Original Article

ADAPTIVE DEFENCE STRATEGIES OF THE STINGLESS BEE, *TETRAGONULA IRIDIPENNIS* SMITH. AGAINST NEST INTRUDERS IN A NEWLY DIVIDED COLONY

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Abstract

A study was conducted to document nest intruders in newly divided colonies of stingless bees. The nature of the damage, the sequence of activities after colony division, and task allocation in the colony were studied. Three insect invaders - solitary resin bees (*Megachile disjuncta*, *M. cephalotes*), ants (*Oecophylla smaragdina* and *Camponotus* sp.) and spiders belonging to the family Salticidae and Lycosidae invaded the colonies during the earlier stages of division. The mean number of resin bees and ant invasions was significantly higher during the first week after division. Spiders invaded the hives and formed webs during the second week after division, resin and honey resources are robbed by resin bees and ants. Nest entrance closure was observed at 4.37±0.74 days after colony division guard bee activity from 6.13±1.24 days and foraging activity from 10.63±1.06 days after division. Observations on the task allocation framework after colony division indicated that 69% of bees were involved in hive entrance repair, 18% in colony architecture development, and 13% in tending to newly emerged bees from brood cells. The bees built a complex nest entrance, guarded activity and demonstrated nest closure behaviour in order to protect the nest against intruders. The results of the study are of prime importance for beekeepers to learn how to watch for hive intruders during colony division and to understand the adaptive defence mechanism to protect colonies.

Keywords: defence, intruders, nest architecture, nest entrance closure

INTRODUCTION

Stingless bees (Meliponini) are an important group of managed pollinators widely employed in the pollination of crops in open fields and protected cultivations (Buchmann, 1983; Sommeijer & de Ruijter, 2000). They are reported to be efficient pollinators of sunflower, strawberry, cherry tomato, cucumber, eggplant and sweet pepper (Slaa et al., 2000; Nicodemo et al., 2013; Del Sarto et al., 2005; Kishan Tej et al., 2017). These social bees build perennial colonies (Slaa, 2006) and store pollen and honey in cerumen pots (Roubik, 2006). Stingless bees commonly use resin and propolis as the involucrum, a nest-building structure and for forming cerumen pots (Schwarz, 1948; Roubik 2006; Rasmussen, 2013). In India, Rasmussen (2013) reported nine species of stingless bees, *Lepidotrigona arcifera, Lisotrigona cacciae, L. mohandasi, Tetragonula aff. laeviceps, T. bengalensis, T. gressitti, T. iridipennis, T. praeterita,* and *T. ruficornis*. Viraktamath and Roy (2022) reported five *Tetragonula* species, *Tetragonula vikrami* Viraktamath, sp. n. (from Karnataka), *T. sumae* Viraktamath, sp. n. (from Tamil Nadu), *T. ashishi* Viraktamath and Jagruti, sp. n. (from Maharashtra), *T. shishirae* Viraktamath sp. n. (from Rajasthan) and *T. shubhami* Viraktamath, sp. n. (from Chhattisgarh). Meliponiaries regularly practice colony division to expand (Mythri et al.,

2018). Under Indian conditions, colony division in stingless bee was performed by collecting mature pupal brood cells with few foragers from the strong colony with some resin, pollen and honey pots in a new hive (Mounika et al., 2019). The successful establishment and development of the divided colonies depend on the acceptance rate of the hive by the foragers, formation of such initial hive architecture as resinous pillars and involucrum, and intrusion by different invaders for the in-hive resources. Arthropod species ants, assassin bugs, black soldier fly, mites, nitidulid beetles, reduviid bugs, resin bees, spiders and wasps were reported to be predators that invade stingless bee colonies (Nisha, 2002, Kiatoko, 2012; Premila et al., 2013; Vijayakumar & Jayaraj, 2013; Devanesan et al., 2017; Pangestika et al., 2018).

