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ORIGINAL RESEARCH ARTICLE

Nest ecology, architecture, and behaviour of the stingless bee (*Meliponula beccarii*) in Baringo County, Kenya

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ABSTRACT
The nesting ecology, architecture, and behaviour of most Afro-tropical stingless bee species are yet to be described, particularly in Kenya. Therefore, we aimed to determine the nest architecture, habitat, and ecology of *Meliponula beccarii* (Gribodo, 1879) in Baringo County, Kenya. Forty-nine (49) nests of *M. beccarii* were conveniently sampled and investigated in detail. All the nests of *M. beccarii* were built underground, mainly in highland forested and farmland habitats. These subterranean nests consist of a well-defined, external entrance, an internal entrance tube, and the nest proper. The external entrance was 1.18 ± 0.49 cm high above the ground with a diameter of 1.39 ± 0.52 cm. The entrance in 74% of the nests was guarded by 2–12 guard bees. The nest proper consists of an area of involucrum layers, the brood-rearing area, as well as food storage pots, where honey and pollen are stored separately. The brood combs were horizontal, constructed in a concentric manner, and had several gyne cells located in the periphery. The nest cavity was fully occupied and was constructed *de novo* and not in pre-existing ground cavities. The nest was lined with a batumen layer to which the brood area and storage pots are anchored *via* short pillars. A canal was located on the nest cavity floor. Behaviourally, the stingless bees were non-aggressive and did not bite even when disturbed. In conclusion, *M. beccarii* in Baringo, Kenya strategically builds subterranean nests in highland forest habitats. The findings of this study can be used to design artificial hives for the development of local meliponiculture.

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KEYWORDS
Meliponula beccarii; *de novo*; Baringo County; nest architecture; highland; behaviour

Introduction

Stingless bees (*Apidae*, *Meliponini*) are eusocial bees, which, unlike the common honey bee (*Apis mellifera*), do not have a sting (Eardley, 2004; Roubik, 2023). The stingless bees play crucial roles as pollinators in Afrotropical ecosystems and honey production (Eardley, 2004). Over 600 stingless bee species belonging to 56 genera have been documented in the tropical and subtropical regions of the world (Roubik, 2023). Of these, over 20 species belonging to six genera (*Hypotrigona*, *Cleptotrigona*, *Liotrigona*, *Plebeina*, *Dactylurina*, and *Meliponula*) have been described in the Afro-tropical region (Eardley, 2004; Eardley & Kwapong, 2013). In Kenya, up to 12 species including *Meliponula bocandei*, *Meliponula lendliana*, *Meliponula ferruginea black*, *Meliponula ferruginea reddish brown*, *Meliponula ogouensis*, *Hypotrigona gribodoi*, *Hypotrigona araujoi*, *Hypotrigona ruspolii*, *Plebeina hildebrandti*, and *Dactylurina schimidti* have been reported to inhabit some parts of Kenya namely; Kakamega forest in western Kenya, Arabuko-Sokoke Forest along the coast, and Mwingi in lower eastern Kenya (Eardley, 2004; Macharia et al., 2007; Ndungu et al., 2019).

The stingless bee species live in colonies consisting of an egg-laying queen and thousands of workers inside purpose-built nests. These nests are built by worker bees inside pre-existing hollow tree trunks, branches, ground cavities, and crevices within rocks (Franck et al., 2004; Kajobe, 2007; Ndungu et al., 2019; Njoya et al., 2017, 2018, 2019; Roubik, 2023). A few species are also known to build their nest cavities inside termite nests (Fabre Anguilet et al., 2015; Namu & Wittmann, 2017), with some also building exposed nests on mud walls or trees (Fabre Anguilet et al., 2015; Kajobe, 2007; Roubik, 2006). Notably, the nest sites, size, and architecture (external and internal) of stingless bee are species-specific (Roubik, 2006). Therefore, nest architecture is

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not only a useful tool in taxonomic identification (Ndungu et al., 2019) but also aids in the rational design of suitable artificial hives for modern meliponiculture (Gela & Hora, 2021). Despite this importance, nest ecology, architecture, and nesting behaviour of most Afro-tropical stingless bees, more so the ground-nesting species, have yet to described (Roubik, 2006). Previously, the nest ecology, nest architecture of *M. beccarii* were described in Cameroon (Njoya et al., 2017), Northern Ethiopia (Jemberie et al., 2020), and the Oromia region of Ethiopia (Hora et al., 2023). However, regional differences in soil types, vegetation, weather patterns, predators, and availability of construction materials could promote adaptations leading to subtle region-specific variation in nesting ecology and biology (Hora et al., 2023). Therefore, information on region-specific adaptation of nesting ecology, behaviour and architecture is of paramount importance in the development of appropriate conservation programs. Moreover, such information is also essential in the design of modern artificial hives that can be used to harness native stingless bee species for pollination, ecotourism and valuable nest products. In Kenya, only the nesting sites and architecture of *H. gribodoi*, *H. araujoi* and *H. ruspolii* species in Kakamega forest and *H. gribodoi* in Mwingi have been described (Ndungu et al., 2019). Therefore, the purpose of this study was to study and describe the nest ecology, nest architecture, and behaviour of the ground-nesting *M. beccarii* in Baringo County.

