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# Species richness and nest entrance characteristics of stingless bees (Hymenoptera: Apidae: Meliponini) in Ujung Kulon National Park, Banten, Indonesia

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**Abstract**. *Miharja J, Atmowidi T, Priawandiputra W, Perwitasari D, Kahono S. 2024. Species richness and nest entrance characteristics of stingless bees (Hymenoptera: Apidae: Meliponini) in Ujung Kulon National Park, Banten, Indonesia. Biodiversitas 25: 4961-4970.* Stingless bees (Hymenoptera, Apidae, Meliponinae) are distributed in tropical and subtropical regions. Ujung Kulon National Park (UKNP), a conservation area of flora and fauna in the western part of Java, was designated by UNESCO in 1992 as a Natural World Heritage site. This study measured the species richness, nesting site, and nest-entrance characteristics of stingless bees in UKNP. Samplings of stingless bees were conducted by road sampling and based on the information from officers of UKNP and the local communities from June to December 2023. Results showed that 163 colonies of stingless bees were found belonging to four species, i,e., *Tetragonula laeviceps, Tetragonula fuscobalteata, Heterotrigona itama*, and *Lepidotrigona terminata.* Based on the number of colonies, *L. terminata* was the most dominant (44%), followed by *T. laeviceps* (41%), *T. fuscobalteata* (12%), and *H. itama* (3%), respectively. The nest of *T. laeviceps* was found in residential house cavities, bamboo and tree holes, and old and abandoned ant nests, showcasing their adaptability and resourcefulness. Meanwhile, the nest of *T. fuscobalteata* was found in the rock holes and tree cavities; *L. terminata* and *H. itama* nests were found in tree cavities. The unique nest entrance characteristics of each species further highlight their fascinating adaptability. This study showed a new distribution record of stingless bees in Ujung Kulon National Park, Banten, Indonesia.

**Keywords:** Banten, distribution record, diversity, nesting sites, road sampling

## INTRODUCTION

Stingless bees (Hymenoptera: Apidae: Meliponinae) are eusocial insects with essential roles in plant pollination, maintenance of plant biodiversity, and producing honey, propolis, and wax (Farida et al. 2020). The distribution of the stingless bees covers tropical and subtropical areas (Neotropical, Afrotropical, and Indo-Malaya), and about 605 species in 45 genera have been described, and about 50 species were found in Southeast Asia (Grüter 2020; Engel et al. 2023). In Indonesia, a diverse range of 46 species of stingless bees belonging to ten genera have been recorded, namely *Austroplebiae, Geniotrigona, Heteretrigona, Lisotrigona, Homotrigona, Lepidoptrigona, Papuatrigona, Pariotrigona, Tetragonula*, and *Wallacetrigona* (Rasmussen et al. 2017; Kahono et al. 2018).

Ujung Kulon National Park (UKNP) is one of the oldest national parks in Indonesia and, in 1991, was designated by UNESCO as a Natural World Heritage Site (unesco.org). In 1883, the eruption of Krakatau volcano in Rakata Island, located in the Sunda Strait between Java and Sumatra, Indonesia, was the most catastrophic in history. This eruption was followed by tsunamis that devastated the coast of the Sunda Strait, including the national park (Paris et al. 2014). Likewise, the latest tsunami due to landslides from the eruption of Anak Krakatau, which occurred in 2018, this area experienced the highest waves and the most severe impacts compared to other coastal areas in the Sunda Strait (Widiyanto and Hsiao 2020). UKNP is a peninsula located at the western tip of the island of Java with an area of 122,956 ha, home to the endemic Javan rhinoceros (*Rhinoceros sondaicus* Desmarest 1822) as a threatened extinction species (Nardelli 2016) and other animals, including many species of stingless bees. As a peninsula, UKNP had a severe impact from tsunamis that affected the survival of animals, including stingless bees. Previously, data of stingless bees reported from Java Island, such as *Tetragonula laeviceps* Smith 1857 and *Tetragonula drescheri* Schwarz 1939, *Tetrigona apicalis* Smith 1857, *Tetrigona vidua* Lepeletier 1836, *Lepidotrigona javanica* Gribodo 1892, *Lepidotrigona terminata* Smith 1878, and *Lepidotrigona ventralis* Smith 1857 (Kahono et al. 2018). The latest reports of stingless bees on Java Island were *Tetragonula fuscobalteata* Cameron 1908, *Tetragonula iridipennis* Smith 1854, and *Tetragonula sapiens* Cockerell 1911 (Trianto and Purwanto 2022). The previous studies showed no available data on stingless bees in UKNP;

therefore, these results showed a new distribution record of stingless bees.

The nesting habitats of stingless bees vary, such as in tree cavities (Atmowidi et al. 2024), ant nests, rocks, and house wall cavities (Grüter 2020), and live in perennial colonies (Roubik 2020). Inside the hive, there is a queen, male bees, and worker bees (Grüter 2020). Stingless bees communicate with each other when foraging by releasing pheromones (Roubik 2020). They use resin and propolis to build and protect beehives from pathogens (Quezada-Euán 2018b). In stingless bees, flavonoid resin functions as an anti-microbial agent in the nest, while terpenoid resin functions to repel ants at the nest entrance (Roubik 2023). The nest structure of stingless consists of a nest entrance, brood cells, food storage (honey and pollen pots), and a layer of cerumen and batumen (Engel et al. 2023). The characteristics of stingless bee nests are related to their defense from natural enemies, and the size of the nest entrance is related to the behavior of nest-guarding bees (Couvillon et al. 2008). Phenotypic observations, such as nest structure, are important for identifying bee species (Roubik 2006), and it is also useful for local meliponiculture to recognize stingless bee species (Rivaldy et al. 2023).

Stingless bees are a part of community pollinators in the forest and agricultural lands. Recently, the decline in natural pollinators has been reported in line with habitat clearing and large-scale habitat destruction due to climate change and forest burning for agriculture (Marchioro et al. 2020; Harianja et al. 2023). Declining stingless bees in the forest are caused by the hunting of bee colonies by local communities, and they sell to breeders in outside areas (Gratzer et al. 2019). These activities may decrease the diversity and sustainability of native bees in the forests, including in UKNP. The lack of information on the species richness of stingless bee colonies in UKNP to be a background of the importance of this research. In this study, we provide data on species richness and nest characteristics of stingless bees in the UKNP in Banten Province, Indonesia.