The hive entrance is commonly coated with resin during the division process of stingless bees colonies in India, as it encourages faster settlement of foragers inside the new hive and the in-hive bees use the resin as an initial building material of the hive (Amala et al., 2023). The resin coating at is often used as a medium by guard bees to entrap and entangle invading arthropods (Shanahan & Spivak, 2021). The protection of newly divided stingless-bee colonies against natural invaders is of paramount importance for the successful establishment of colonies in the meliponiary. Such natural defence strategies as standing and hovering guards (Karcher & Ratnieks, 2009) and suicidal biting behaviour (Shackleton et al., 2015) were well documented in older perennial colonies of several stingless-bee species. Challenges to the establishment of newly divided stingless-bee colonies are attack by natural enemies, rate of hive acceptance (Bayeta & Hora, 2021) and in-hive food resources (Roubik, 1982). Documentation of hive intruders threatening the establishment of the colony during the earlier stages of colony division must be closely monitored. The authors noticed an invasion of a few natural arthropod enemies and recorded an interesting phenomenon of nest closure behaviour and complex nest entrance in the newly divided stingless-bee colonies. The present study was conducted to document the different invaders in the newly divided stingless-bee colonies, to understand the natural defence mechanism operated in the newly established colony, to evaluate the nature and extent of damage caused by intruders and to determine the tasks of the bees in the newly divided colony.

MATERIAL AND METHODS

Study site

The study was conducted at the experimental farm of the ICAR-National Bureau of Agricultural Insect Resources (NBAIR) Bengaluru, Yelahanka Campus (13.096932N, 77.56759E) which is located in the heart of the rapidly growing capital city of the South Indian state of Karnataka.

Maintenance and division of colonies of stingless bee, *T. iridipennis*

Stingless-bee colonies were maintained in wooden square box hives (17.5 cm x 17.5 cm x 11.5 cm) in the meliponiary located at the study site. Colonies with more than fifty pollen and honey pots with a higher volume of larval and pupal brood cells with relatively higher hive traffic of incoming and outgoing foragers were considered strong. The identified strong colonies were formed through the collection of approximately 25-30 pupal brood cells, a queen cell, ten pollen pots and honey pots and two scoops of resin from the strong colonies and placed in a new wooden square box hive. Fifty foragers were also added to each rectangular hive during the division. Ten replicates of similar colonies were maintained for our observations. A small hole 1.0 cm in diameter was made in the bottom of the newly used wooden square box hive, and a polyethylene transparent tube (1.0 cm in dia.) was inserted to serve as an entry/exit for foragers. Resin was also applied to the outer surface of the polyethylene transparent tube to enable outgoing foragers to navigate back to their nest in the newly divided colony.

Documentation of arthropod invaders in newly divided colonies of *T. iridipennis*

Ten newly divided colonies of stingless bees were selected and established colonies were monitored weekly for attack by invaders. The observations were recorded for a period of twenty-eight days after division from 7.00 am to 6.00 pm, as this is

a crucial period for the initial acceptance of the new hive and colony establishment. The invading arthropods were collected, pinned, preserved and taxonomically identified. The nature of the invaders and the number of attacks per week for a period of four weeks were recorded. The number of nest closure events per month, mode of entrance closure and material used for the closure of the entrance were also recorded. The period of nest closure and time taken for guard bee activity was recorded for every 24-hour interval for a period of one week. The initiation of foraging activity was recorded three days after the division of the colonies. The change in the architecture of the inner hive after the invasion of the enemy was also recorded.

Observations on task allocation by bees in newly divided colonies of *T. iridipennis*

The bees introduced during colony division were monitored at an interval of two hours from the date of division for a period of two weeks by opening the top lid of the hive during the nest closure period. The activities of the introduced bees within the hive were recorded. The number of days needed for nest closure, guard bee activity at the hive entrance and forager activity were also recorded. The percentage of bees undertaking the initial colony establishment activities of in-hive architecture formation, hive entrance repair and tending the emerging bees from the brood cells were recorded.

Observations of damage caused by intruders in newly divided *T. iridipennis* colonies

An experiment documented the nature and extent of damage caused by intruders in the newly divided colonies. Two treatments were used for the study, one set of newly divided colonies exhibiting natural defence against the intruders and a control set with of a newly divided colony where natural defence mechanisms exhibited by the colonies were excluded. The closure of the nest entrance, the formation of a complex nest entrance and the resin applied to the entrance tube were considered as the natural defence mechanisms the stingless bees. The natural nest defence mechanisms exhibited by the bees were removed through the dismantling of the nest entrance tube with the use of a fine needle to allow the invaders into the colony. The effect of the intruder's attack on brood emergence and the robbing of storage pots in both treatments were recorded for a period of twenty-one days.

Data analysis

Data on various parameters studied were statistically analysed. The mean ± SD of the number of bees repairing the hive, guarding and tending the brood was calculated. Analysis of variance (GLM in SAS 9.3; SAS Institute, Cary, NC) was used to compare the number of invasions in the first four weeks after the division of the colonies with the effect of colony defence over the percentage of brood emergence and the percentage of resource robbery. Where a significant difference was detected, treatment means were separated using the Tukey HSD Test (0.5%).