Materials and methods

Study site

This study was conducted in Baringo County (0°40′0″ N and 36°0′0″ E), which covers a total land area of 10,976.4 km^2. The county comprises seven administrative sub-counties: Koibatek, Marigat, Mogotio, Baringo Central, Tiaty East, East Pokot, and Baringo North. Notably, Baringo County has a diverse topography ranging from flatlands to steep hilly terrains and covers humid, sub-humid, semi-humid, semi-arid, arid, and very arid climatic zones (Koskei et al., 2018; Odada et al., 2006). The mean annual rainfall in these climatic zones varies greatly, ranging from as low as 450 mm in the semi-arid to a high of 1100–2700 mm in the humid zones. The county experiences a dry season from January to mid-March, a rainy season from mid-March to mid-July, and a second dry season between July and September, followed by a short rainy season up to December. Ecologically, Baringo County is divided into three major zones: namely, the highlands, midlands, and lowlands, which can be further subdivided into up to eleven distinct sub-ecological zones (Koskei et al., 2018). Several rivers and seasonal streams also run across the county, mainly from the highlands towards lakes Baringo and Bogoria in the lowland southern parts. This ecological diversity provides a wide range of nesting sites for stingless bee species, which are yet to be described. The current study sampled nesting sites from Koibatek, Baringo Central, and Baringo North sub-counties (Figure S1). This was based on our previous surveys, which indicated that medicinal stingless bee honey in Baringo County is mainly sourced from the three sub-counties (Kiprono et al., 2022).

Recruitment of local wild stingless bee honey collectors

Wild honey gatherers with the knowledge of native stingless bee habitats and experience in locating nesting sites were recruited from Eldama Ravine, Baringo Central, and Baringo North sub-counties to assist in the location of nests. The recruitment was done with the help of elders, community opinion leaders, key informants, local administrators, market honey vendors, and local community forest associations (CFAs). The information provided by those key informants was used to conveniently map the potential sampling sites and the number of nests that could be identified in those sites. The wild honey gatherers were then requested to locate the nests before field expeditions, which were undertaken during the dry season of February to April 2022.

Sampling technique

Owing to the inherent difficulties in locating the wild-occurring stingless bee nests, a total of 49 nests were conveniently sampled and investigated across the three sub-counties (Figure S1).

Geospatial data

The exact geographical coordinates and altitude of the identified nests were registered with the Global Positioning System (GPS, Garmin Etrex 20, Garmin USA). The registered geographical coordinates were then analysed with ArcView GIS (Geographical Information Systems) to determine stingless bee nesting positions in the study area.

Nest ecology and nest architecture

The nest site and the surrounding areas were photographed (Sony Cyber shot digital Camera, SONY Corp) to capture any unique vegetation cover and terrain. The distance to the nearest water point was then estimated, and the habitat type was recorded as farmland, forest, or riverine. The topography of the nest site was also documented. The external nest structures, external nest height and nest entrance diameter, presence or absence of guards, height above the ground, shape, and orientation were documented. The diameter and height of the entrance were measured using a standard ruler and tape measure. The nest was then carefully excavated using garden hoes and a machete to expose the underground nest architecture as previously described (Barbosa et al., 2013). Photographs of the excavated nest were taken using a digital camera (Sony Cyber shot digital Camera, SONY Corp). The nest depth below the ground surface, length of the internal entrance tube, nest cavity shape, nest proper shape, location, and dimensions of the brood area, combs location and dimensions (diameter, height, and shape) shape of the honey pots, location and dimensions of the brood area, combs location and dimensions (diameter, height, and shape) shape of the honey pots, location and dimensions of pollen pots, presence of waste area, presence and position of any tunnels/canals on the nest cavity floor among other features were measured, counted and recorded (Barbosa et al., 2013).

Stingless bee sample collection

A sample of 4–8 worker bees was collected from each excavated nest, put in sterile, air tight 1.5 ml plastic tubes with alcohol (75%), labelled with unique numbers, date, and location, then shipped to the National Museums of Kenya, Nairobi, for taxonomical studies and identification.

Taxonomic identification

The wet bee samples were drained of alcohol, then pinned through the thorax using a stainless steel entomological pin. The appendages were then set to ensure that all the body parts were visible for easy identification. The specimens were then dried in an oven set at 36 degrees Celsius for 24 h. With the aid of a stereomicroscope, morphological features that included: the number of sub-marginal cells in the forewing, presence or absence of corbicula in the hind tibia, visibility of the vain Rs, the shape of the outer surface of the hind tibia, the colour of the mesosoma dorsum, the colour on the face, the colours on the legs and the colours of the antenna and scutum (Figure S2) were recorded and used to identify the stingless bee samples as *M. beccarii* using the scientific voucher specimen collections at the Centre for bee biology and pollination ecology at the National museums of Kenya and according to published guide of morphological taxonomic keys (Eardley, 2004). The pictures of the queen and worker bees are shown in Figure S3.

Statistical analyses

The data on nesting site characteristics, external and internal nest entrance architecture, Nest cavity, nest proper architecture, brood comb architecture, and Nest cavity floor canal were tabulated in MS Office Excel 2007. Individual means, standard deviation, and range were calculated using MS Office 2007 Excel. The Statistical Package for Social Sciences (SPSS), version 20 software (SPSS Inc., Chicago, Illinois, USA) was used for the frequency data analysis.

Results

Nesting sites characteristics

All the nests of *M. beccarii* that were found in the study area were subterranean. The altitude of nesting sites ranged from 2374 to 2611 m. Most ($N = 35$; 71%) of the nests were located in indigenous and plantation-type forests. Eleven (23%) of the nests were located in the farmlands along the edges of the forests, and a few were found in riparian land ($N = 2$; 4%) or by the roadside ($N = 1$; 2%; Table 1). Among the nests found in the forests, the majority were located in areas densely shaded by large trees and thick undergrowth vegetation (Figures 1(A–D)). However, few were in open, unshaded grazing fields within the forest (Figures 1(E–I)). Notably, all the nests were located within an estimated average distance of 0.73 km (range, 0.02–2 km) from water points (streams, rivers, or small dams). The ground inclination for most of the nests was a moderate slope with well-drained black, reddish brown, or red volcanic loam soils (Table 1).

Table 1. Main features of *M. beccarii* nesting sites in Baringo County, $N = 49$.