## MATERIALS AND METHODS

### Study area

This research was conducted from June until December 2023 in several areas of Ujung Kulon National Park (UKNP), Pandeglang District, Banten Province, Indonesia (6°49'31,397" S and 105° 27' 52,776"E). The coastal area vegetation in the study was dominated by *Ipomoea pes-caprae*, *Spinifex littoreus*, *Desmodium umbellatum*, *Pandanus* sp., and *Sophora tomentosa*. While in the lowland forest, vegetation was dominated by Annonaceae, Myrtaceae, Moraceae, Lauraceae, Euphorbiaceae, Arecaceae, Clussiaceae, Ebenaceae, Sapindaceae, Symplocaceae, and Salicaceae (Purwaningsih and Atikah 2018). The average rainfall at the research location was 4,068 mm/year. Eleven sampling sites were used to collect stingless bees, i.e., in the mainland peninsula (Taman Jaya, Ujung Jaya, Legon Pakis, Karang Ranjang, Kalejetan, Cigenter, Cidaon, Cikelang, Nyawaan), Peucang Island, and Panaitan Island (Figure 1). The sampling sites were selected by using the purposive sampling method (Etikan et al. 2016).

### Observation of stingless bee colonies

At each site, we observed the stingless bee colonies by tracking them on sunny days, and we used information from national park officers using the phrase *teuweul* (Sunda language). During observations, environmental parameters, i.e., air humidity, temperature, humidity, light intensity, and wind speed, were recorded using Lutron LM8000A four-in-one measurer. After the stingless bee colony was found, the nest characteristics were measured and described. The nest properties observed were nesting site location, nest-entrance shape, texture, and color. Then, we measured the nest entrance (funnel length, horizontal and vertical diameters of nest opening) using a caliper (Kelly et al. 2014).

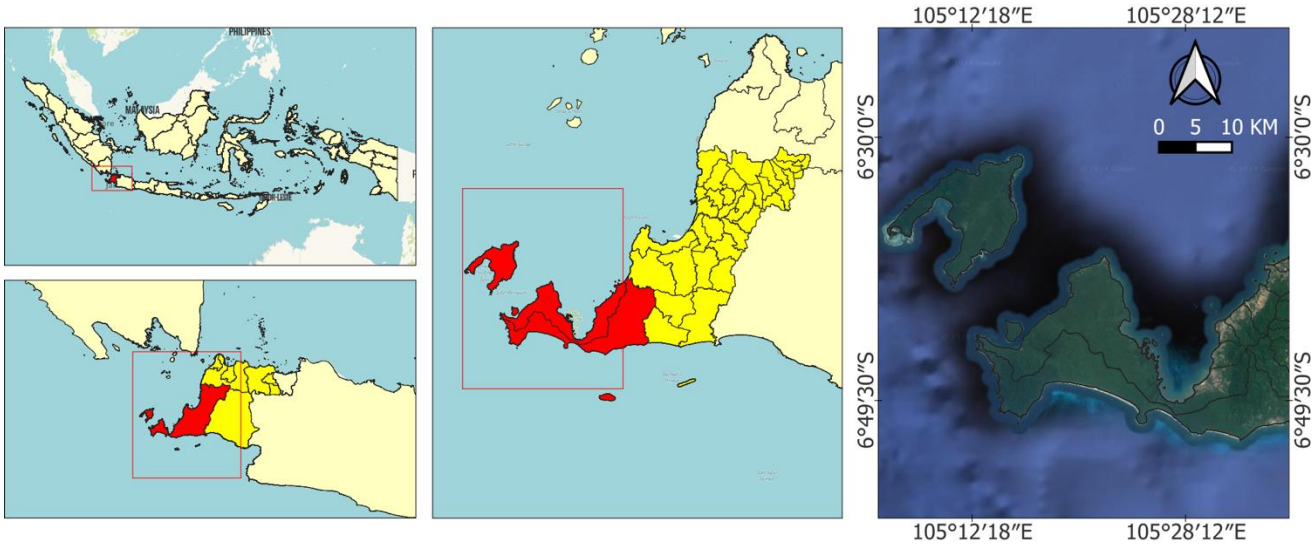


**Figure 1.** Study sites for the sampling of stingless bees in Ujung Kulon National Park, Banten, Indonesia

**Specimen collection and identification**

A collection of workers' stingless bees from each colony was carried out using a sweep net. Fifty individual worker bees were collected from each colony, and the specimens were put into a bottle containing 90% ethanol. Then, the samples were preserved using a dry method. Stingless bee specimens were identified based on Sakagami et al. (1990) and Engel et al. (2019). The identification was carried out at the Laboratory of Animal Biosystematics and Ecology, Department of Biology, Institut Pertanian Bogor, Bogor. Then, the specimens were verified and deposited as voucher specimens at the Research Center for Ecology and Ethnobiology, Research and Innovation Agency (BRIN), Cibinong, Bogor, West Java, Indonesia. Some specimens were kept in the Laboratory of Animal Biosystematics and Ecology, Institut Pertanian Bogor.

**Observation of nest entrance and brood cell characteristics**

We observed each nest found and documented it. The nest entrances measured were shape, opening diameter, nest height from the ground, and nest entrance ornamentation and color. The nests of stingless bees were observed from two locations in UKNP and then characterized in cluster, semi-comb, or comb. The brood cells were observed and measured, such as shape, diameter, height, color, and columnar or lamellate pillars. All measurements were using Image Raster v.4.0.

**Data analysis**

A one-way analysis of variance (ANOVA) test was used to compare the diameter, funnel length, nest entrance height, and nest height from the ground among stingless bee species using Paleontological Statistics (PAST) ver. 4.09 (Hammers 2022). The species composition of stingless bees from all study sites was summarized in the table.

