




Biology of bamboo nesting stingless bees of southwest China

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Abstract – More than 550 stingless bee species have been found in the tropical and subtropical areas across the world. Different stingless bee species inhabit various types of nests, such as tree hollows, walls, lime stone crevices, or even co-nest with other live creatures such as ants and termites underground. These cavity-nesting habits make it difficult to estimate the colony size of the stingless bees. Stingless bee species native to southwest China are sympatric with many species of bamboo, and the straight shape of bamboo provides an easier method to estimate the size of the colony and the volume preference of stingless bee in selecting trap nests. Here, we reported bamboo nest characteristics measurement with its height, diameter, entrance size, a calculation its inner volume capacity to determine the stingless bee nesting preference in bamboo. The results showed that two stingless bee species, *Lepidotrigona flavibasis* and *Tetragonula gressitti*, all nest in the bamboo; the size of entrance that was preferred by *T. gressitti* was around $10.71 \pm 2.38 \text{ cm}^2$, compared with the preference by *L. flavibasis* for small nest entrance area around $1.33 \pm 0.25 \text{ cm}^2$. Accordingly, the volume of the internode of the bamboo was $2272.37 \pm 126.7 \text{ mL}$ compared to $4493.35 \pm 466.91 \text{ mL}$ chosen by *L. flavibasis* and *T. gressitti*, respectively. Interestingly, both stingless bee species preferred to living bamboo rather than the dead bamboo as a nesting site. This study indicates that cheap and easily accessible bamboo could be used as trap nests for stingless bees, and the preference volumes of different species suggest what the various colony sizes of stingless bee swarms might be. Selecting a proper species-specific characteristics of bamboo internode as trap nest benefits us in researching, conserving, and keeping for stingless bees.

Nest volume / Trap nests / Stingless bee conservation / Meliponiculture

1. INTRODUCTION

Meliponini is the largest group of social bees that not only interact with plants via providing pollination services but also rely on plants for nesting (Michener 2013). There are approximately 550 stingless bee species distributed in subtropical and tropical areas around the world with approximately 100 species yet to be described (Grüter 2020; Michener 2013). These

stingless bee species are playing a crucial role as pollinators that benefit 215 different families and 1434 genera of flowering plants around the world (Bueno et al. 2021). Up to 90 crop species benefit from the pollination of stingless bees (Heard 1999). In China, some medicinal herbs, including *Amomum villosum*, benefit from stingless bee pollination to increase seed set (Wang et al. 1984; Qu et al. 2022); meanwhile, almost all these stingless bee species are cavity-nesting, either nesting underground, in stone crevices, walls, hollowed plants, or other man-made containers (Roubik 2006). Some species, such as *Lepidotrigona flavibasis*, *Tetragonula laeviceps*, have been driven by either forest fragmentation or

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innately adapt to nest in multiple cavities conditions such as nesting in brick walls and hollowed tree cavities (Roubik 2006; Li et al. 2021). *T. bengalensis* was found to prefer nesting in wood and sometimes in bamboo in India (Rahman et al. 2015). The diversity of species and their unique behaviors provide an interesting model of study in social insects.

There have been seven stingless bee species found in China, mainly in Yunnan Province (Wu 2000). With improvements in surveys, 11 stingless bee species have been confirmed in Yunnan, Guangxi, Hainan, Taiwan, and Tibet Provinces of China (Li et al. 2021; Qu et al. 2022). These species belong to four different genera that mainly prefer nesting in hollowed plants, walls of old buildings, stone crevices, and termite mounds underground (Li et al. 2021). *Tetragollina collina* is an exception, as it nests in active termite mounds. All other species can be attracted to man-made wooded boxes for keeping (Qu et al. 2022). The traditional stingless bee beekeeping practice originated from the trapping of *Apis cerana* swarms with wooden logs, and in the process occasionally getting stingless bee swarms. Local people moved the trapped stingless bee colonies next to their home for keeping and harvesting its honey only once or twice per year. In most cases, people need to either chop down the tree trunk or dig out the nests from underground, and these methods of harvesting honey from stingless bee colonies not only cause damage to the nesting plants, but also to bee colonies and the local environment, with a very low payoff of stingless bee honey.

