**Original article**

# Pollen columns and a wax canopy in a first nest description of *Bombus* (*Cullumanobombus*) *morrisoni* (Apidae)

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**Abstract** – In this study, we describe the first reported nest of *Bombus morrisoni*, a species with an extensive range in the arid Intermountain Region of the Nearctic. The mature, naturally terminated nest consisted of 424 nest cells (cocoons), with 328 non-gyne cells and 94 gyne cells. The nest also had two kinds of understudied structures associated with bumble bee nests: pollen columns and a wax canopy. We found five pollen columns rising amid the cocoons. A 0.3-mm-thick wax canopy spanned over the entire nest. An estimated 40 million pollen grains were incorporated into the 19 g wax canopy, demonstrating that *B. morrisoni* devotes a significant amount of pollen to this non-dietary purpose. *Bombus morrisoni* is a species of conservation concern due to an observed reduction in their historic distribution. The data generated in our study contributes to the much-needed comparative accounts of bumble bee nesting biology and has consequential implications in supporting management and conservation decisions.

**Anthophila / bumble bee / cocoons / wax / pollen**

## 1. INTRODUCTION

Colony development is a key component of the bumble bee life cycle, reflecting the colony's health, its influx of pollen and nectar, and habitat quality (Heinrich 2004; Michener 1974; Sakagami 1976). Published descriptions of colony characteristics, production of offspring, nest position (e.g., ground nesting, above ground nesting), and habitat associations began more than a century ago. Nest studies are widespread, though often cursory, and incomplete for many species in diverse habitats. A recent report by Liczner and Colla (2019) synthesized multiple studies that describe some element of bumble bee nesting biology, sometimes including overwintering biology or ecology across 13 of the 15 recognized bumble bee subgenera. Examining colony structure and function in the context of systematics can generate testable hypotheses relating to the evolution of larval feeding modes and nest location in the environment (Plath 1934; Michener 1974). In our study, we describe for the first time, the nest structure and incidental nesting biology of the Morrison bumble bee, *Bombus morrisoni* Cresson (Hymenoptera: Apidae), from a mature nest from northern Utah (Figure 1A). We elaborate on two rarely characterized structures within the bumble bee colony, pollen columns (cylinders), and a wax canopy and briefly discuss the terminological discrepancies found in the literature.

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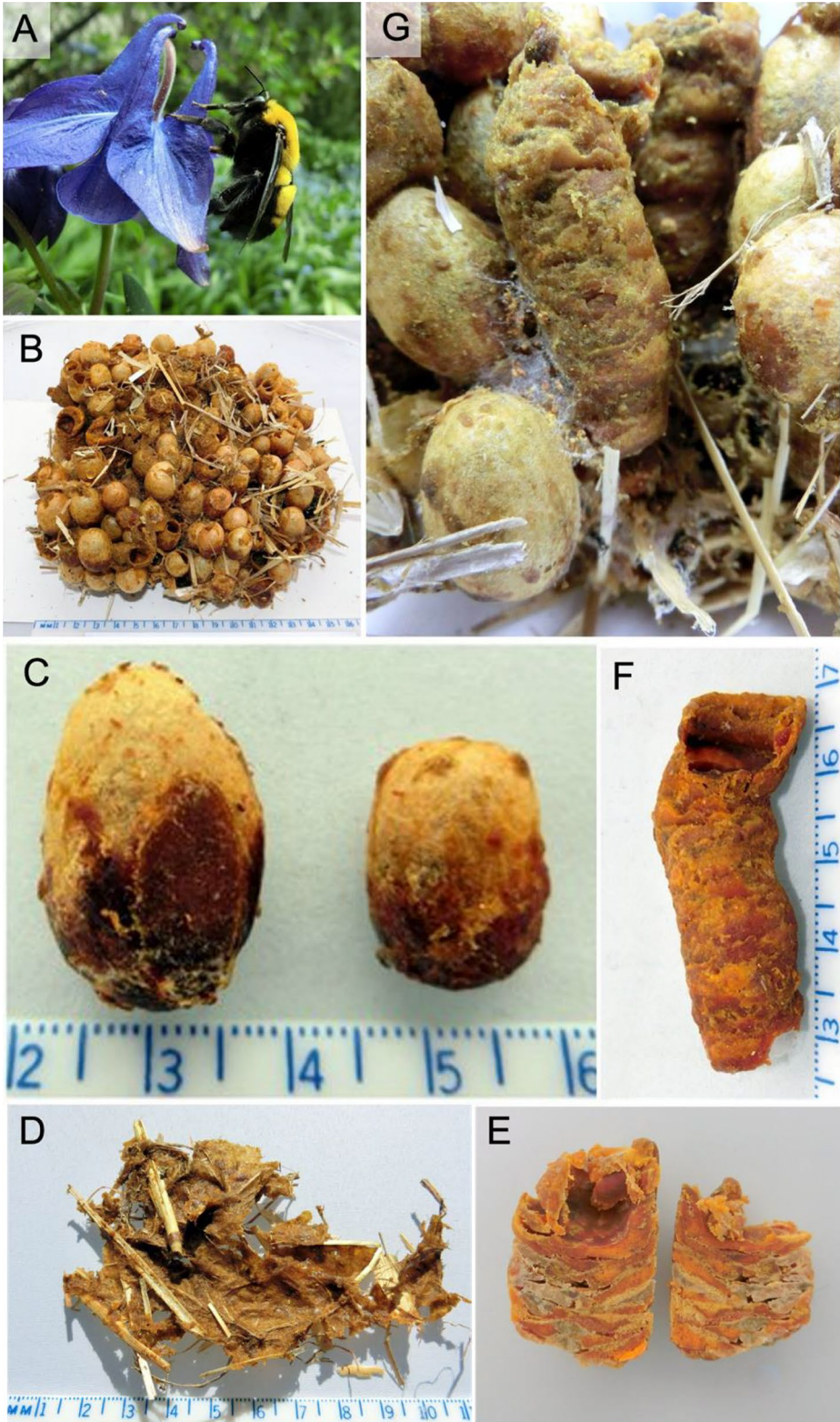
◂**Figure 1.** Plate of *B. morrisoni* nest and associated structures. **A** Female foraging on *Aquilegia × vulgaris* blossom, **B** habitus view of nest (cm scale), **C** aborted gyne (left) and non-gyne (right) pupal cells (cm scale), **D** a sample of the wax canopy with straw (cm scale), **E** midline dissection of two pollen columns, **E** pollen column (cm scale), **G** pollen column among the nest cells.