## RESULTS AND DISCUSSION

**Species richness of stingless bees**

Results indicated four species of stingless bees (163 colonies) were found in several locations in UKNP, namely *Tetragonula laeviceps* Smith 1857, *Tetragonula fuscobalteata* Cameron 1908, *Heterotrigona itama* Cockerell 1918, and *Lepidotrigona terminata* Smith 1878 (Figure 2). In the peninsula areas of this park were found 112 colonies of stingless bees, i.e., Taman Jaya (6 colonies), Ujung Jaya (3 colonies), Legon Pakis (9 colonies), Kalajetan (11 colonies), Karang Ranjang (32 colonies), Cigenter (2 colonies), Cikelang (2 colonies), Nyawaan (4 colonies), and Cidaon (42 colonies). Meanwhile, on Peucang Island, we found 26 colonies, and on Panaitan Island, 22 colonies. *Lepidotrigona terminata* was found as a dominant species (72 colonies, 44%), followed by *T. laeviceps* (67 colonies, 41%), *T. fuscobalteata* (19 colonies, 12%), and *H. itama* (5 colonies, 3%) (Table 1).

**Nesting sites of stingless bees**

The nesting site of stingless bees in UKNP was found in tree cavities of many plant species, mainly in the *Ficus* tree (Moraceae). Nests of *T. laeviceps* were found in *Ficus benjamina* (24.0%), *Hibiscus tiliaceus* (16.4%), *Sumbaviopsis albicans* (9.0%), *Dendrocalamus asper* (9.0%), *Intsia bijuga* (7.5%), *Calophyllum inophyllum* (6.0%), *Cynometra ramflora* (3.0%), *Calophyllum soulattri* (3.0%), *Syzygium densiflorum* (3.0%), *Pongamia pinnata*, *Vitex pinnata*, *Carallia brachiata*, *Leucaena leucocephala*, *Archidendron pauciflorum*, *Parkia speciosa*, *Pterocarpus indicus*, and *Sonneratia caseolaris* (each 1.5%). Nesting sites of *T. fuscobalteata* were found in tree cavities of *F. benjamina* (26.3%), *C. ramiflora* (10.5%), and *Garcinia dioica* (5.3%). Furthermore, nests of *T. fuscobalteata* also were found in coral rocks (15.8%), house wall cavities (21.1%), and former ant nests (5.3%) (Table 2). Nest of *L. terminata* were found in tree cavities of *F. benjamina* (56%), *C. inophyllum* (28%), *P. pinnata* (4%), *Pterospermium javanicum* (3%), *Gonystylus macrophyllus* (3%), *G. dioica* (3%), *S. albicans* (1%), and *Drypetes neglecta* (1%). Of the five colonies found of *H. itama*, 80% of them were found in the tree cavities of *F. benjamina*, while 20% of the nest was found in *S. albicans*.

**Nest entrance characteristics**

Of the 163 colonies of stingless bees, we found varied nest entrances in shape, color, and texture. The nest entrance of *T. laeviceps* was characterized by round, oval, irregular nest-opening, and funnel. Most of the nest opening was irregular (30 colonies), followed by an ellipse (11 colonies), round-oval (7 colonies), funnel (13 colonies), and round (7 colonies) with hard- and soft textures. Several nest entrances of this species have a short funnel (8 cm in length, 7 cm in horizontal diameter) and 5 cm in vertical diameter on average). The color of the funnel was light brown, dark brown, black, and black yellowish (Figure 3).

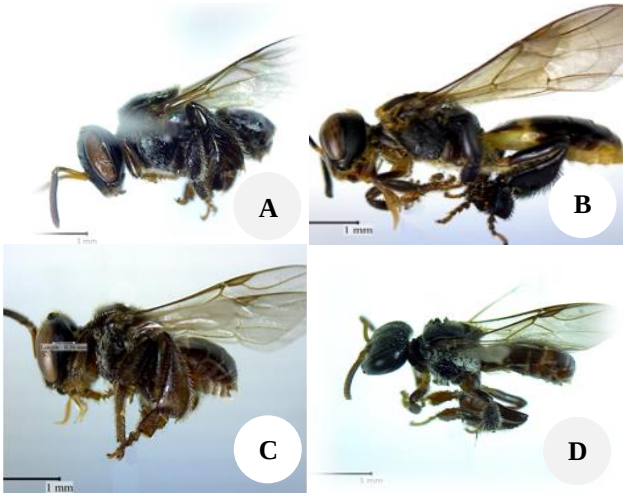


**Figure 2.** The worker of stingless bee species in Ujung Kulon National Park, Banten, Indonesia. A. *Tetragronula fuscobalteata*; B. *Lepidotrigona terminata*; C. *Heterotrigona itama*; D. *Tetragronula laeviceps*

**Table 1.** Number of colonies found and nest location of stingless bees in Ujung Kulon National Park, Banten, Indonesia