In Brazil, it is illegal to harvest wild bee colonies via cutting trees or damaging their original colony in the field (Oliveira et al. 2012). The noninvasive trap nesting method became a suitable way to attract stingless bee colonies from nature. Oliveira et al. (2012) reported the successful trapping 61 swarms of stingless bees. The density of swarms, the seasons, the number of potential cavities, and the character of the man-made traps all affect the success rate of attracting stingless bee swarms with trap nests.

The lack of nesting biology knowledge and the inability to design trap nests based on species-

specific preferences often result in failure to obtain stingless bee swarms from the field. Unlike honey bee swarms, the old queen leaves the mother colony to look for a new nesting site in only few hours to a few days (Seeley 1977). In stingless bee swarms, the scouts first locate a new nesting site and transport wax and resin to store honey and pollen in, before the virgin queen is ready to move into the new nest. This procedure can take up to a few weeks or even several months (Grüter 2020). Any interruption or harvesting of the trap nest before the queen gets into the new colony results in failure. The characteristics of trap nests, such as volume, entrance size, entrance direction, and even the height of the trap nest, have all been well studied in the honey bee *Apis mellifera* by Seeley and Morse (1978).

Nest characteristics such as volume size, diameter of the hollowed plants, and the size of the entrance were reported important for trapping stingless bee swarms. Previous studies have proved stingless bees would prefer 3 L to the smaller size for trapping species (Oliveira et al. 2012). Stingless bees *T. fuscobalteata* (26 colonies) and *T. sapiens* (7 colonies) were reported nesting in bamboo stems with a volume range from 0.7 to 3 L in the Philippines (Starr and Sakagami 1987). Diameter of the hollowed plants would be a limiting variable for nesting, since there were no cavity or small cavities for bees to choose (Hubbell and Johnson 1977; Eltz et al. 2003; Silva et al. 2013; Silva et al., 2014; Kapitanhitu et al. 2018). Although most of giant bamboo may offer several hollowed internodes for bees to nest, the preferred diameter size still needs to be determined for different stingless bee species. Inoue et al. (1984) used a bamboo internode with an entrance of 1.2 cm in diameter, as a trap nest to study the colony multiplication of the stingless bee of *T. laeviceps* (Inoue et al. 1984).

However, these data did not clear up the nest size preferences of different species of stingless bees, in which populations may vary from a few hundred to tens of thousands and body sizes ranging from 2 mm up to 12 mm (Grüter 2020). The entrance shape and size were an overlooked characteristic in previous studies, since there are huge differences in entrance types for different

stingless bee species (Bänziger et al. 2011; Shackleton et al. 2019).

Bamboo distribution varies from temperate to tropical areas around the world, which is coincidentally sympatric with the global stingless bee distribution area (Chen et al. 2019). The giant bamboo internode could provide a suitable and natural trap nest after some bamboo borers or rodents burrowed. The regular shape of the bamboo internode provides us a natural trap nesting studying case in stingless bees to analyze the species-specific preference characteristics of trap nests.

Here, a preliminary study placed 13 bamboo trap nests placed in Xishuangbanna Tropical Botanical Garden, successfully attracting two swarms of stingless bee, *L. terminata* and *T. laeviceps*. The bamboo volumes were 2.9 and 1.96 L, respectively (Wang et al. 2022). Even with some initial success in trapping stingless bee colonies with bamboo internodes, the limited data size could not show the preferences of stingless bees when selecting trap nests. In the present study, we hypothesize that different stingless bees show species specific preferences to the characteristics of trap nests, such as volume, nest entrance area, and diameter of the bamboo. In the present study, we accessed a meliponary of Yunnan, China. All stingless bees nesting in bamboo internodes were photographed and measured in a noninvasive way to determine the trap nest characteristics and determine species specific preferences.