*Bombus morrisoni* is endemic to arid western North America and overlaps extensively with the Great Basin (Thorp et al. 1983; Williams et al. 2014; Koch et al. 2012). The species is quite common throughout the Intermountain West, with many specimens from Utah in collections (Koch et al. 2012), but surprisingly, no nest has been reported or described. Based on digitized *B. morrisoni* museum labels associated with the US National Pollinating Insect Collection (Logan, Utah, USA), spring queens are active beginning in April, workers forage from late April to late September, and males and fall gynes fly primarily from August until late October in Cache County, Utah (Koch et al. 2012). *B. morrisoni* belongs to the monophyletic subgenus *Cullumanobombus* Vogt., which now includes 23 described species globally (Williams 2021). Seven species plus *B. morrisoni* compose a Nearctic clade (Cameron et al. 2007). In the Western United States, *B. morrisoni* is hypothesized to have undergone range retraction from the Pacific Northwest and northern California (Hatfield et al. 2014).

To date, limited nesting biology reports of the Nearctic *Cullumanobombus* have been published, with some of the most recent reports being completed nearly 60 years ago (e.g., Hobbs 1965). In the subgenus, *B. griseocollis* is known from only a few wild nests, most of which were on the ground surface, with a capacity to produce more than 100 nest cells during the peak of summer (Plath 1934). In contrast, nests of *B. rufocinctus*, another subgeneric relative, can be either subterranean or above ground and sometimes large, producing more than 430 cocoons in a season (Hobbs 1965). Furthermore, similar to the observations we report in our study, *B. rufocinctus* has been found to produce "wax-pollen" cylinders for storing pollen on the periphery of the brood mass and has been described as a "prolific producer of wax" as evidenced by the development of a wax canopy to waterproof nest and protect the developing offspring (Hobbs 1965).

Detailed reporting of bumble bee nesting biology is a critical component of species conservation status assessments as they clarify reproductive output of sexuals (i.e., gynes, males) and non-sexuals (i.e., workers) (Liczner and Colla 2019). From an evolutionary perspective, characterizing the location of nests relative the ground surface, the production of progeny, and approaches to the storage of pollen and nectar provide opportunities to systematically study the evolution of nest architecture, progeny output, and larval feeding strategies (Plath 1934). Thus, our discovery and description of a wild *B. morrisoni* nest is a consequential contribution to bumble bee nesting biology knowledge as it provides increased taxonomic coverage on an understudied subgenus of bumble bees, some which are of conservation concern.