| Location | Coordinates* | Species | No. of colonies | Nest location |
|---|---|---|---|---|
| Taman Jaya | 6°43'49,248" S; 105° 32' 2,051" E | *Tetragonula laeviceps* Smith 1857 | 4 | Tree holes |
| | 6°43'27,211" S; 105° 31'48,159" E | *Heterotrigona itama* Cockerell 1918 | 2 | Tree holes |
| Ujung Jaya | 6°48' 31,486" S; 105° 29' 51,634"E | *Tetragonula laeviceps* Smith 1857 | 2 | Tree holes, house wall |
| | 6° 48' 31.4856"S; 105° 29' 51.633"E | *Heterotrigona itama* Cockerell 1918 | 1 | Tree holes |
| | 6° 48' 24.8394"S; 105° 28' 52.1148"E | | | |
| Legon Pakis | 6°49'31,397" S; 105° 27' 52,776"E | *Lepidoptrigona terminata* Smith, 1878 | 5 | Tree holes |
| | 6°49' 9,948 " S; 105° 27' 52,776"E | *Tetragonula laeviceps* Smith 1857 | 4 | Tree holes |
| | 6°49' 31,404" S; 105°28' 12,036" E | *Tetragonula fuscobalteata* Cameron 1908 | 1 | Tree holes |
| Kalejetan | 6° 49' 33,085" S; 105° 28'12,000"E | *Tetragonula laeviceps* Smith 1857 | 6 | Bamboo, tree holes |
| | 6° 49' 25, 165" S; 105° 28'18,012"E | *Heterotrigona itama* Cockerell 1918 | 1 | Tree holes |
| | 6° 49' 48, 036" S; 105° 29'4, 920" E | *Lepidoptrigona terminata* Smith 1878 | 3 | Tree holes |
| | 6° 50' 28, 892" S; 105° 29'16,800"E | *Tetragonula fuscobalteata* Cameron 1908 | 1 | Tree holes |
| Karang Ranjang | 6° 49' 32, 995"S; 105° 28'12,167" E | *Tetragonula laeviceps* Smith 1857 | 14 | Tree holes, house wall |
| | 6° 50' 18,846" S; 105° 26' 59,82" E | *Lepidoptrigona terminata* Smith 1878 | 18 | Tree holes |
| | 6° 50' 22,542" S; 105° 27' 6,941" E | | | |
| Cigenter | 6° 41' 54,276" S; 105° 20' 3, 876" E | *Lepidoptrigona terminata* Smith 1878 | 1 | Tree holes |
| Cikelang | 6° 40' 35, 91" S; 105° 22' 06,331" E | *Lepidoptrigona terminata* Smith 1878 | 2 | |
| Nyawaan | 6° 45' 13,716" S; 105° 24' 05,724" E | *Tetragonula laeviceps* Smith 1857 | 1 | Tree holes |
| | 6° 45' 3,085" S; 105° 14' 52,055" E | *Lepidoptrigona terminata* Smith 1878 | 3 | Tree holes |
| Cidaon | 6° 44' 30,437" S; 105° 16' 41,009" E | *Tetragonula laeviceps* Smith 1857 | 8 | Tree holes |
| | 6° 45' 80,280" S; 105° 15' 53,341" E | *Heterotrigona itama* Cockerell 1918 | 1 | Tree holes |
| | 6° 44' 45,154" S; 105° 16' 16,280" E | *Lepidoptrigona terminata* Smith 1878 | 28 | Tree holes |
| | 6° 45' 48,913" S; 105° 15' 51,998" E | *Tetragonula fuscobalteata* Cameron 1908 | 4 | Abonded ants |
| Peucang Island | 6° 44' 19,302" S; 105° 16' 39,749" E | *Tetragonula laeviceps* Smith 1857 | 8 | Tree holes, bamboo |
| | 6° 44' 43,980" S; 105° 15' 46,526" E | *Lepidoptrigona terminata* Smith, 1878 | 12 | Tree holes |
| | 6° 44' 4,841" S; 105° 16' 47,644" E | *Tetragonula fuscobalteata* Cameron 1908 | 7 | Tree holes, rock hole |
| | 6° 44' 34,069" S; 105° 16' 27,368" E | | | |
| Panaitan Island | 6° 36' 20,326" S; 105° 11' 30,502" E | *Tetragonula laeviceps* Smith 1857 | 20 | Tree holes |
| | 6° 36' 42,365" S; 105° 11' 24,986" E | *Tetragonula fuscobalteata* Cameron 1908 | 6 | |
| | 6° 37' 55,225" S; 105° 11' 30,908" E | | | |
| | 6° 38' 35,513" S; 105° 11' 59,568" E | | | |
| | 6° 38' 38,631" S; 105° 12' 59,312" E | | | |
| | 6° 32' 926" S; 105° 12' 59,601" E | | | |
| | 6° 32' 821" S; 105° 12' 59,765" E | | | |
| Total colonies | | | 163 | |

Note: (*): Not all nesting site coordinates were shown

Meanwhile, *T. fuscobalteata* has a varied nest entrance opening, such as funnel, round pipe, oval, and ellipse, with ornaments around the entrance opening. The funnel of the nest entrance ranged from 0.97-1.0 cm in horizontal diameter, 3 cm in vertical diameter, and 2-5 cm in length with dark brown and black colors (Table 3). Of the 16 colonies, we found a nest entrance funnel (6 colonies), round pipe (4 colonies), round (4 colonies), irregular (3 colonies), and ellipses (2 colonies) with a hard texture. The species of *L. terminata* was the most with a long funnel nest entrance and oval opening. The color of the nest entrances was light brown, blackish brown, black and white, yellowish, and dark brown. The nest entrance funnel is 1 cm in horizontal diameter, 1.2 cm in vertical diameter, and the length ranges from 5-30 cm. Interestingly, we found old nests with 2-5 branches of the nest entrance. Of the 72 colonies observed, we found variations in nest entrance, i.e., ellipse (8 colonies), oval (29 colonies), funnel (27 colonies), and trumpet with a soft texture. The large-size stingless bee, *H. itama*, in UKNP of the current study varied in nest entrance, i.e., oval opening (2 colonies), funnel (2 colonies), ellipses (1 colonies) with a soft texture and ornaments around the entrance. The size of the nest entrance funnel was 5-10 cm in horizontal diameter, 3 cm in vertical diameter, and 8-13 cm in length with dark brown and light brown in colors.

We observed the nest internal structure of two species, i.e., *T. laeviceps* and *L. terminata*. The nest internal structure of *T. laeviceps* observed in the tree of *H. tiliaceus* and *D. asper* formed clusters and semi-clusters. Brood cells are connected to other cells through flat structures (Figure 4). Oval and elongated brood cells are light brown and dark brown (young larval cells). The pollen pots have a regular shape located at the end of the hive, along with honey pots. The size of pollen pots ranged from 9-15 cm in length and 0.6-0.8 cm in diameter. Honey pots sized 1.0-1.56 cm in width and 18 cm in length with dark brown and black in colors. The total length of the nest space is 27-34 cm. The nest internal structure of *L. terminata* in the dead tree of *C. inophyllum*, the brood cells stem form combs with a spiral layer. The brood cells are light brown and dark brown (young larval cells). The pollen pots are a regular shape located in the middle of the hive, along with the honey pots. The size of pollen pots ranged from 9-15 cm in length and 0.6-0.8 cm in diameter. The honey pots are 1.0-1.76 cm wide and 12 cm in length, with dark brown and black. The total length of the nest is 40 cm (Table 4).