Feature	*N* (%)
Vegetation cover	
Dense cover	22 (45)
Undergrowth cover	13 (27)
Under a tree	9 (18)
No cover	5 (10)
Habitat type	
Forest	35 (71)
Farmland	11 (23)
Riparian	2 (4)
Roadside	1 (2)
Soil type	
Black loam	37 (76)
Red loam	11 (22)
Red volcanic	1 (2)
Topography	
Moderate Slope	35 (71)
Flat area	13 (27)
Steep slope	1 (2)

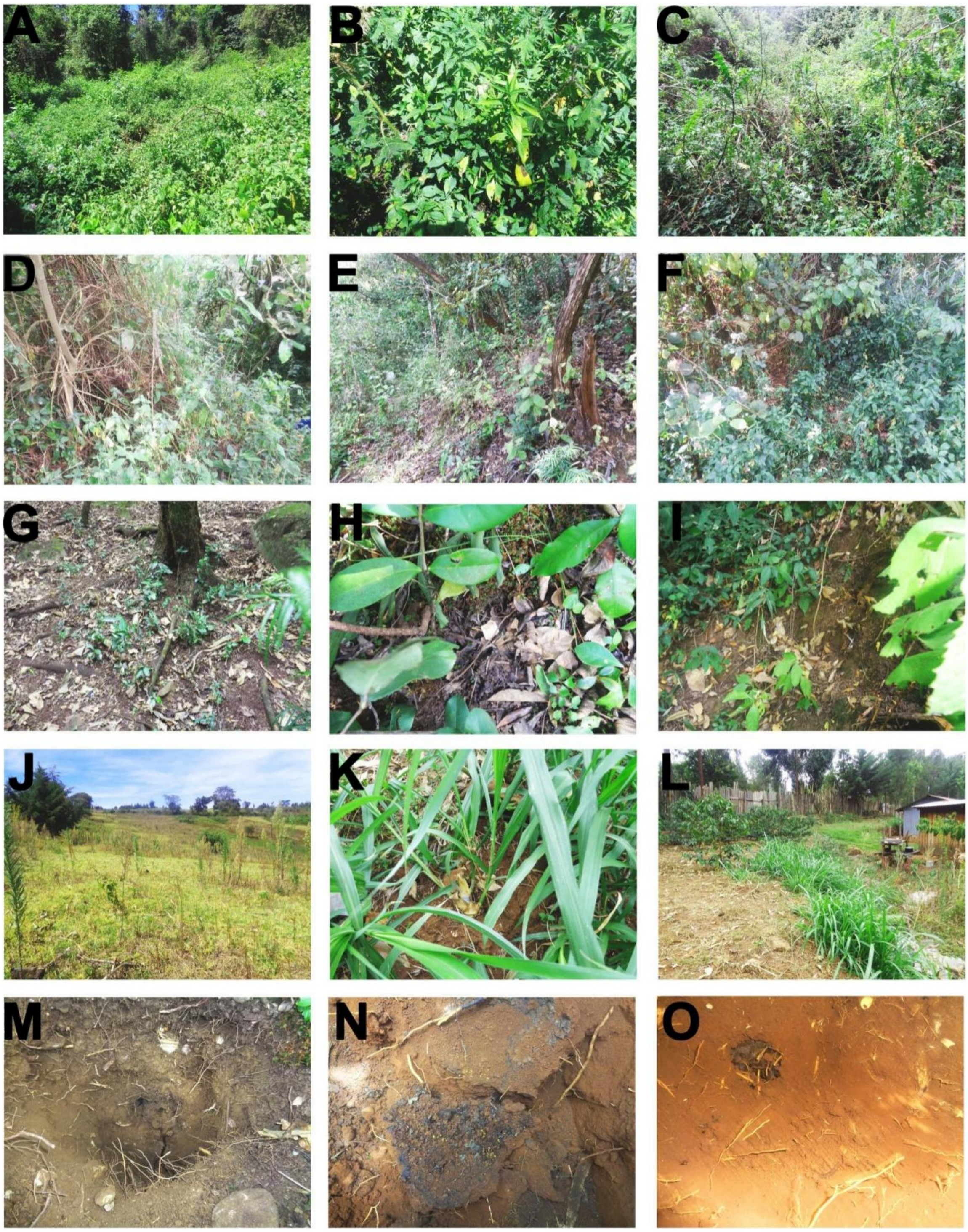

Figure 1. Representative photographs showing *M. beccarii* nesting sites characteristic. (A–D) Densely covered and shaded areas within indigenous forests, (E–I) sparsely covered and less shaded areas within indigenous forests, (J) un-shaded open grazing land within a plantation forest, (K,L) Napier grass and coffee farmland close to a homestead, (M) excavated black soil nesting site, (N) partially excavated reddish-brown loam soil nesting site, and (O) partially excavated red volcanic soil nesting site.

External and internal nest entrance architectures

All the studied *M. beccarii* subterranean nests had one external entrance leading to the outside environment (Figures S4(A–G)). Of these, the majority ($N = 26$; 53%) were exposed and could easily be spotted, while 47% ($N = 23$) were concealed under shrubs, twigs, or dry leaves and could not be easily spotted unless the nest site was first cleared to expose them. The external entrance in most of the nests was ovoid (oval) in shape ($N = 33$; 68%), whereas in 16 (32%), the entrance was circular (Figure S4(M)). The external entrances were made either of cerumen substance ($N = 42$; 82%), cerumen with dry leaves ($N = 7$; 16%), or a mixture of cerumen and soil ($N = 1$; 2%) (Figure S4(M)). The colour of the external entrance varied from dark brownish to black in colour. The height of the external entrance was on average 1.18 ± 0.49 cm (range, 0.5–1.8 cm) above the ground and with a diameter of 1.39 ± 0.52 cm (range, 0.5–2.2 cm). In the majority of the nests, the external entrance was facing either North West or South West. An internal entrance tube measuring an average of 24.05 ± 6.95 cm (range, 14–49 cm) in length connects the external entrance and the subterranean nest cavity (Figures S4(H,I)). In the majority of the nests ($N = 37$; 76%), this internal entrance is vertical (Figures S4(H,I)), was inclined in 4 (8%) and meandering in 8 (16%). The walls of the internal entrance were lined in the majority of nests ($N = 42$, 86%) by a black brittle substance. In the remainder 7 (14%) nests, the internal entrance channels were lined with cerumen. In most of the nests ($N = 39$; 80%), the internal entrance entered the nest cavity at the top part (Figures S4(H,I)), while in only 10 (20%) of the sampled nests, the internal entrance entered the nest cavity at the sideway.