2. MATERIALS AND METHODS

2.1. The measurements of bamboo nests of stingless bees

All colonies (142 in total) of stingless bees in the bamboo nests were naturally occurring in the mountain areas of Lincang and Xishuangbanna, Yunnan, China, where many bamboos exist in nature. These colonies were collected and moved to a meliponary in Jinuo Mountain, Xishuangbanna Yunnan, China. We identified the species of stingless bees nesting in bamboo and the

species of bamboo via collecting samples and identifying with their morphological characteristics in the laboratory (Li et al. 2021). We took pictures of the bamboo nests with a ruler (50 cm) as references attached to each nest. The height, diameter, and wall thickness were all measured to parameterize the stingless bee nests with the distance measure function of Image J (<https://fiji.sc/>). The volume size was calculated in the formula below:

$$\text{vol} = \pi \times (d/2)^2 \times h.$$

Vol means the volume capacity, d means the inner diameter of the bamboo, and h means the height of the bamboo internode.

We analyzed the area of the nest entrance by selecting the nest entrance with region of interest of the picture area by Image J software (<https://fiji.sc/>). The ruler was used for set scale for each picture.

2.2. Statistics analysis

We measured 142 bamboo nests of stingless bees, containing 19 colonies of *T. gressitti*, the other 123 colonies of *L. flavibasis*. A Wilcoxon rank sum test (Mann–Whitney U test) was used to determine the preference characteristics of the host bamboo, such as the entrance size, height, inner diameter of the internodes, and the volume, as chosen by *L. flavibasis* and *T. gressitti*.

The cross-table Chi-square test was used to test whether stingless bees prefer to choose an living or dead bamboo as a nest site. All statistics were calculated with R studio (version 1.3.1073).

3. RESULTS

3.1. The measurements of bamboo nests of stingless bees

The diameter of bamboo internodes chosen by *L. flavibasis* range from 8.21 to 18.44 cm, with an average of 11.85 ± 0.19 cm (Figure 1A) and ranged from 10.58 to 17.53 in those chosen by

T. gressitti, with an average of 13.75 ± 0.48 cm (Figure 1A). The inner diameter of each internode was much larger in those chosen by the *T. gressitti* ($W = 598$, $p < 0.001$, Figure 2A).

The height of bamboo interval-nodes chosen by *L. flavibasis* ranged from 8.25 to 47.01 cm, with an average of 19.15 ± 0.68 cm (Figure 1B) and ranged from 12.04 to 63.82 cm in those chosen by *T. gressitti*, with an average of 29.39 ± 2.7 cm (Figure 1B). The height of internode was much higher in those chosen by *T. gressitti* ($W = 506$, $p < 0.001$, Figure 2B).

Accordingly, the volume of each internode of bamboo was 2272.37 ± 126.7 mL compared to 4493.35 ± 466.91 mL chose by *L. flavibasis* and

T. gressitti, respectively (Figure 1C). The preference capacity was approximately twice that chosen by *T. gressitti* than by *L. flavibasis* ($W = 424$, $p < 0.001$, Figure 2C).

The preexisting entrance(s) on the bamboo were always utilized by stingless bees when scouts were entering. The preference size of the entrance was 1.33 ± 0.25 cm² and 10.71 ± 2.38 cm² for *L. flavibasis* and *T. gressitti*, respectively (Figure 1D). In most cases, *T. gressitti* chose the bigger entrance up to 30 cm² made by some rodents and occasionally, they were also found in smaller entrance with less than 1 cm² caused by Lepidoptera. On average, *T. gressitti* chose a much bigger entrance than *L. flavibasis* ($W = 470$, $p < 0.001$, Figure 2D).