**Table 2.** Nesting sites of stingless bees in Ujung Kulon National Park, Indonesia, Banten, Indonesia

| Nesting sites | | | Species of stingless bees | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Family** | **Species** | **Local name** | ***T. laeviceps*** | **%** | ***T. fuscobalteata*** | **%** | ***L. terminata*** | **%** | ***H. itama*** | **%** |
| Tree cavities | | | | | | | | | | |
| Malvaceae | *Pterospermium javanicum* | *Bayur* | - | - | - | - | 2 | 2.8 | - | - |
| Calophyllaceae | *Calophyllum inophyllum* | *Nyamplung* | 4 | 6 | - | - | 20 | 27.8 | - | - |
| Moraceae | *Ficus benjamina* | *Beringin* | 16 | 24.0 | 5 | 26.3 | 40 | 55.6 | 4 | 80 |
| Thymeleaceae | *Gonystylus macrophyllus* | *Kakaduen* | - | - | - | - | 2 | 2.8 | - | - |
| Moraceae | *Cynometra ramiflora* | *Kibatok* | 2 | 3.0 | 2 | 10.5 | 1 | 1.4 | - | - |
| Fabaceae | *Pongamia pinnata* | *Malapari* | 1 | 1.5 | 1 | 5.3 | 3 | 4.2 | - | - |
| Lamiaceae | *Vitex pinnata* | *Laban* | 1 | 1.5 | - | - | - | - | - | - |
| Rhizophoraceae | *Carallia brachiata* | *Kicelang* | 1 | 1.5 | 1 | 5.3 | - | - | - | - |
| Euphorbiaceae | *Sumbaviopsis albicans* | *Tangkele* | 6 | 9.0 | - | - | 1 | 1.4 | 1 | 20 |
| Clusiaceae | *Garcinia dioica* | *Kihasem* | - | - | 1 | 5.3 | 2 | 2.8 | - | - |
| Putranjivaceae | *Drypetes neglecta* | *Cerelang* | 3 | 4.5 | - | - | 1 | 1.4 | - | - |
| Poaceae | *Dendrocalamus asper* | *Bambu* | 6 | 9.0 | - | - | - | - | - | - |
| Malvaceae | *Hibiscus tiliaceus* | *Waru laut* | 11 | 16.4 | - | - | - | - | - | - |
| Cluciaceae | *Calophyllum souattri* | *Kampis* | 2 | 3.0 | 1 | 5.3 | - | - | - | - |
| Mimosaceae | *Leucaena leucocephala* | *Petai Cina* | 1 | 1.5 | - | - | - | - | - | - |
| Mimosaceae | *Archidendron pauciflorum* | *Jengkol* | 1 | 1.5 | - | - | - | - | - | - |
| Fabaceae | *Parkia speciosa* | *Petai* | 1 | 1.5 | - | - | - | - | - | - |
| Fabaceae | *Pterocarpus indicus* | *Angsana* | 1 | 1.5 | - | - | - | - | - | - |
| Lythraceae | *Sonneratia caseolaris* | *Pidada merah* | 1 | 1.5 | - | - | - | - | - | - |
| Mirtaceae | *Syzygium densiflorum* | *Jambu kopo* | 2 | 3.0 | - | - | - | - | - | - |
| Fabaceae | *Intsia bijuga* | *Marbo* | 5 | 7.5 | - | - | - | - | - | - |
| Other substrates | | | | | | | | | | |
| Rock cavity | | - | - | - | 3 | 15.8 | - | - | - | - |
| House wall cavity | | - | 2 | 3.0 | 4 | 21.1 | - | - | - | - |
| Ant Nest | | - | - | - | 1 | 5.3 | - | - | - | - |
| Total | | | 67 | 100 | 19 | 100 | 72 | 100 | 5 | 100 |

Note: (-): no available data


**Figure 3.** Variation of nest entrance of stingless bees in Ujung Kulon National Park, Banten, Indonesia. A-D. Nest entrance of *T. laeviceps* with short funnel, wide in diameter, sticky propolis covering the surface of entrance; E-H. Nest entrance of *L. terminata* with long funnel, trumpet- and funnel-shaped, sticky propolis covering the surface, branched of nest entrance; I-L. Nest entrance of *T. fuscobalteata* with small and short funnel, blackish brown; M-P. Nest entrance of *H. itama* with a long and wide opening, blackish in color, sticky propolis covering the surface. Scale: 1 cm

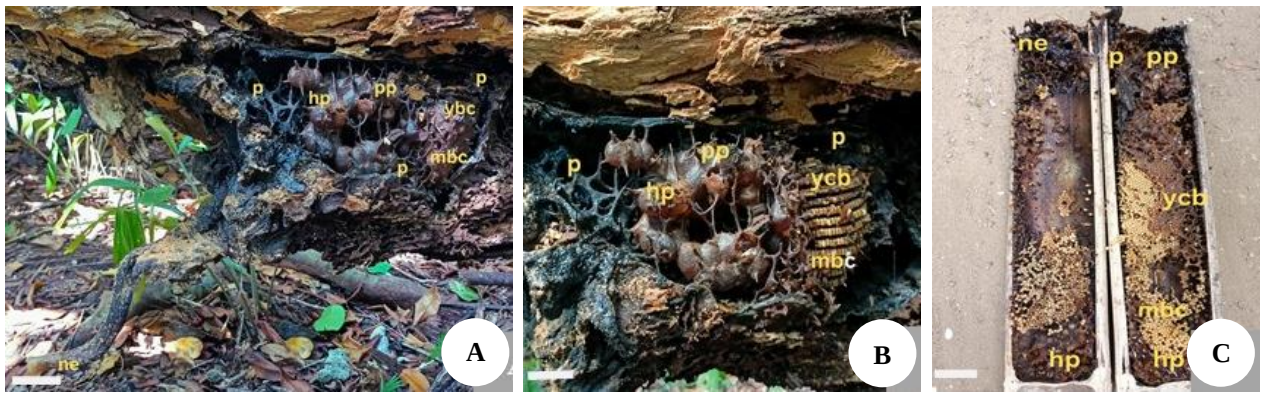


**Figure 4.** The internal nest structure of stingless bees. A-B: regular layered comb of brood cells of *L. terminata*; C: semi-cluster comb of brood cell of *T. laeviceps;* Ne: nest entrance; p: pillars; hp: honey pots; pp: pollen pots; ycb: young brood cells; mbc: mature brood cells. Bar: 1 cm