Nest cavity and nest proper architecture

The nest cavity was located 24.05 ± 6.95 cm (14–49 cm) below the ground surface, which is equivalent to the length of the internal entrance tube. In all the excavated well-established nests, the cavity was filled by the nest proper with no observable spaces (Figure 2(A)). The nest cavity exhibited different shapes, ranging from conical ($N = 30$; 61%), oval ($N = 9$; 8%), pear-shaped ($N = 8$; 8%) to spherical ($N = 2$; 6%). As shown in Table 2, the mean height of the nest cavity of *M. beccarii* was 27.43 ± 8.52 cm (range, 15–58 cm) with an estimated upper part, middle part, and lower part diameters of 15.02 ± 4.47, 21.25 ± 4.82, 20.71 ± 5.99, respectively. The cavities in most, but not all, nests were lined with a single layer of water-impermeable batumen lining (Figure 2(A), green arrow head). The upper part of the nest proper of *M. beccarii* was covered on the outside by 6–8 involucrum layers, with the outermost layers being dark and brittle. In contrast, the inner layers that were closer to the brood area are softer and dark brown (Figures 2(A–D) and 3(A–C)). The involucrum sheets were brown and shiny and arranged in alternating layers for easy movement of bees in between the layers and to the brood area. Notably, the thickness of the involucrum area varied from nest to nest, with the larger, well-established mature nests having thicker layers of involucrum. The brood area was located on the upper part of the nest cavity and connected directly to the widened internal entrance

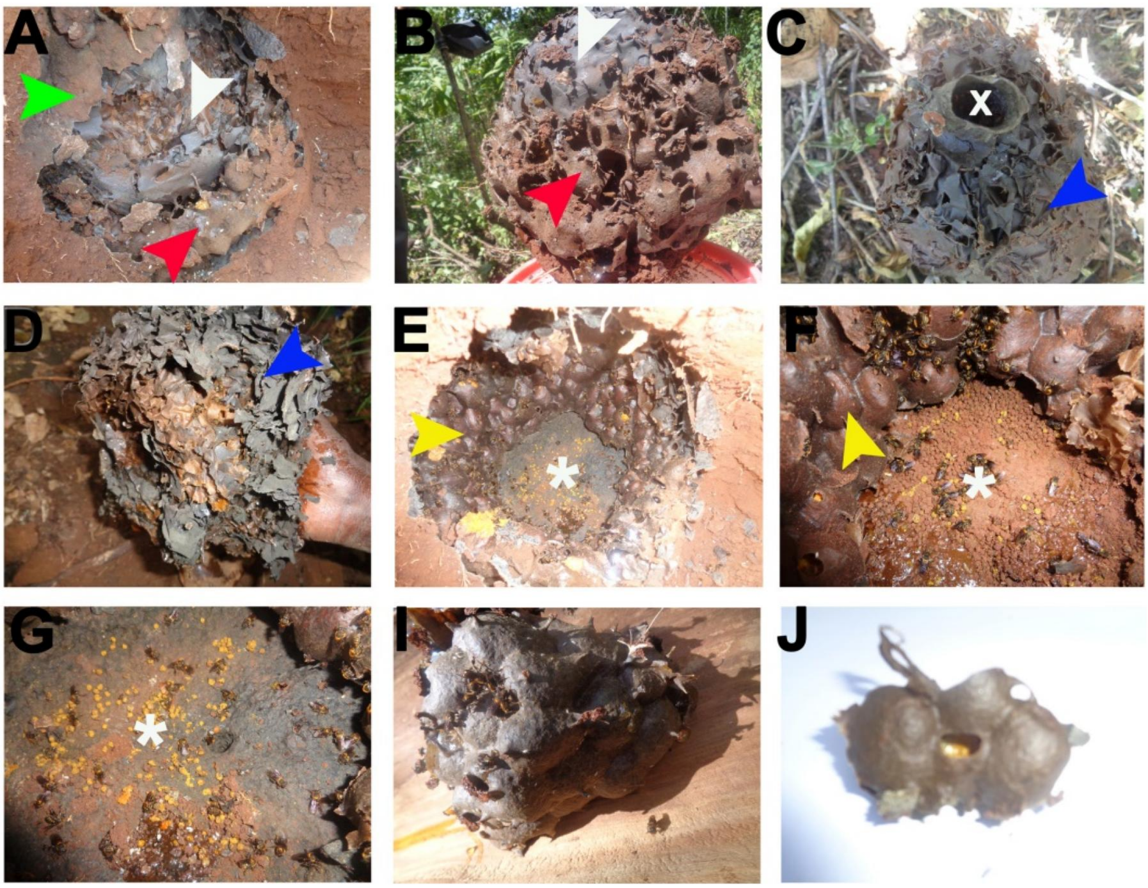

Figure 2. Nest cavity and nest proper architecture. (A) Shows the side view of a partially excavated nest, green arrow head-batumen lining, red arrow-storage area, white arrow-involucrum layers, (B) shows the entire intact nest proper, white arrow-brood area, red arrow point to the storage area, (C,D) shows the brood area which is directly accessed by internal entrance, (E–G) shows the intact storage area and nest floor upon removal of the brood area, (H) depicts a group of excised intact honey pots, and (I,J) depicts a group of excised honey and pollen pots.