RESULTS

Nest intruders after the colony division of stingless bee, *T. iridipennis*

The newly divided colonies of stingless bees were observed to be invaded by two species of solitary resin bees (Fig. 1), *Megachile cephalotes, M. disjuncta*, two species of ants *Camponotus* sp. and *Oecophylla smaragdina*, and an unidentified spider species belonging to family Salticidae (one female and one spiderling), wolf spider, *Pardosa* sp. (Lycosidae: Araneae). A parasitic wasp species *Leucospis* sp. was observed near the nest entrance (Fig. 2). We did not observe nest entry/invading activity by the parasitic wasp.

The sequence of activities during the initial stages of colony division are presented in Fig. 3A-D. The foragers sealed the nest entrance with a thin layer of yellowish-brown coloured resin which restricted entry by invaders. Complete nest closure was sometimes observed at the outer part of the entrance tube and sometimes at the inner part of the entrance tube which protruded into the colony. The behavioural response of the stingless bees in the colony to invasion from different natural enemies was is in Tab. 1. Resin bees stole resin at the nest entrance of the newly



Fig. 1. Resin robbing by *Megachile* sp.



Fig. 2. *Leucospis* sp. in the hive of newly divided colony.

divided colonies. In two colonies, resin bees were trapped in the polyethylene tube fitted in the entrance and died from a lack of further movement and asphyxiation. We also observed a deposition of fresh brown-coloured sticky resin droplets at the entrance in the mud pot hives during the hiving of wild stingless-bees colonies, which is a direct defence strategy to trap any intruder in the colony.

Intruder attacks in newly divided colonies of stingless bee, *T. iridipennis*

A significant difference was observed in the invasion by resin bees ($F_{3,15}$=5.90; P<0.0001) during the four weeks after colony division (Fig. 4). The highest mean number of resin bee invasions was recorded during the first week of colony division (11.67±1.53 invasions) followed by a relatively lower number of attacks during the second (2.00±0.31 invasions), third (1.15±0.67 invasions) and no invasion four weeks after division. No significant difference in spider invasion was observed during the four weeks after colony division. The mean number of spider attacks was highest during the second week after division (4.67±1.04 invasions) followed by 3.00±1.00 invasions during the third week and 1.00±0.57 invasions during the fourth week after division. Ant invasion in the colony differed significantly during the four weeks of colony division ($F_{3,15}$=8.19; P<0.0001). The mean number of ant invasions during the first week (4.33±1.15 invasions) after colony division was the highest followed by the second (1.02±0.16 invasions), the third week (1.00±0.08 invasions) and no invasion four weeks after colony division.

Task allocation of stingless bees during the initial stages of establishment in the newly divided colonies of *T. iridipennis*

Nest closure was observed for a period of 4.37±0.74 days after the division and the guard bee activity and outgoing activity of foragers for resource collection for periods of 6.13±1.24 days and 10.63±1.07 days, respectively (Tab. 2). Of the fifty introduced bees in the newly divided rectangular hive, 18.40% participated in the initial activities of hive architecture, namely hive entrance repair, attachment of the brood cells using resinous pillars and forming involucrum to protect the brood cells. Around 69.20% of them were observed to participate in the hive entrance repairs by completely rebuilding the entrance with a resinous papery multilayered tubular material. The bees were also observed to tend to the new emerging bees from the given pupal brood cells (13%) in the colony (Fig. 5).

Damage caused by intruders in stingless bee colonies of *T. iridipennis*

Among the three major invaders of the newly divided colonies, ants and resin bees were observed to rob resources and damage the

