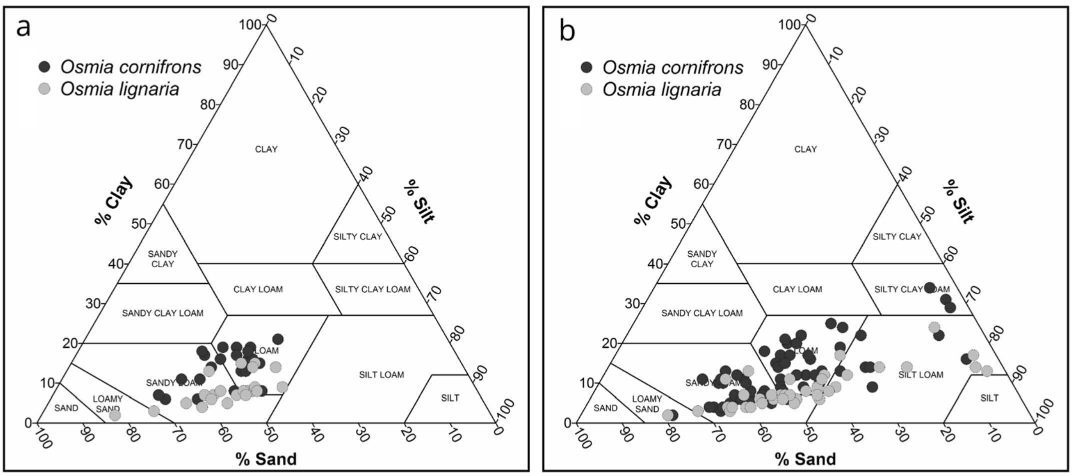

Figure 2. Texture of soil samples from **a** the composite nest (all partitions in a nest) and **b** individual partitions within nests of *O. cornifrons* (black) and *O. lignaria* (gray).

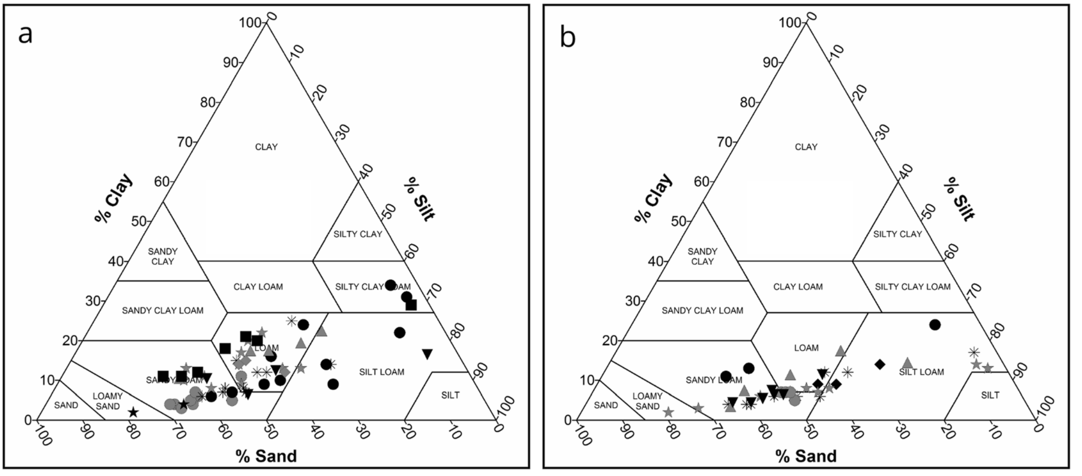

Figure 3. Textures of soil samples from individual partitions in the nests of **a** *O. cornifrons* and **b** *O. lignaria* . Dots with the same color and shape correspond to partitions from the same nest.

non-native species. To the best of our knowledge, this is the first report of the textures of soil materials collected by *O. cornifrons* and *O. lignaria* .

Earlier reports of soil use by mason bees indicate that they prefer soft, moist soils with high clay content (Rau and Mo 1937; Medler 1967; Mader et al. 2010). For both bee species, most of nest samples had loam or sandy loam textures, and individual partitions also exhibited considerable variation in textures, suggesting that clayey soil is not essential for successful nesting. The question of what type of soil is selected by mason bees from the available options should be addressed by future experiments in an enclosed setting where female bees can select from soil of different textures. We predict that species will differ in their soil preferences, as suggested by the differences found in the soil clay content collected by the two species studied here. This experimental setting could allow for exploration of texture as well as other potentially important factors such as soil moisture and organic matter.

One possible reason for the generally low clay content of the soils collected by both species is that clayey soil was absent from most sampled locations. Furthermore, some kinds of clays will crack upon drying, allowing entry of parasites. In using mainly coarser-textured soils, females may also need a sticky substance to bind the soil particles which might come from saliva, given that many other bees secrete substances to waterproof the nest or keep the building materials together (Michener 2007).

The relatively low textural variation of the soils at the study site could help explain why bees nesting at different locations all collected similar textured soil. It is also possible that bees could fly out of the study area to find their preferred soil type, since individual flights can extend beyond 600 m (Rust 1990). In that case, the texture variation across the research station would have less influence on the soil found in the nests.

In general, texture was similar across the positions in the nest for both species, indicating that soil selection is relatively consistent. However, the larger texture variations observed within some nests shows it is possible for females to change soil textures over time. Additionally, the different colored soil patches observed within individual partitions indicates soil collection from more than one location during the several trips needed to gather material for one partition. Future studies should consider the investment (amount of soil) that different species allocate to building partitions, and the adaptive benefits of using particular soil types.