Table 2. *Meliponula beccarii* nest characteristics.

Nest features	*N*	Mean ± *SD*	Range
External entrance tube diameter (cm)	49	1.39 ± 0.52	0.5–2.2
Height of external tube entrance (cm)	49	1.18 ± 0.49	0.5–1.8
Length of internal entrance tube (cm)	49	24.05 ± 6.95	14–49
Height of nest (cm)	49	27.43 ± 8.52	15–58
Upper part nest diameter (cm)	49	15.02 ± 4.47	7–36
Middle part nest diameter (cm)	49	21.25 ± 4.82	14–42
Lower part nest diameter (cm)	49	20.71 ± 5.99	6–32
Brood area diameter (cm)	49	12.83 ± 2.02	8.4–17.5
Brood area height (cm)	49	16.02 ± 3.60	8–23
Brood comb number	49	10.42 ± 2.25	5–14
Brood comb diameter (cm)	49	8.39 ± 1.66	5–11
Brood combs stack height (cm)	49	8.37 ± 1.43	5–12
Brood cell height (cm)	49	0.714 ± 0.18	0.6–1
Brood cell diameter (cm)	49	0.542 ± 0.17	0.3–0.8

SD: standard deviation.

channel (Figures 2(C,D)). The food storage area consists of pots located on the sides of the lower part of the nest, with no observable involucrum layers, and covers the lower half of the brood area (Figures 2(A–B,E,F)). The pots were made of cerumen (Figures 2(I,J)) and were connected to the nest cavity batumen lining by short, strong pillars. The honey and pollen were stored in separate, but interspersed pots, with no discernible arrangement patterns. The average honey yield per nest was 0.82 ± 0.37 L; range (0.15–1.5 L). The floor of the nest in some nest was flat and round-bottomed in some. The nest floor acts as the waste collection area, as demonstrated by observable pollen wastes and small round moulded mud in most ($N = 42$; 86%) of the nests (Figures 2(E–G)). Unpaired *t*-test showed that the nests from Baringo Central had significantly bigger diameters than those from Koibatek ($p < 0.05$). All the other characteristics were similar between the two sub-counties (Table S1). Only one nest was excavated from Baringo north and therefore was not included in the comparative analysis.

Brood rearing area architecture

In most of the nests, the brood area was "heart-shaped," being broad at the top and narrow at the lower side (Figures 3(A,B)), and a few were cylindrical shaped (Figure 3(C)). The brood area, which is covered by soft layers of involucrum, had an average height of 16.02 ± 3.6 cm (range, 8–23 cm) and an average diameter of 12.83 ± 2.02 cm (range, 8.4–17.5 cm (Table 2). Within the brood area, the brood cells were arranged in horizontal circular combs (Figures 3(D–F)). Gyne cells, about two times larger than the worker brood cells could easily be identified at the edge of combs and were white in colour (Figures 3(D–F)). On average, the nests had 10 combs (range, 5–14) that were stacked on top of each other to a mean height of 8.37 ± 1.428 cm. Each comb had an average diameter of 8.39 ± 1.66 cm which ranged 5–11 cm, with the smaller-diameter combs being the top and bottom. The combs were firmly connected to one another and to the involucrum by pillars. The individual worker bee brood cell had a mean height of 0.7 cm, a diameter of 0.5 cm, and those with larvae or pupae were rounded both at the top and the bottom (Table 2). The newly constructed brood cells were covered with wax and were dark brown in colour (Figures S5(A,B,D,F,H)). The combs were constructed in a concentric manner, beginning at the centre towards the periphery, resulting in spiral-shaped combs (Figures S5(A–I)). However, in some nests, all the combs were completely flat or concave (Figure S5(J)). Importantly, the brood area in large well-established/mature nests consisted of two sets of comb stacks that could easily be split into an upper (8–10 combs) and a lower stack (3–6 combs).

Nest cavity floor canal

We observed the presence of one blind-ended canal that extended downwards from the floor in the majority ($N = 46$; 96%) of the nests that were surveyed (Figures S6(A–F,I)). Of these canals, 27 (55%) were vertically oriented and straight, while 19 (45%) were vertically oriented but meandering. The opening to the canals varied in diameter, with an average diameter of 1 cm (Figures S6(A–F)). Interestingly, canals' opening in some of the nests was lined with a waxy material and rises above the nest floor by 0.5–1 cm (Figures S6(A,C)). We further determined whether these nest floor canals were aligned with the external entrance and internal access channel. In the majority of the nests ($N = 44$; 90%), the nest floor canals were not aligned with the external entrance and internal access channel (Figures S6(G,H,J)) and were placed 7.6 cm (range, 3–16 cm) from the walls of the nest cavity.

Meliponula beccarii construct their subterranean nests *de novo*

The complexity and consistency of the *M. beccarii* nest architecture in three separate ecologies that we sampled prompted us to hypothesize that the nests were designed and built from scratch. We searched and found such nests that were still at the preliminary stages of construction at short distances from old nests that had been destructively harvested by local traditional honey gatherers. As shown in Figures 4(A,B), fresh soil mounds excavated and dumped outside by the workers were visible at the entrance of intact nests under construction. However, we observed that most of the excavated soils were dumped far away from the nest, perhaps to conceal the ongoing construction of the new nests. Excavation of one of the most nascent nests under construction revealed only a short