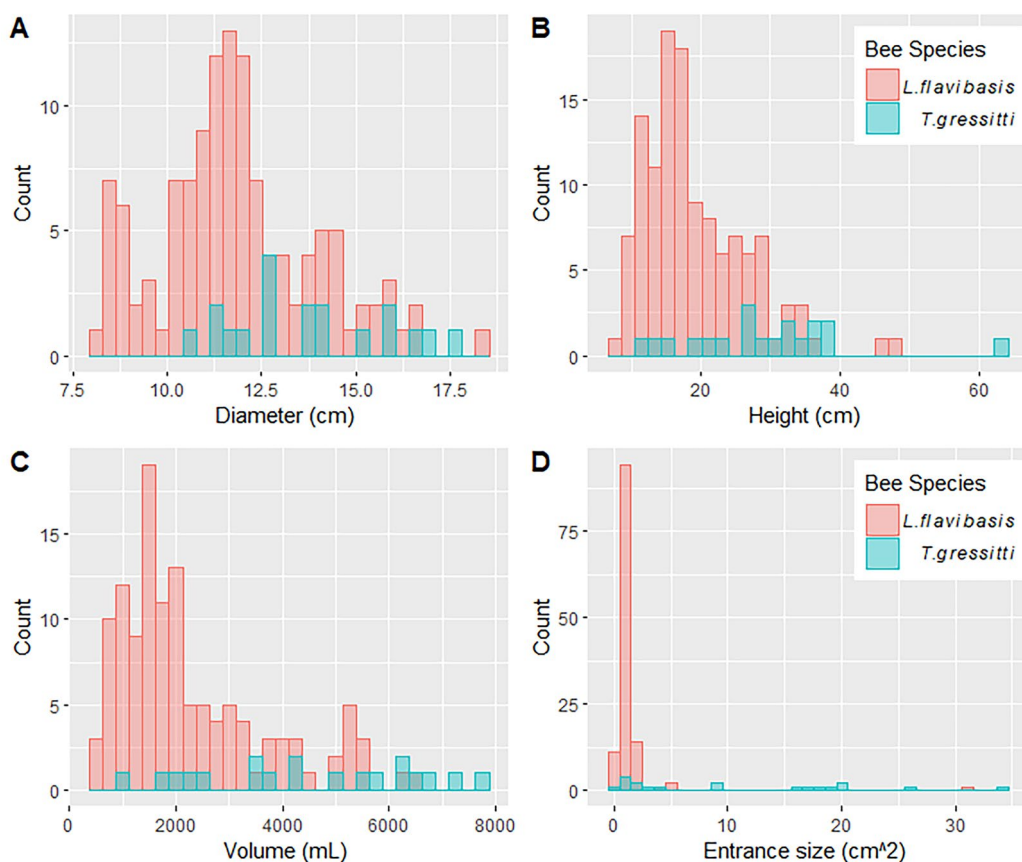


Figure 1. Histogram of characteristics of stingless bee bamboo internode nests. Here we showed the distribution of diameter (A), height (B), volume of bamboo nest (C), and the entrance size (D) of *L. flavibasis* ($N = 123$, red) and *T. gressitti* ($N = 19$, blue).