## 2. MATERIALS AND METHODS

The *B. morrisoni* nest we examined and dissected in our study was discovered beneath chopped straw on the plywood floor of a vacant doghouse in Richmond, Cache County, Utah, USA (41.92° N 111.81° W). The doghouse was stored in a large outdoor shed through whose open doorway JHC observed workers, many males and gynes flying on 15 August 2020. We left the nest alone until after the flight season ended, yielding a fully matured, expired nest.

We collected the nest from the field in November 2020. During our systematic dismantling of the nest in the lab, the nest proved to be in excellent condition (Figure 1B). We photographed, weighed, and measured the entire nest, its waxen canopy, and counted silk cocoons (= cells) sorted by size into those of larger gynes and smaller workers/males (i.e., non-gynes). We measured the individual weights of cocoons with pharate adults and subsequently removed the pharate adults to estimate the weight of the emptied cocoons. We also measured the total weight of all emptied

cocoons from which adults emerged. Finally, five embedded pollen columns were further assessed for material composition, weight, and dimensions.

We measured cocoon volumes using water weight (1 g water = 1 mL volume). In brief, 50 cocoons were randomly selected from the nest, 25 which represented "large cocoons" and 25 which represented "small cocoons." Each cocoon was cut in half, their pupal cadaver (pharate adult) removed, and the empty cocoon weighed. The two halves were then filled with water and weighed, from which cocoon volume was easily calculated. We tested for differences in cocoon volume between the two size classes using a simple $t$-test. In addition to volume, we report on the dimensions of each cocoon by estimating the equatorial diameters and lengths with calipers of 10 cocoons.

The five pollen columns appeared to be built from pollen and nectar. Alford (1975) and others have asserted that the columns have waxen walls too. To evaluate this claim, a column was sliced across its rim, middle, and base. Half of each slice was heated to a temperature that melted beeswax (~62–64 °C). The remainder was soaked and agitated in 40% ethanol, which should dissolve sugars and some pollenkitt, but not wax. The amount of pollen, if any, in the wax canopy was estimated, as most authors assert that pollen is mixed into the pliable wax canopy, but without evidence. We dissolved 1/20 of our nest's canopy in 20 ml of chloroform to dissolve the wax and then plated 15 uL of the agitated suspension on a slide. Once dry, we added fuchsin gel and visually counted stained pollen using a haemocytometer. The deconstructed *B. morrisoni* nest (Accession # KNEST001) is stored at 4 °C in a vacuum sealed package at the US Department of Agriculture-Agricultural Research Service, Pollinating Insect Research Unit in Logan, Utah, USA.

## 3. RESULTS

The nest we obtained and dissected was late in the phase of producing sexuals. The nest spanned 270 cm$^2$, stood 9 cm tall, and weighed 196 g. Sparse straw adhered to the wax. The colony's 424 cells were stacked in roughly three tiers (Figure 1B). Of these, 25% were sealed cells containing dead pupae of 35 gynes, 3 males, and 68 workers. Twenty-five gyne cells averaged 2.41 ± 0.06 ml in volume (maximum = 3.11, minimum = 1.8), five of which measured an average 2.36 ± 0.02 cm tall × 1.55 ± 0.03 cm across. Twenty-five non-gyne cells averaged 1.17 ± 0.04 ml in volume (maximum = 1.4 ml, minimum = 0.64 ml), five of which measured an average 1.71 ± 0.05 cm tall and 1.18 ± 0.01 cm across. Nest cells of *B. morrisoni* fell into one of two distinct size classes for gyne and non-gyne, with gyne cells being twice as large as non-gyne cells ($t = 17.25$, $df = 48$, $P < 2.2e-16$) (Figure 1C). Furthermore, deceased non-gyne pupae weighed 0.13 ± 0.04 g ($n = 10$), and deceased gyne pupae weighed 0.28 ± 0.09 g ($n = 10$).

In addition to sealed gyne and non-gyne cells, we counted 252 emerged smaller cells that likely held non-gynes (workers or males) and 19 larger cells that likely held developing gynes. An emerged cell is an open and empty nest cell that is not filled with bumble bee honey (i.e., honeypot). In total, we estimate the weight of all emerged and emptied cells (cells with deceased pharates removed in our study) to be 83 g, with the average empty gyne cell weighing 0.35 ± 0.11 g ($n = 10$) and empty non-gyne cell weighing 0.17 ± 0.06 g ($n = 10$). We found 40 large and 5 small uncapped cells filled with 37 g of bumble bee honey (i.e., honeypots); the cells' sizes corresponded with those of gynes and non-gyne nest cells, respectively.