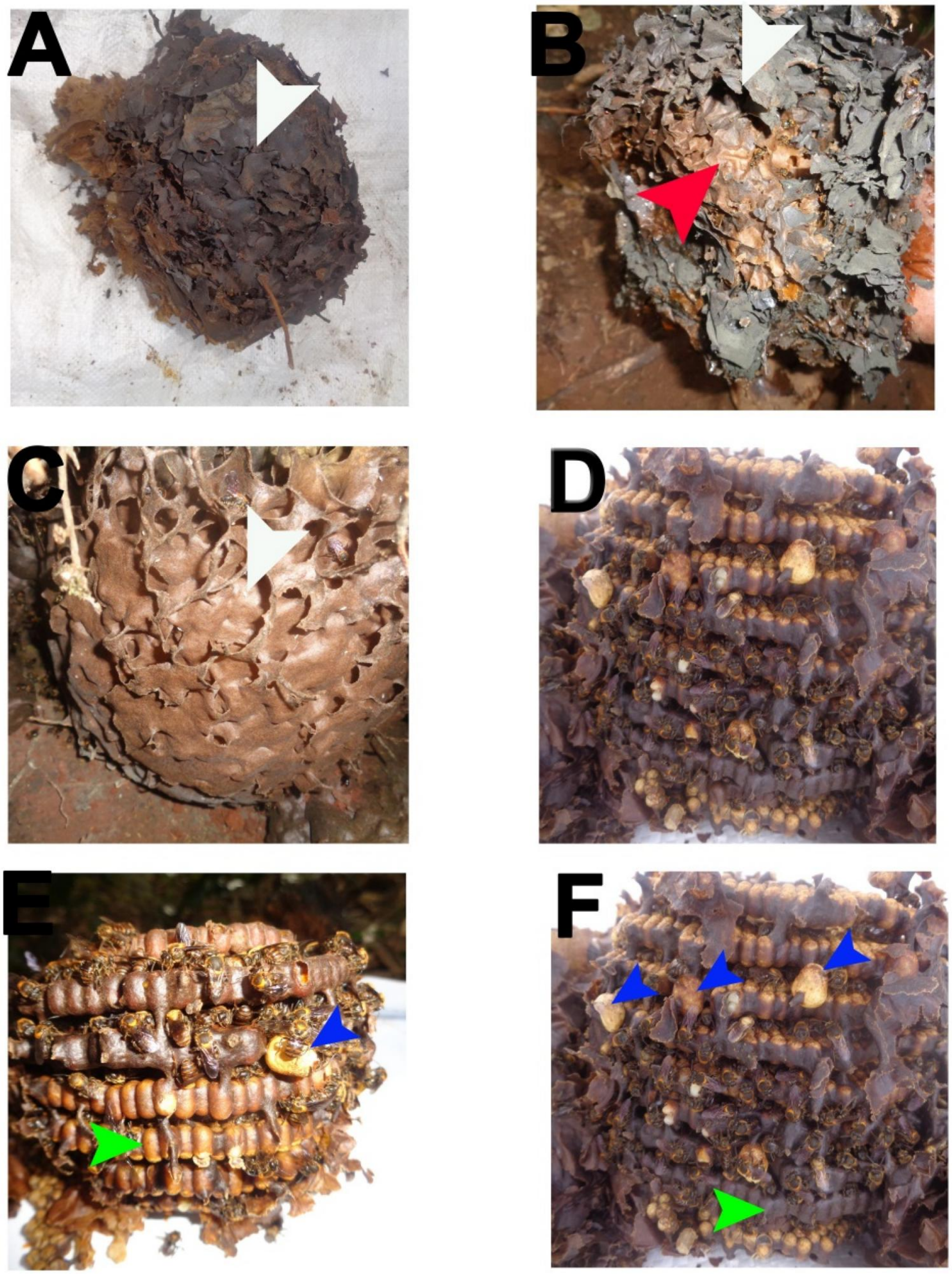

Figure 3. Brood area architecture. (A,C) Show brood area from a newly constructed nest note the texture and brownish colour of the involucrum layers, (B) shows brood area from a mature well-established nest, (D–F) shows representative horizontal combs stacked on top of each other and connected with vertical pillars. The blue arrow heads in (E,F) points to the gyne cells.

blind-ended access channel, with no nest cavity, brood area, storage area, or involucrum sheets (Figure 4(C)). Figures 4(D–F) shows newly constructed nests that have been occupied, but with only a small rudimentary brood area, no storage areas, thick layers of involucrum, nest floor, and floor canals that we observed in well-established nests (Figures 2 and S6).

Meliponula beccarii behaviour

The entrance in 74% of the surveyed nests was guarded by 5 bees on average (range, 2–12), with foraging bees leaving the nest and others arriving (Figures S4(A–G)). However, upon sensing or sighting any human movement, all flights into or out of the nest were completely halted. The bees did not exhibit any aggressive behaviour, for example, biting or entering the eyes and nostrils during excavation, but increased their movements and buzzing sound within the nest. The worker bees were also seen to feed on the honey in the honey pots upon disturbance of the nest. The queen bee had a larger and bigger abdomen than the worker bees (Figure S2(A)), and was often found in the brood area, remained docile, even when the nest was disturbed.