**Table 3.** The size, shape, and color of stingless bee nest entrances in Ujung Kulon National Park, Banten, Indonesia

| Species | Opening diameter (cm) | | | Funnel length (cm) | | | Nest height from the ground (cm) | | | Entrance shape | Entrance color | Nest tree |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M | R | SD | M | R | SD | M | R | SD | | | |
| Taman Jaya and Ujung Jaya | | | | | | | | | | | | |
| *T. laeviceps* | 2.0 | 1.0-5.0 | 1.7 | 2.5 | 1.0-5.0 | 1.6 | 232 | 30-500 | 159 | El. Ir, Ov, | Bk, Db, Lb | Bm, H,T |
| *H. itama* | 2.0 | 0.9 | 0.4 | 5.2 | 4.0-5.8 | 1.6 | 181 | 60-400 | 189 | Cl, Bl | Db | T |
| Legon Pakis and Kalejetan | | | | | | | | | | | | |
| *T. laeviceps* | 2.1 | 1.0-5.0 | 1.4 | 5.6 | 1.0-16.0 | 5.7 | 92.4 | 30-200 | 68 | El. Ir, Ov, | Bk, Db, Lb | Bm, T |
| *T. fuscobalteata* | 1.3 | 1.0-1.5 | 0.4 | 2.5 | 2.0-3.0 | 0.7 | 103 | 33-174 | 0.4 | Bp, Bl | Bk, Db, | T |
| *L. terminata* | 1.7 | 1.3-2.3 | 0.4 | 12.2 | 2.5-22.0 | 7.4 | 111 | 55-200 | 57.9 | Ov, CI, Ct | Lb, BW, By | T |
| *H. itama* | 1.8 | 1.5-2.0 | 0.4 | 6.5 | 6.0-6.5 | 0.7 | 85 | 75-100 | 21.2 | Ov | Db, Lb | T |
| Cigenter and Nyawaan | | | | | | | | | | | | |
| *L. terminata* | 1.3 | 1.2-1.4 | 0.1 | 7.0 | 5-8 | 1.8 | 167 | 0.8 | 69.9 | Ov, CI, Ct | Lb, By | T |
| Cidaon | | | | | | | | | | | | |
| *T. laeviceps* | 2.9 | 1.4-5.5 | 1.8 | 6.6 | 5-10 | 2.1 | 98 | 8-182 | 61.6 | El. Ir, Ov,Ro | Bk, Db, Lb | |
| *T. fuscobalteata* | 1.3 | 0.8-2.2 | 0.6 | 3.8 | 2-7 | 2.2 | 146 | 84-250 | 74.8 | Bp, Ro | Bk, Db, | BS, T |
| *L. terminata* | 1.5 | 0.8-2.5 | 0.5 | 12.7 | 2-30 | 7.3 | 170 | 15-300 | 82.4 | Ov, CI, Ro | Lb, BW, By | T |
| Peucang Island | | | | | | | | | | | | |
| *T. laeviceps* | 2.4 | 1.1-3.7 | 0.6 | 1.1 | 1.0-2.2 | 0.6 | 128.5 | 60-260 | 86.9 | El. Ir, Ov,Bl | Lb, Bk, Db | Bm,T |
| *T. fuscobalteata* | 1.2 | 0.9-1.3 | 0.1 | 3.9 | 3.0-7.0 | 2.2 | 42.4 | 10-80 | 30.3 | Bp, Bl | H, CT | Bm,K,T |
| *L. terminata* | 1.6 | 1.0-2.2 | 0.7 | 9.1 | 6.0-21.0 | 4.3 | 168.9 | 30-310 | 94.6 | Ov, CI, Ct | Lb, BW, By | T |
| Panaitan Island | | | | | | | | | | | | |
| *T. laeviceps* | 1.6 | 1.0-6.0 | 1.0 | 2.8 | 2-11 | 1.7 | 90.9 | 30-232 | 0.8 | El. Ir, Ov,Bl | Lb, By, Bk, Db, Lb | T |
| *T. fuscobalteata* | 1.8 | 1.5-1.8 | 0.3 | 2.6 | 1-5 | 2.0 | 145 | 80-250 | 74.2 | Ir | Bk, Db | T |
| Karangranjang | | | | | | | | | | | | |
| *T. laeviceps* | 2.3 | 0.9-4.0 | 1.2 | 3.6 | 0.7-10.1 | 2.7 | 136.4 | 50-350 | 108.7 | El, Ir, Ro,BI | Lb, By,Bk, Db, Lb | H, T |
| *T. fuscobalteata* | 1.6 | 1.3-2.1 | 0.5 | 1.7 | 1.0-3.0 | 1.2 | 140 | 70-300 | 65.6 | Ro,BI | Bk, Db | H, T |
| *L. terminata* | 2.3 | 1.0-3.3 | 0.7 | 15.5 | 5.0-45 | 13.4 | 312 | 50-900 | 86.9 | El,Ov, CI, Ct, | Db, Lb, BW, By | T |

Notes: The number of colonies measured were Taman Jaya and Ujung Jaya (9 colonies), Legon Pakis and Kalejetan (20 colonies), Cigenter and Nyawaan (4 colonies), Cidaon (41 colonies), Peucang Island (26 colonies), Panaitan Island (25 colonies), and Karangranjang (32 colonies). M: Mean; R: Range; SD: Standard deviation; Shape: El: ellipse, Ir: irregular, Ov: oval Cl: wide funnel, Ro: round Bl: short round tube; Bp: round pipe, Ct: trumpet, Color: Bk: black, Db: dark brown, Lb: light brown, BW: black and white, By: black and yellow), Nest location: T: tree, K: coral, H: house wall, BS: ant nest, Bm: bamboo