The colony's 19 g wax canopy formed a thin (0.3 mm), pliable roof above the nest (Figure 1D). No supports were evident, being held aloft by adhesion to the cavity's straw dome. Its caramel color suggests additional constituents, which others believe to be pollen (Alford 1975; Hobbs 1964, 1965; Michener 1974). We calculate that this nest's wax canopy contained about 40 million embedded pollen grains. Distinctive grains included a few resembling *Hibiscus* (massive and polyporate, with bottle-shaped stout spines) and many more hexacolpate grains of one or more species of Lamiaceae. Many others were unknown tricolpate morphs.

The five cylindrical pollen columns that we found were built from stacked corbicular pellets, as seen in cross-section (Figure 1E). The five pollen columns averaged 4.81 ± 0.94 g in weight, ranging in size from 13 × 19 mm to 17 × 50 mm (Table I) (Figure 1F). To estimate corbicular load pollen pellet weights, we turned to Allen et al. (1978), who estimated that returning *B. vosnesenskii* Radoszkowski foragers carried 20 mg loads. From the collective weight of the pollen columns (24 g), we can calculate that each pollen column therefore represented 240 pollen loads, or about 1200 pollen loads stored in all five columns. Furthermore, the various colors represented by the corbicular pollen loads in the column imply that multiple flowering species contributed to the surplus pollen composing a column (Figure 1E). Finally, dissection of the pollen columns did not reveal evidence for eggs or larvae, a phenomenon observed by Hobbs (1967) in the pollen "cylinders" of a wild *B. huntii* Greene nest.

When fragments from the rim, middle, and base of one column were warmed to a temperature that melted a crumb of beeswax, no molten liquid formed. Further heating simply charred the fragments. Soaking them in 40% ethanol generated a suspension of pollen that settled out over time. Several flat flakes of apparent wax were left from the basal slice, but slices from the middle and top of a column disintegrated completely. An unexpected collection of 10–20 bare anthers was also left, ones that foragers must have inadvertently removed from stamens while foraging.

**Table I** Weight and dimensions of pollen columns in *B. morrisoni* nest

| Pollen column ID | Weight (g) | Dimensions (length × width) (mm) |
|---|---|---|
| Pollen column 1 | 5.16 | 40 × 13 |
| Pollen column 2 | 7.20 | 43 × 15 |
| Pollen column 3 | 6.11 | 50 × 17 |
| Pollen column 4 | 3.77 | 28 × 14 |
| Pollen column 5 | 1.83 | 13 × 19 |

## 4. DISCUSSION/CONCLUSION

Bumble bee diversity reflects successful colony stages in the overall bumble bee life cycle. However, bumble bee nesting biology is generally far less studied than foraging ecology, particularly for wild nests in the field (but see Allen et al. 1978). Our detailed and quantified nest description of *B. morrisoni* contributes to much needed comparative accounts of bumble bee nesting biology, with implications for management and conservation decisions. For example, the baseline data we present on the number gynes produced from a single colony gives researchers a sense of reproductive output. Furthermore, the presentation of data on the pollen columns and wax canopy lays the foundation for determining if the placement of resources along the vertical axis of the columns is correlated to flowering phenology. Our study also raises unanticipated questions, such as the purpose of pollen addition to wax canopies, and why this large *B. morrisoni* nest expired despite large pollen and nectar surpluses and a bevy of worker and gyne pupae ready to emerge.

In the literature, freestanding pollen columns are hypothesized to be structures that are the result of pollen storage behavior (Sladen 1899; Michener 1974) (Figure 1G). Workers presumably draw upon these stores to feed larvae during periods of floral dearth, which for *B. morrisoni* typically ensues by midsummer at lower elevations (Koch et al. 2012). F.W.L. Sladen is credited with being the first scientist to describe "pollen storer" bumble bees (Michener 1974). Sladen (1899) described pollen storers as species that "store the newly gathered pollen in waxen cells specially made for the purpose, or in old cocoons specially set apart to receive it, from which it is taken and given to the larvae through the mouths of the nurse-bees are required." Moreover, Michener (1974) described that these pollen columns (= cylinders) can stand "several centimeters high." The definition presented by Sladen (1899), and size observations presented by Michener (1974) support our justification that the pollen columns we observed in the *B. morrisoni* nest are the result of "pollen storer"

behavior. Furthermore, Sladen (1899) describes the pollen columns in the context of nurse bees taking pollen from the columns to feed larval offspring. This nuance suggests that Sladen observed nurse bees interacting with the structure and extracted pollen for provisional larval feeding, as opposed to being inferred by the mere presence of the structure.