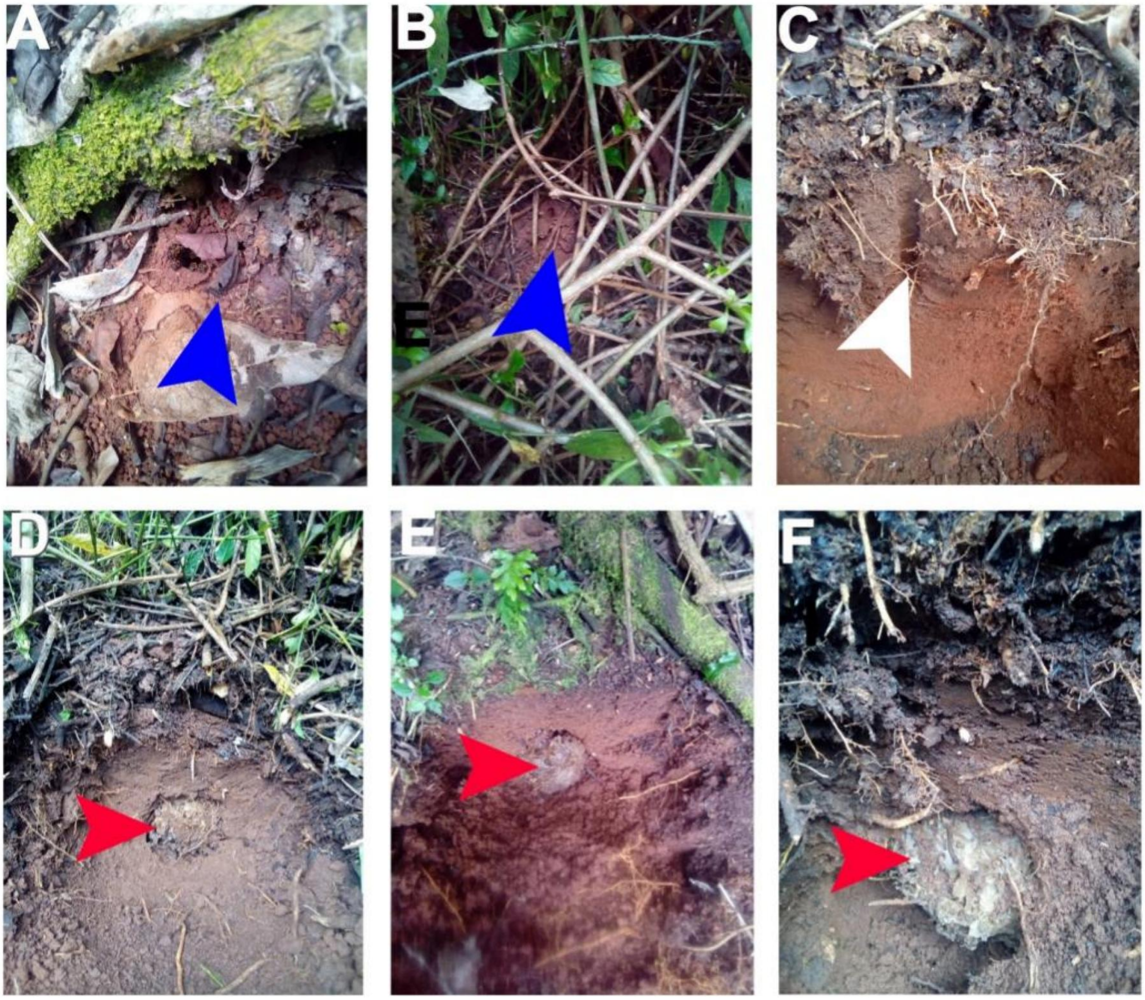

Figure 4. *De novo* construction of *M. beccarii* nests. (A,B) Representative photos of nests under construction showing freshly excavated soil on the entrance (blue arrowheads), (C) an excavated nest showing only a short blind-ended entrance tube (white arrow), with no nest cavity, brood area and storage areas yet, (D–F) excavated newly constructed nests at different stages, note the small round- shaped brood areas, with no storage areas, nest floor, or the floor canals observed in well-established nests.

Discussion

Stingless bees are known to construct their nests in diverse habitats, but mainly in natural forests, plantation forests, grassland, and open croplands (Jemberie et al., 2020; Kajobe, 2007; Njoya, 2010). These nests, which vary in size and complexity, can be constructed in subterranean cavities, cavities in tree trunks, active or abandoned subterranean termite mounds, abandoned ant nests, rock crevices, active bird nests, as well as crevices in mud walls and roofs (Mduda et al., 2023; Namu & Wittmann, 2017; Njoya et al., 2019; Roubik, 2006; Sayusti et al., 2021). In this study, the majority of the subterranean *M. beccarii* nests were found deep inside the natural indigenous and plantation forests in the highlands, followed by farmlands along the edges of these forests, but rarely along the riparian habitats. This is similar to the report of *M. beccarii* nesting sites in the Bermenda highlands of western Cameroon (Njoya et al., 2017). In contrast, a recent study reported that most of *M. baccarii* nests in Oromia Regional State, Ethiopia, were mainly found in the open croplands near forests (Hora et al., 2023). Highland forests have several advantages that make them a preferred nesting habitat for *M. beccarii*. First, the forest soils are soft, which makes it easy for the *de novo* construction of nest cavities by *M. beccarii* stingless bees. Secondly, the cool highland temperature and forest cover protect the underground nests from the extreme heat that can melt or destroy the structural properties of the materials used to construct the nest, that is, the waxes, geopropolis and propolis. Additionally, the biodiversity of highland forest plants may provide unique sources of floral and nest construction materials for *M. beccarii*. We found that all the nests were located within <1 km from a water source. Therefore, the availability of water might also be a key factor restricting *M. beccarii* to the highland forests, where water is much more readily available compared to other habitats. This is further supported by the finding of a few *M. beccarii* nests built along rivers outside the forest ranges.

Stingless bee nests consist of external and internal entrances that connect the nest proper to the outside environment. The external nest entrance serves several functions, including defense, foraging guidance, and regulation of internal physicochemical characteristics (Roubik, 2006). The characteristics of the nest entrances are species-specific and are dependent on various factors, including age of the nest, need for defense against predators, foraging traffic, and local climatic conditions (Roubik, 2006). In Bamenda Afromontane forests of Cameroon, *M. beccarii* nests have one circular-shaped external entrance protruding 0.5–0.6 cm above the ground and with a diameter of 1–1.4 cm (Njoya et al., 2017). This contrasts with our study in which the external entrance was mainly ovoid-shaped, with a higher average height above the ground (1.18 ± 0.49 cm) and a broader diameter of 1.39 ± 0.59 cm (range 0.3–2.5 cm). In Tanzania, the external entrance tube of *M. beccarii* nests is oval in shape, which is similar to our finding (Mduda et al., 2023). However, the height above the ground of the Tanzanian *M. beccarii* external nest entrance is comparatively shorter than in our case and that reported for *M. baccarii* in Oromia, Ethiopia (Hora et al., 2023). These differences in external entrance height might be due to differences in the perceived threats at the nesting sites and materials used for their construction. We found that the external entrance is oriented north or southwest direction. This was mainly due to preferential nesting on slopes with north or southwest orientation. This may be to protect the nests from direct sunlight during the hot mid-morning and afternoon hours of the day.