**Table 4.** Nest entrance and brood cells characteristic of stingless bees in Ujung Kulon National Park, Banten, Indonesia

| No entrance | *T. laeviceps* (n=67 colonies) | *T. fuscobalteata* (n=19 colonies) | *L. terminata* (n=72 colonies) | *H. itama* (n=5 colonies) |
|---|---|---|---|---|
| Nest characteristics | | | | |
| Opening shape | Ellipse, irregular, round, oval | Round, round pipe, irregular | Oval, wide funnel, round-ringed, ellipse | Oval, wide funnel |
| Horizontal diameter (cm) | 2.3 ± 0.5 | 1.4 ± 0.3 | 1.6 ± 0.4 | 2.4 ± 0.5 |
| Vertical diameter (cm) | 2.3 ± 0.9 | 1.6 ± 0.1 | 2.0 ± 0.2 | 3.2 ± 1.6 |
| Funnel length (cm) | 4.0 ± 1.8 | 3.0 ± 0.9 | 11.3 ± 3.3 | 6.5 ± 3.5 |
| Ornamentation | Enlargement of propolis with droplets, thick and hard structure | Enlarges the spread of propolis with a hard structure | Droplet, sticky of propolis | Droplet, sticky of propolis |
| Color | Black, blackish brown, yellowish | Blackish brown, greyish brown, light to dark brown | Black and white, light and dark brown, yellowish | Light to dark brown |
| Funnel texture | Hard and soft | Hard | Soft | Soft |
| Length of pollen pot area (cm) | 9-15 | Na | 14 | Na |
| Pollen pots diameter (cm) | 0.6-0.8 | Na | 0.5-1.0 | Na |
| Honey pots length (cm) | 18 | Na | 12 | Na |
| Honey pots diameter (cm) | 1.5 | Na | 1.8 | Na |
| Total length nest (cm) | 27-34 | Na | 40 | Na |
| Brood cells | | | | |
| Arrangement | Cluster, semi-cluster | Na | Comb brood cells with a regular layer | Na |
| Shape | Sub-spiral | Na | Elongated | Na |
| Length of brood cell area (cm) | 15 | Na | 28 | Na |
| Cell height (cm) | 0.3 | Na | 0.6 | Na |
| Cell width (cm) | 0.3 | Na | 1.2 | Na |
| Color | Light brown, dark brown | Na | Light brown, dark brown | Na |
| Pillar (connectives) | Columnar | Na | Lamellate | Na |

Notes: The number of brood cells measured were *T. laeviceps* (2 colonies) and *L. terminata* (1 colony). Na: no available data

**Discussion**

This study was the first comprehensive research of stingless bee species in wide areas of UKNP including in satellite islands, i.e., Peucang and Panaitan islands. In total, 163 colonies of stingless bees were observed (Table 2), belonging to four species, namely *T. fuscobalteata, T. laeviceps, L. terminata*, and *H. itama* (Figure 2). The description of these stingless bee species referred to morphological observations (Sakagami 1978; Sakagami et al. 1989; Sakagami et al. 1990). The highest number colony found was *L. terminata* (72 colonies, 44%), and the lowest was *H. itama* (5 colonies, 3%) (Table 1). Nests of stingless bees were commonly found in tree and bamboo cavities, coral crevices, and former ant nests (Quezada-Euán 2018a). The current study found 21 species of nesting trees, and *Ficus* (*F. benjamina*) was as dominant tree for nesting sites. The characteristics of this tree were many cavities in the trunk that were suitable for the nesting site. We also found that one tree of *F. benjamina* was housed by several stingless bee colonies. In addition, a cavity as a nesting site could protect the colony from predators and regulate nest temperature. In *T. fuscobalteata*, the nesting sites were found in bamboo and tree cavities, coral crevices, and ant nests. A previous report on the nesting habitat of 145 species of stingless bees in the ground (11.7%), cavities in trees (65.5%), in active termite nests (9%), in active ant nests (2.1%) and exposed or partly exposed (11,7%) (Grüter 2020). Species of the genera *Tetragonula, Tetragonisca, Paratrigona*, and *Pertamona* build nests in solid substrates or tree trunks (Roubik 2006; Jesajas et al. 2023). The characteristics of the nest entrance of this species in UKNP were a short funnel compared to three other species. We found that *T. laeviceps* nests were more likely to live together in one tree with *L. terminata* at a slightly greater distance and opposite position. In *T. fuscobalteta*, we found more nest colonies together with *T. laeviceps* than other species. The nest of *H. itama* tended to be high and far from other species. This could be due to the characteristics of the bee, which is aggressive towards other types of bees. Aggressive stingless bee nests were found individually on certain tree trunks, while non-aggressive bee colonies were generally close to colonies of other species (Roubik 2006). In *T. laeviceps* and *T. fuscobalteata*, we found that they have aggressive colony defense characteristics against human disturbance by attacking directly and guarding behavior around the nest. Colony-level defense is a selective defense method greater than the rare stingless bee predation of individual worker bees when foraging (Shackleton et al. 2019). *Trigona* and *Patramona helleri* worker bees are very aggressive in defending their nest (Shackleton et al. 2015). Our study showed aggressive and defensive behavior in stingless bees in UKNP, such as in *T. laeviceps* and *T. fuscobalteata*. These species attacked humans who stood close to the nest entrance by attacking the human head, hair, ears, face, and other parts of the body. Defensive adaptations allow bees to perform suicidal self-defense through biting as an example of self-sacrificial altruism in protecting the nesting colony (Shackleton et al. 2015).

The nest locations of stingless bees in the UKNP forest were commonly found in coastal areas. We supposed that stingless bees need water for the colony and related to thermoregulation and nest temperature. The nest of stingless bees was affected by environmental temperature. For example, *Melipona beecheii* and *Melipona fuliginosa* maintain the nest temperature range from 23-30°C in ambient temperature 18.2-36°C (Moo-Valle et al. 2000), and *Melipona subnitida* remained in the 27-33°C in ambient temperature 22.9-34.6°C (Dantas 2016). As a social bee, stingless bees need to maintain the nest temperature for colony development (Nacko et al. 2023). The thermoregulation ability of stingless bees is partly due to the thermal insulation and endothermic characteristics (Carvalho 2009). The nest entrance of stingless bees varies greatly in opening diameter, funnel length, and color. The variation of nest entrance properties may be influenced by the nest age, predation, bee genetics, and the microenvironment, such as rainfall and sunlight (Grüter 2020; Roubik 2020). In *L. terminata*, we found 3-5 branches from one entrance funnel. The branched entrance funnel indicated the old nest. The nest entrance of stingless bees varied in shape, such as trumpet-like, wide funnel, short funnel, and rounded. In the peninsula area (Karangranjang and Cidaon), the nest funnel length of stingless bees was longer (average ranging of 5-45 cm) than in Peucang Island (9.09 cm on average). The diameter of the nest entrance of *T. laeviceps* in Panaitan Island is also smaller (1.57±0.99 cm) compared to peninsula areas (2.3±0.5) and Peucang island (average 2.39 cm). The size of the nest entrance of social insects is an important factor in the colony-level trade-off between defense and efficiency in foraging (Couvillon et al. 2008).