The vocabulary used to describe vertically standing pollen storehouses built by *Bombus* are diverse. They include "columns" as we state here (Alford 1975; Sladen 1912), "cylinders" (Plath 1922, 1934; Michener 1974), and "tubes" (Plath 1934). Vertical bee-made pollen storage structures have been reported from the nests of several other bumble bee species from diverse subgenera including the *Bombus s. str.* (i.e., *B. terrestris* (Linnaeus), *B. terricola* Kirby, *B. affinis* Cresson) (Alford 1975; Plath 1934), *Thoracobombus* (i.e., *B. fervidus* (Fabricius)) (Plath 1934), *Melanobombus* (i.e., *B. lapidarius* (Linnaeus) (Sladen 1899), and *Pyrobombus* (i.e., *Bombus huntii*) (Hobbs 1967). However, in addition to the storage of pollen in columns, Sakagami (1976) enumerated the diversity of strategies and structures of pollen storage by referencing the work of Weyrauch (1934). Weyrauch (1934) identified seven different structures/approaches to storing pollen in the nest, some of which require wax for structure, with the assumed purpose of provisioning larval offspring.

Given the vertical disposition of these pollen columns (e.g., Plath 1927), it follows that pollen loads located near the top of the column are progressively newer (akin to a sediment deposition chronology). Many details of the process in column development remain unknown. For example, how dynamic is pollen column use, are they sometimes exhausted, or later replenished, are multiple columns built concurrently or sequentially? Do columns arise during a phase of colony development or in response to a burst of local bloom or a surplus of foragers relative to progeny demand? Do colonies often expire with a huge surplus of pollen as in our *B. morrisoni* nest? (but see Sakagami 1976). Furthermore, pollen storage methods by bumble bees appear diverse and perhaps species-specific as articulated by Sakagami

(1976) and Weyrauch (1934). For example, in wild *B. huntii* colonies, Hobbs (1967) and Medler (1959) found that queens would lay eggs inside the pollen "cylinders"; however, it is unclear how big these cylinders were or their precise location within the nest. Understanding the prevalence, diversity, and scale of pollen storage approaches in wild bumble bee nests will require nest dissections of additional species that can then be placed in a phylogenetic context (Michener 1974; Sakagami 1976).

Williams et al. (2014) state that *B. morrisoni* is a ground-nesting species. However, our observation of a *B. morrisoni* nest in situ in a protected area on the ground surface differs from the assertion made by Williams et al. (2014). Additional observations of *B. morrisoni* nests in situ would show if the species is flexible in their nesting approach. For the New World clade that includes *B. morrisoni* (Cameron et al. 2007), only nests of *B. griseocollis* are known. The three colonies of *B. griseocollis* (= *B. separatus*) available to Plath (1927) were surface nests, while Williams et al. (2014) state that *B. griseocollis* also nests underground. In 2013 and 2017, two additional of *B. griseocollis* nests were found at the University of Wisconsin Arboretum, one in a tree hollow and the other underground (Susan Carpenter, personal communication). Given these observations, we hypothesize that both *B. morrisoni* and *B. griseocollis* are versatile in their nesting habits, nesting either below or above ground.

Alford (1975) states that only large nests of some ground-nesting bumble bees have waxen canopies. Depending on the species, G.A. Hobbs has described this structure as a "wax to plaster the roof of the brood chamber" in *B.* (*Alpinobombus*) *balteatus* Dahlbom (Hobbs 1964) with the intent to "waterproof the ceiling" in *B. rufocinctus* (Hobbs 1965). However, alternative hypotheses (e.g., insulation and nestmate recognition) on the function of wax canopies remain to be tested (Breed et al. 1995). Like pollen columns, the wax canopy layer has been variously described as a "waxy sheet" (Michener 1974) or a "wax envelope" (Sakagami 1976). Because it forms the interior roof of the nesting cavity but has no walls, we prefer the term "canopy."