We found that the internal entrance in most nests of *M. beccarii* is vertical and connects to the ceiling of a completely filled-up nest cavity, which is located at an average depth of 24.05 ± 6.95 cm (range 14–49 cm) below the ground surface. This internal entrance length and thus the depth of the nest cavity below the ground surface is closer to those reported for *M. beccarii* nests in Bermenda region of Cameroon (Njoya et al., 2017), in the Amhara region of Ethiopia (23.4–35.4 cm) (Jemberie et al., 2020) and the Oromia region of Ethiopia (Hora et al., 2023). Altogether, these findings indicate slight variation in the subterranean depth of *Meliponula* nest cavities across East and Central Africa.

The nest proper of *M. beccarii* in this study consisted of a brood area, involucrum layers, and storage pot areas. Within the brood area are brood combs, which were horizontally arranged and exhibited a concentric construction mode. The honey and pollen pots covered the lower part of the brood area. Again, this architectural design is consistent with the descriptions of Cameroonian (Njoya et al., 2017) and Tanzanian *M. beccarii* (Mduda et al., 2023), as well as the ground-nesting *M. beccarii* in the Amhara (Jemberie et al., 2020) and Oromia (Hora et al., 2023) regions of Ethiopia.

A blind-ended tunnel located on the nest cavity floor of several Afrotropical ground-nesting stingless bee species, including *M. beccarii*, *P. lendiana*, *M. tanganyikae medionigra*, and *P. hildebrandti* (Araujo, 1963; Hora et al., 2023; Namu & Wittmann, 2017; Njoya et al., 2017). The exact function of this blind-ended canal that seems to be consistently present in stingless bee ground nests is not yet entirely clear, still it is generally accepted to serve the purpose of draining water that might inevitably enter the nest (Araujo, 1963; Namu & Wittmann, 2017; Njoya et al., 2017). The floor canal has also been considered to serve as a defecation pit (Gela & Hora, 2021). We found a similar tunnel in all the well-established *M. beccarii* nests, with the exception of one nest in the Baringo region. The canal in our study was not aligned with the entrance tube and was not at the centre of the nest cavity floor. However, unlike the previous findings (Araujo, 1963; Namu & Wittmann, 2017), the floor canal was not located on the lowest part of the floor in all the nests. Moreover, we found that some of these floor canals are constructed to rise above the floor by ∼1 cm, closely resembling the external entrance tube. Such design features might impede the generally accepted role of the floor canal in the drainage of water from the nest.

Some ground-nesting stingless bee species, including *P. hildebrandti* and *Geotrigona subterranea* build their nests in active and inactive termite hills, abandoned ant nests, cavities between the ground and a masonry structure, and chambers formed by rainwater (Barbosa et al., 2013; Namu & Wittmann, 2017; Roubik, 2006). However, studies in Cameroon did not find evidence suggesting that *M. beccarii* build their nest in pre-existing cavities (Njoya et al., 2017). In Tanzania, also, *M. beccarii* underground nests are not associated with termite nests, and it is not clear how the nest cavities were formed. In this current study, we found *M. beccarii* nests with freshly excavated soil mounds dumped outside the entrance of nests, only a short burrow measuring about 5 cm in length below the ground, and rudimentary nest architecture. Altogether, these observations indicate that indeed, *M. beccarii* construct their nests from scratch and not in pre-existing underground cavities. This raises an intriguing question of where the entire *M. beccarii* colony, whose nest has been destroyed, stay during the *de novo* construction of the new nest. This question needs to be addressed in future studies.

Meliponiculture is not yet well developed in Africa, including Kenya, where only a few tree-nesting stingless bee species have been successfully domesticated using artificial wooden hives in the western part of the country. Notably, attempts to adapt the ground-nesting species, including *M. beccarii,* in available artificial wooden hives often exhibit as high as 100% colony failure rates (Araujo, 1963; Gela & Hora, 2021). Therefore, the development of appropriate hives that closely resemble their natural nest design is essential for the successful domestication of *M. beccarii*. Indeed, Gela and Hora (2021) recently demonstrated the successful adaptation of *M. beccarii* colonies in clay pot hives that incorporated the key design features of their natural nest architecture and ecology. Therefore, the results presented herein form the basis for developing appropriate meliponiculture technology to conserve and harness the economic potential of *M. beccarii* in Baringo County. One limitation of this study was that some of the key nest features, including the number and sizes of the queen cells, number of the worker cells, pillar thickness, and height, diameter and volume of the honey pot and pollen pot, were not documented. Nevertheless, this limitation does not limit the use of the reported information as the basis of designing novel hives.

Conclusions

In conclusion, the subterranean nests of *M. beccarii* in Baringo County are majorly in the highland forest habitats. The nests have the general basic architecture of Afrotropical ground-nesting stingless bees that has previously been reported, including an external entrance, internal entrance, brood area, pot storage area, and involucrum layers. Several gyne cells are found in the brood area of most nests. The nests in Baringo Central have a bigger diameter compared to those found in Koibatek forests. These findings can be used to design different artificial hives, which should then be evaluated for suitability in the development of local meliponiculture programmes.

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Author contributions

TB and SKJ collected and analyzed the data and wrote the first manuscript draft. JM and HA contributed to the design, data collection, and taxonomic identification. KJK contributed to the design, data analysis, and manuscript review. BNO and GM contributed to data analysis and critical review of the final manuscript. SK conceptualized the project and reviewed the final manuscript. All authors read and approved the content of this manuscript.

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Data availability statement

All relevant data are within the paper and its Supporting Information files.

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