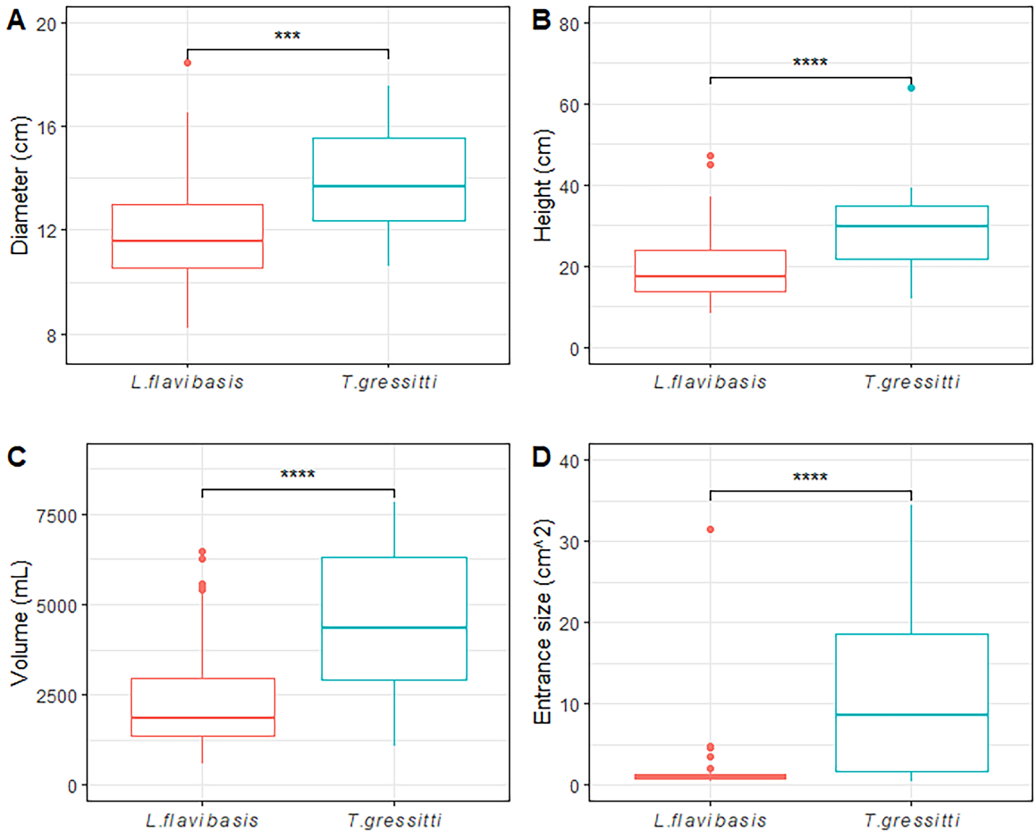


Figure 2. Preference of bamboo internode nests chosen by stingless bees (*L. flavibasis* (red box, N = 123), *T. gressitti* (blue box, N = 19)). *** and **** indicated $P < 0.001$ and $P < 0.0001$.

Furthermore, the diameter of the bamboo was measured and ranged from 10.1 to 22 cm, with an average of 14.2 ± 0.21 for *L. flavibasis*; while *T. gressitti* chose bamboo diameters ranging from 12.94 to 19.95 cm with an average of 16.23 ± 0.5 cm. The outer diameter was larger in bamboo chosen by *T. gressitti* than *L. flavibasis* ($W = 605$, $p < 0.001$).

Stingless bees prefer living bamboo to dead bamboo as nesting sites. Both *L. flavibasis* and *T. gressitti* choose 86.99% and 89.47% living bamboo as nests, respectively. Only 16 out of 123 colonies of *L. flavibasis* and 2 out of 19 colonies of *T. gressitti* nested in dead bamboo (cross-table Chi-square test: $\chi^2 = 37.30$, $df = 1$, $P < 0.001$ in *L. flavibasis*; $\chi^2 = 5.27$, $df = 1$, $P < 0.02$ in *T. gressitti*, Figure 3).