Michener (1974) observed that the presence of these wax canopies occurred more commonly in large underground nests as opposed to small surface nests. Furthermore, Plath (1927) did not describe the presence of a wax canopy in the surface nests of *B. griseocollis* (= *B. separatus*) he intercepted. In our study, the wax canopy that we observed came from a large surface nest of *B. morrisoni* and does not concur with the conclusions made by Alford (1975). However, Michener (1974) stated that wax canopies are more common in large underground nest (= ground-nesting), leaving our observation of the large surface nest of *B. morrisoni* with a wax canopy perhaps being an aberrant phenomenon.

Sakagami (1976) provides an insightful narrative of the wax canopy, hypothesizing that most species have the capacity to build a wax canopy and it is a facultative behavior in response to a nest's environmental and colony conditions. Both Michener (1974) and Sakagami (1976) speculate that a wax canopy likely fills some homeostatic function, a way for the colony to better regulate temperature, moisture, desiccation, and wind exposure, while barring dust and debris sedimentation falling from the cavity ceiling onto developing offspring below. Interestingly, Sakagami (1976) reported that pollen pockets may also be found on the lateral part of the wax canopy. This structure was defined as *pollentasche* by (Weyrauch 1934) in the German language. We saw no pollen pockets associated with the wax canopy of our *B. morrisoni* nest.

The construction of the wax canopy may be facultative in part due to need, but also for its cost in materials and labor to construct. Although the canopy was thin, it was still about 4 × thicker than cell walls of fresh honey bee comb (in Seeley 1985). It should have required about 4 g of dietary sugar to synthesize, presuming that its weight was mostly wax (calculated from Seeley 1985). It was about 12% of the nest's weight, after subtracting away the weights of the 106 dead pupae (~19 g) and the five pollen columns. Its construction should also divert some workers' time away from other activities (e.g., guarding, larval provisioning, foraging), although a spate of bad weather may leave some workers otherwise idle.

Wax canopies of bumble bee nests are frequently described as being made of "pollen-wax" (Michener 1974; Sakagami 1976). However, no study has looked for pollen or estimated how much pollen is found in a wax canopy. For the first time, we have extracted pollen grains from a *Bombus* nest canopy and estimated how many were incorporated in a canopy, in this case a *B. morrisoni* nest canopy. From pollen counts in ten samples (sum 1 g) of the canopy, we estimate that 40 million pollen grains were incorporated in the 19 g canopy. This many grains seem an unlikely contaminant, but rather that mixing pollen into the canopy was an intentional part of canopy construction. Foraging for pollen is typically regarded as an activity that satisfies larval dietary needs and ultimately reproductive output and survival of the species. However, we demonstrate that some pollen influx is also diverted to a structural element – the canopy – of some *Bombus* nests for as yet unknown benefit.

In conclusion, we present the first nest description of *B. morrisoni*, increasing the knowledge of bumble bee nest biology within the subgenus *Cullumanobombus*. Of notable importance, we document the presence, dimensions, and location of a nest relative to the ground surface and significance of pollen columns and the wax canopy of a mature, naturally terminated nest. Unlike honey bees, the pollen storage capacity of bumble bees is rarely considered, nor is wax production included in a colony's nectar budget. A brief review of the literature reveals diverse vocabulary to describe these bumble bee nest structures which confuse their interpretations. Scientists could better integrate and synthesize their descriptions of *Bombus* nests by publishing photographs and measuring various internal structures. Photographs should help resolve terminological ambiguities, as will presenting more quantitative evidence as we demonstrate in our study and in other past studies. While the results of our study are based on a single nest, we have expanded the phylogenetic diversity of wild bumble bee nest studies, which may increase our capacity to test hypotheses associated with larval provisioning strategies and location of

the nest relative to the ground surface. Finally, *B. morrisoni* is a species of conservation concern that the IUCN classifies as "Vulnerable." Thus, we expect the data collected in our study to be useful to conservation and management assessments of *B. morrisoni* and potentially other bumble bee species.

## AUTHOR CONTRIBUTION

All authors contributed to the study conception and design. Material preparation, data collection analysis, and writing of the manuscript were performed by Jonathan Berenguer Uhuad Koch and James H. Cane. All authors read and approved the final manuscript.

## DATA AVAILABILITY

The datasets generated during the current study are available in the figshare repository, https://doi.org/10.6084/m9.figshare.17965553.v1.

## CODE AVAILABILITY

Code and data for analysis can be found at this link: https://github.com/jbkoch/KochCane_BmorrisoniNest_Apidologie.

## DECLARATIONS

**Ethics approval**    Not applicable.

**Consent to participate**    Not applicable.

**Consent for publication**    Not applicable.

**Competing interests**    The authors declare no competing interests.

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