The difference in funnel length may related to the availability of resins and natural enemies of stingless bees in both areas. In some nest entrances of *L. terminata*, the funnel is covered by a sticky and fresh propolis with varied colors, such as black, yellow, and light brown. At the same time, the nest entrance of *H. itama* was a light brown color and was oval in funnel opening with a fairly large nest entrance. The resin on the nest entrance was used to protect the nest from predators and prevent rain (Drescher et al. 2014). The color variation of the nest entrance, i.e., yellow and dark brown, is related to resin sources at each sampling location. Stingless bees have the ability to select nesting locations and mutualism with plants (Roubik 2023). The resin was taken from plants around the nest that was used by stingless bees to build nests and protect the colony from microbes and natural enemies (Shanahan and Spivak 2021). Predators of stingless bees included arachnids (*Menemerus bivittatus, Crossopriza lyoni, Pholcus phalangioides*) (Gopinatha and Basavarajappa 2022), cockroaches (Blattidae), hysterid beetles (*Platysoma leconti*), nitidulid beetles (*Carpophilus* sp.), and ants (*Pheidole* sp.) (Wicaksono et al. 2020). Natural enemies of stingless bees include salticid spiders and lizards such as *Tropidurus hispidus* in the Neotropics and *Hemidactylus mabouia* worldwide and their macropredators such as pangolins, monkeys, civets (Roubik 2023). Stingless bees adapt guarding behavior at nest entrances (Shackleton et al.

2019) and the existence of variations in the shape of the nest entrance, which is useful for protection from natural enemies (Pangestika et al. 2020; Sayusti et al. 2021). By bees, the entrance also helps worker bees recognize their nest after foraging for foods (nectar and pollen) and resin. We found that some nests of stingless bees had a bright and striking yellow color. In particular stingless bees, such as in *Partamona helleri*, the outer nest entrance is larger (about 40x) than the inner entrance, which is related to the effectiveness of worker bee movement (Couvillon et al. 2008). Nest entrance variation is related to polyphenism, which occurs when two or more phenotypic bees originate from the same genotype. Polyphenism is influenced by environmental conditions that impact phenotype preferences in neurochemical and hormonal pathways related to nest-building behavior (Simpson et al. 2011).

In general, the structure of internal of stingless bee nests consists of a nest entrance, an inside entrance tunnel, brood cells, storage pots (honey and pollen pots), and layers of cerumen (Roubik 2020). The internal nest structure of *T. fuscobalteata* was hard texture with a cerumen and mud mixture and dark brown and black. In conditions where the wax concentration is higher than the resin, the texture of the nest becomes harder, plus the presence of cerumen and mud mixtures that form batumen (Roubik 2020; Roubik 2023). Based on observations of the structure of brood cells in two species of *T. laeviceps* nests, cells were arranged in clusters and semi-cluster. The shape of the *T. laeviceps* brood cell is sub-spiral with a diameter and height of 0.30 ± 0.03 cm and 0.28 ± 0.04 cm, respectively, and a length of brood cell area of 15 cm with light- and dark brown colors. Spaces between brood area, batumen, and storage pots are occupied with a columnar-pillar system (Figure 4). In observations of one *L. terminata* nest, we found the structure of brood cells, cells arranged in a comb with regular layers. Lamellate pillars surround the nest without sheeted involucrum. There is a tendency for the nest architecture to be round with food storage pots and brood cells, including pillar shapes (Roubik 2020). The diameter and height are 0.58 ± 0.03 cm and 1.2 ± 0.04 cm, respectively, and the length of the brood cell area of 28 cm in light- and dark-brown colors. Pollen cells in the *T. laeviceps* species obtained a pollen pot area length of 9-15 cm. Pollen pots diameter 0.6-0.8 cm, honey pots length 18 cm, and honey pot diameter 1.52 cm. In the pollen cells of the *L. terminata* species, the length of the pollen pot area was 14 cm. Pollen pots had a diameter of 0.5-1 cm, a honey pot length of 12 cm, and a honey pot diameter of 1.76 cm (Table 4).

This study concludes that the availability of suitable plants for nesting, nectar and pollen sources, water availability, and environmental factors, such as temperature, humidity, wind speed, and altitude, greatly influence the distribution of colonies found in each study site. Lowland forest vegetation in the UKNP is an ideal area for habitat of stingless bees. We found that stingless bees choose varied nesting sites, such as house cavities, tree cavities, unused dry ant nests, or bamboo, and are safe from rainwater, wind, or natural enemies. The shape of the nest entrance varies depending on the habitat conditions of the stingless bees. In this study, the colony of *T. laeviceps* was distributed across all habitat types. It showed that *T. laeviceps* colonies are well adapted to the environment. This species has been reported to visit various species of agricultural crops, such as fruit plants (Alpionita et al. 2021) and vegetable plants (Mubin et al. 2022). The small body size allows *T. laeviceps* to build nests in narrow spaces, in rock crevices, in soil cavities, in rock cavities, and in tree branches or trunks (Engel et al. 2020). We also found that *L. terminata was* found in many forest zones far from disturbance areas. In all areas inhabited by humans, we did not find a colony of *L. terminata.* The use of agricultural chemicals (Hernández et al. 2022), smoke activity from residential homes, and the lack of food resources may caused *L. terminata* to migrate to the forest. Conservation in the UKNP habitats area is very important for the conservation and sustainability of native stingless bees.

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