4. DISCUSSION

In the present study, we accessed 142 colonies of stingless bees nesting in bamboo internode. The curtailed bamboo internodes gave us the chance to measure its entrance size and volume capacity preferences of different stingless bee species. In this study, we observed 86.62% (123 out of 142 colonies) of *L. flavibasis* and 13.38% of *T. gressitti* colonies nesting in the bamboo internodes of two bamboo species, *Dendrocalamus sinicus* and *D. giganteus*. Nest entrance area preference was as small as 2 cm² for *L. flavibasis*, while the chosen range was larger for *T. gressitti*. Accordingly, *T. gressitti* prefer a 4 L bamboo capacity, which is about twice that of *L. flavibasis*. These results indicate that different species

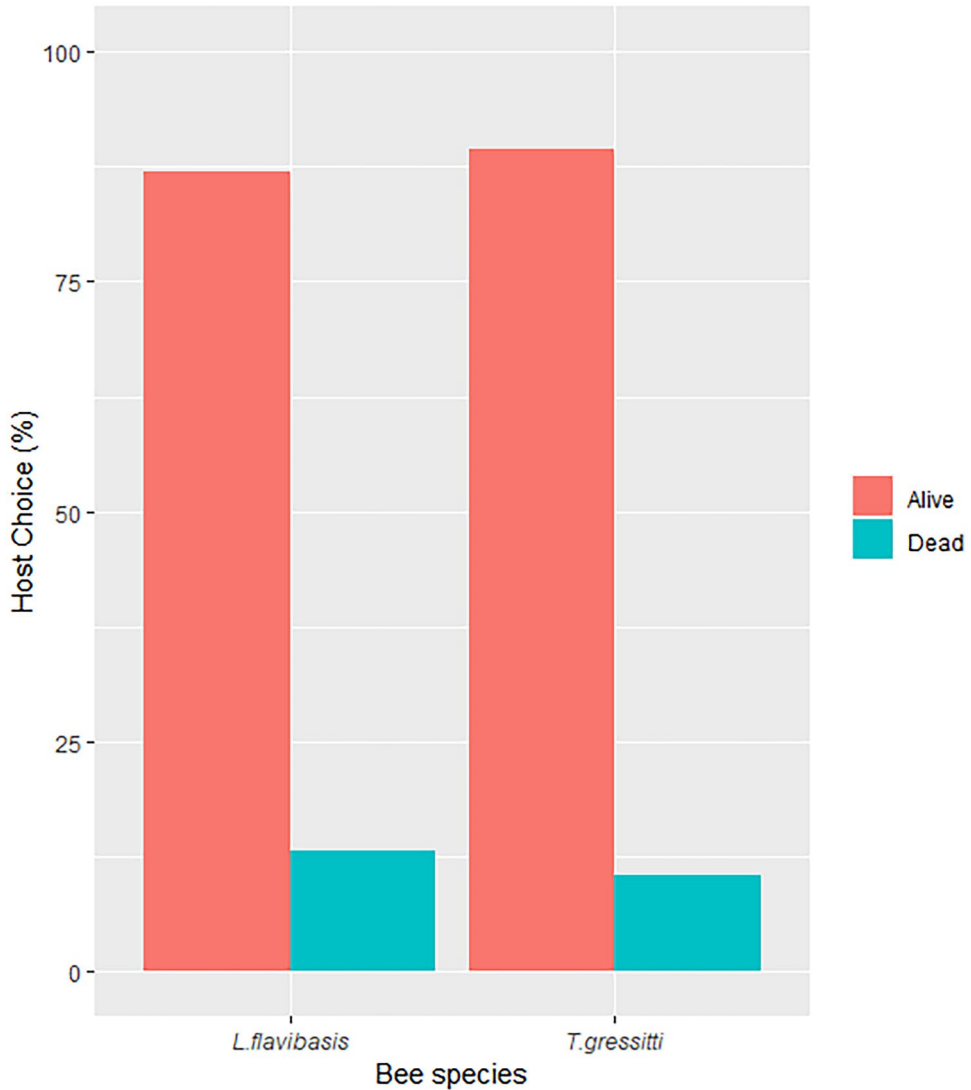


Figure 3. Host choice of stingless bees (*L. flavibasis*, N=123, *T. gressitti*, N=19) in alive vs dead bamboo.

of stingless bees have different nesting preferences, such as volume and nest entrance area. These different nesting preferences may benefit for less nest competition among sympatric stingless bee species.