5. CONCLUSIONS

We found that *O. cornifrons* and *O. lignaria* collect soil from a broader range of textures than previously reported, with species differing in the

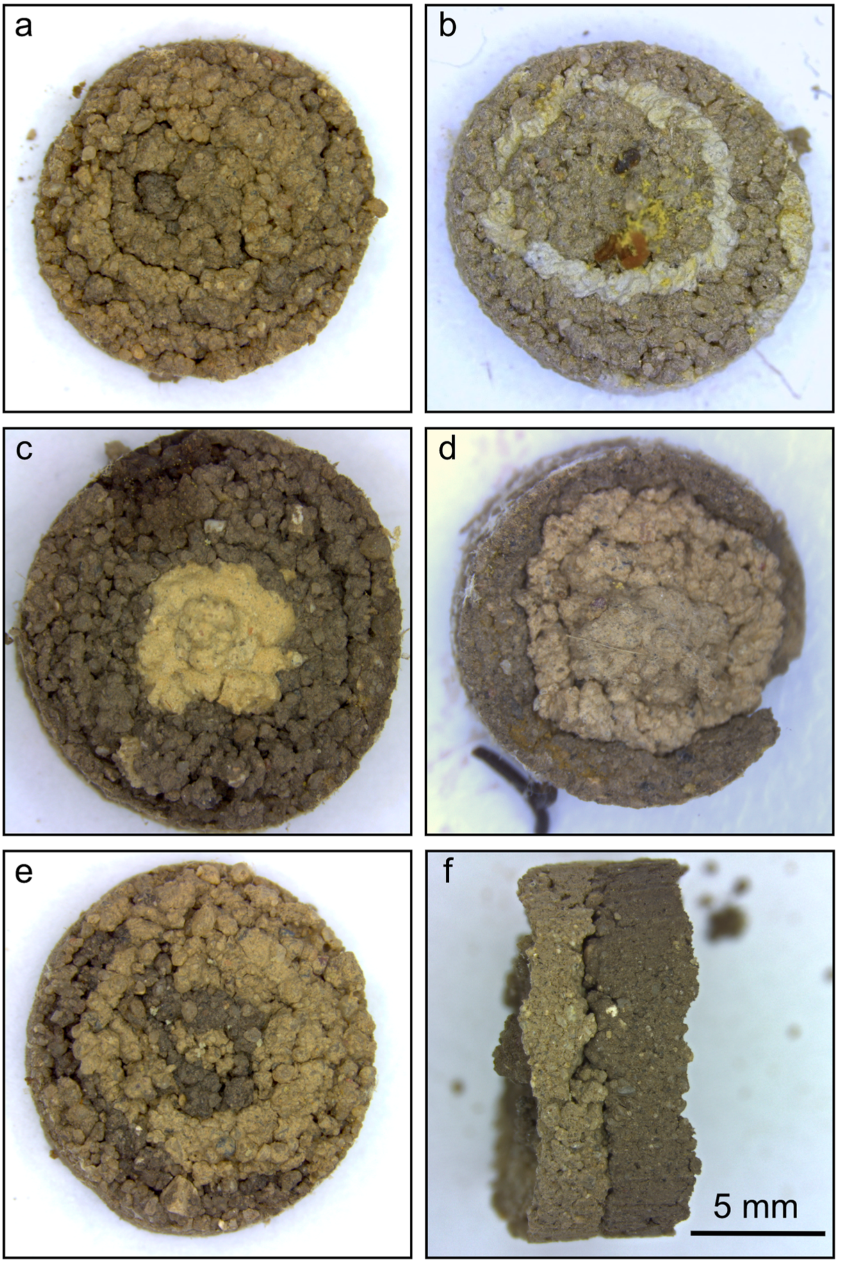

Figure 4. Photographs of nest partitions of *O. cornifrons* and *O. lignaria* . Partitions can have a uniform color (**a**) or more than one color with arrangements that resemble the construction pattern of concentric circles (**b-d**) or spotted arrangements (**e**). Partitions can exhibit varying colors in each layer (**f**). Soils of different color suggest that they were collected at different location.

clay content of the soil in nest partitions. This provides strong evidence that soil with high clay content is not essential for successful nesting. Their partitions can vary widely in soil texture, with females bringing soil from different locations to build single partitions. Despite the remaining gaps in our understanding of soil use by *Osmia* bees, our results provide an important step toward a more complete understanding of how mason bees utilize soil resources and the factors driving their soil selection. This study also demonstrates that laser particle size analysis can be applied to the study of mason bee nest partitions, providing new opportunities for understanding this important resource.

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AUTHORS' CONTRIBUTIONS

MPG and RI conceived this research and designed the experiments. JC contributed to the experimental design and data analysis. MPG did the field work and data collection and wrote the manuscript with RI. All authors were involved in manuscript revisions.

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Les textures du sol des cloisons de nidification faites par les abeilles maçonnes *Osmia lignaria* et *O. cornifrons* (Hymenoptera: Megachilidae)

***Osmia lignaria* / *Osmia cornifrons* / Analyse granulométrique par laser / abeille gérée alternative**

Bodentextur der Brutzellwände von den Mauerbienen *Osmia lignaria* und *O. cornifrons* (Hymenoptera: Metachilidae)

Blaue Obstbiene / gehörnte Mauerbiene / Laser-Partikelanalyse / gemanagte solitäre Biene

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