Bamboo, especially with giant bamboo internodes, provides a suitable potential choice for sympatric stingless bees who prefer living in tree hollows. In the present study, we found that the common distribution of bamboo species in Southern

Yunnan works as natural trap nests for sympatric stingless bee species. This bamboo–stingless bee nesting interaction has been observed and utilized in several countries of China-Indo-Australian tropical areas, such as Australia, India, Philippines, Malaysia, Indonesia, and China (Inoue et al. 1984; Starr and Sakagami 1987; Kumar et al. 2012; Salim et al. 2012; Singh 2013; Suriawanto et al. 2017; Kapitanhita et al. 2018; Abduh et al. 2020; Wang et al. 2022).

Many nest characteristics can be evaluated by scouts of swarming social bees, such as the diameter of the trap nest, size of entrance, volume, and even the height of the cavities. The honey bee has a larger body size as well as population density than most stingless bees, showing a preference for trap nests with a larger entrance (12.5 cm^2) and overall volume (20–100 L with an average of 40 L). Interestingly, the volume size was irrelevant with swarm populations (Seeley 1977; Seeley and Morse 1978). Concerning the similarities and differences between swarms of stingless bee and honey bee, the scouts and a group of stingless bees would evaluate a potential nest first, and move wax and pollen to start the nest activity before the virgin queens emerged and enter the new nests. The scouts of stingless bees also evaluate the size of the entrance and the volume of trap nests. In the present study, we observed that *T. gressitti* had a preference for nests with an entrance area of $10.71 \pm 2.38 \text{ cm}^2$ which contrasts with the smaller entrances observed in other stingless bee species, for example $1.33 \pm 0.25 \text{ cm}^2$ for *L. flavibasis* (this study), 1.2 cm^2 in *T. laeviceps* (Inoue et al. 1984), and 0.4–1.1 cm in width for other species (Kapitanhиту et al. 2018).

Oliveira et al. (2012) reported that stingless bees prefer the 3 L of trap nest in volume compared with 1 and 2 L. This finding was consistent with our results, in which we observed that *L. flavibasis* chose 2.27 L. Nevertheless, *T. gressitti* preferred volumes about twice as large (4.47 L) as *L. flavibasis*. These findings indicate that different species search for different cavity capacities. Inoue et al. (1984) reported that *T. laeviceps* nested in small volume of bamboo nest (0.7 L) in Indonesia, while in China, we found the same species was trapped with a bamboo internode of 1.96 L (Wang et al. 2022). Starr and Sakagami (1987) reported that *T. fuscobalteata* and *T. sapiens* nest in bamboo ranging from 0.7 to 3 L, with an average of 2 L.

Different nesting volume and sizes of entrance preferences between species of *T. gressitti* and *L. flavibasis* may benefit both sympatric species by avoiding nest competition. Nest usurpation occurs often in both intraspecific and interspecific species, especially during swarming season

(Gloag et al. 2008; Cunningham et al. 2014). Stingless bees often fight to the death to take over a potential nest, even if there is a living colony still nesting inside. A preference bias would reduce the possibility of fighting. In the present study, we still found one colony of *L. flavibasis* took over a *T. gressitti* nest, with a large entrance. That could be because the large entrance (31.489 cm^2) was first sealed by *T. gressitti* and was later usurped by *L. flavibasis* during its swarming by utilizing its smaller modified entrance (1.66 cm^2).

L. flavibasis showed a species-specific preference to diameter, height, volume, and entrance size while *T. gressitti* showed a homogeneous preference to these parameters. It may difficult for us to conclude that the stingless bees are selecting a potential nest by one of the parameters over others. It may still be needed more strict comparative data on stingless bee selecting on each parameter with other parameters been equalized in future as trap nests setting in previous works (Oliveira et al. 2012).

Six times more colonies of *L. flavibasis* than *T. gressitti* were observed in the bamboo trap nests. All these natural nests of stingless bees in bamboo internodes have been collected by local farmers regardless with discrimination of species. In the present study, 123 *L. flavibasis* colonies versus 19 *T. gressitti* colonies were harvested in bamboo nests. This suggests that *L. flavibasis* was the most abundance stingless bee species in the study site as reported in previous study (Li et al. 2021), and the *T. gressitti* was a new record in this area and prefer habitat in higher altitude mountains (up to 1100 m, Pan et al. 2021). The projected waxy entrance of *L. flavibasis* also makes their wild colonies easier to be found than the concave entrance of *T. gressitti* colonies. Several other reasons will affect the number of stingless bee colonies to be found in nature, such as the densities of stingless bee species, the height of the in vitro nests, and their entrance directions, and these still need further study in the future.

The bamboo surface color and the entrance position showed that the bamboo was alive when newly colonized. Up to 88% and 89% of bee

colonies tended to nest in living bamboo. This was consistent with a previous study that stingless bees prefer nesting in living than dead trees in Malaysia (91.5% vs 8.5%, Eltz et al. 2003; Macedo et al. 2020).

4.1. Advantages of stingless bee bamboo trap nests

Bamboo nests are easily accessible for bees since stingless bees are distributed sympatrically with giant bamboo species. The bamboo nodes could act as an easy and economic trap nest prepared for stingless bees, just as coconut shells are also used for keeping stingless bees in India and the Philippines (Udayakumar et al. 2021). A giant bamboo could produce dozens, or up to 50 suitable nodes as potential trap nests. An additional advantage is that bamboos naturally regrow each year. Therefore, using bamboo trap nests could be an important alternative to collecting stingless bee nests from other plant species.

The relatively small entrances in bamboo internode nests likely take less energy from stingless bees to seal with propolis, which could help to isolate from the light and invaders. Like most cavity-nesting bee species, their brood and young adults are always kept in dark and safe hives. The number of entrances has been considered a negative effect for trap nests designed for stingless bees. And the hardened wall of the bamboo nests also repels most invaders, such as ants, moths, and beetles which invade into the hive. Only few stingless bee colonies had been invaded by predators and parasites such as cockroaches, beetles, and ants in bamboo nests (Pangestika et al. 2018).

There is good reusability of bamboo trap nests, the bamboo can grow up to 40 m tall, with several nodes, and the separate plate between nodes can also be tilted or burrowed in by bamboo borer larvae. Stingless bees can make great use of this extensibility by either sealing or opening the hole (through the separate plate in bamboo) to expand the cavity. Two bamboo trap nests with large entrance sizes

were first used by *T. gressitti* and were later taken over by *L. terminata* and *L. flavibasis*. This finding indicates that the bamboo trap nest has great reusability. The bamboo with a larger entrance of up to 30 cm² may be preferred by *T. gressitti*; after they modified the nest entrance area, the hive soon became a candidate trap nest for other stingless species who prefer smaller entrance sizes.

Taken together, bamboo nests are easily accessible and manageable to be used in modern meliponiculture. The bamboo node can be set as a trap nest and then can be easily transferred into artificial boxes for beekeeping. Based on these observations, bamboo trap nests can play crucial role in stingless bee research, conservation, and meliponiculture in the future.

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AUTHOR CONTRIBUTIONS

YFQ and ZWW conceived this research and designed experiments; YFQ, XXW, and YXW performed experiments and data analysis; and YFQ and ZWW wrote the paper. All authors read and approved the final manuscript.

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AVAILABILITY OF DATA

Data and original figures will be available from corresponding author on reasonable request.

CODE AVAILABILITY

Custom code for data analysis in R.

DECLARATIONS

Ethics approval This is an observational study that no ethical approval is required.

Consent to participate Not applicable.

Consent for publish Not applicable.

Competing interests The authors declare no competing interests.

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