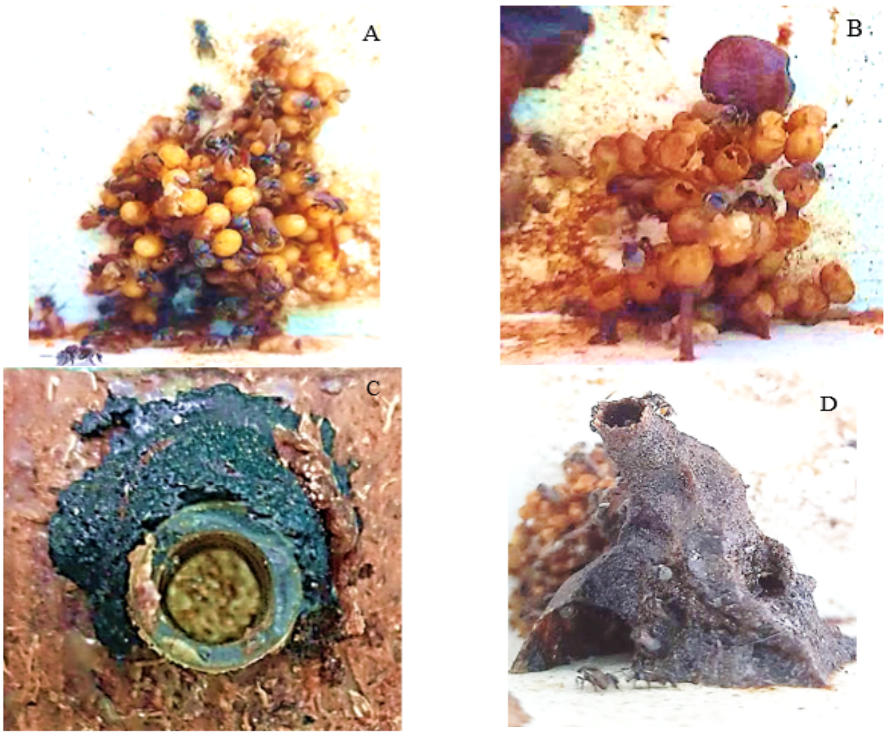


Fig. 3. Ethogram of different behaviours of stingless bees, *T. iridipennis* after colony division.
A. Emergence of bees from pupal brood cells; B. Pillars and connectives to attach brood to the hive;
C. Nest entrance closure by the bees; D. Hive entrance repair activity by the bees.

Table 1.

Nest defence behaviour recorded in response to the attack by the enemies

Natural enemy	Nature of damage caused by the intruder in the unprotected colony	Nature of nest entrance closure	Type of defence behaviour exhibited by the stingless bees
Resin bee	Resin-robbing activity noticed at the nest entrance as well as inside the colony	Full closure of nest entrance from inside for a week period. Partial outside closure at the entrance tube	Guard bees were sighted near the entrance tube during the resin robbing by the *Megachile* bee.
Ant	Destroyed the developing pupal broods inside the brood cells Consumed the honey in the honey pots	Nest closure not observed	In a few colonies, the ants were seen trapped in the entrance tube whereas, in other few colonies, some individuals were observed in a dead form as further navigation into the colony was arrested by the formation of complex nest architecture made by the bees inside the colony.
Spider	Formed webs in the colonies invaded by ants and resin bees with lost resources	Nest closure not observed	The spider was seen entangled and killed inside the entrance tube by a layer of mud mixed resin.

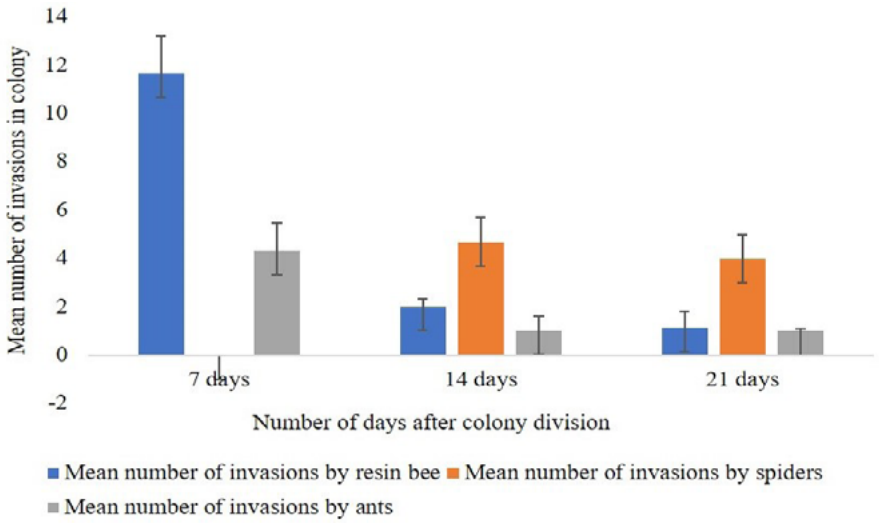


Fig. 4. Mean number of invasions by different invaders in the newly divided colonies.

Table 2.

Events in the newly divided colony of stingless bees

Sequence of events	Mean ± SD (days)
Nest closure	4.37 ± 0.74
Guard bee activity	6.13 ±1.24
Foraging activity	10.63 ±1.06

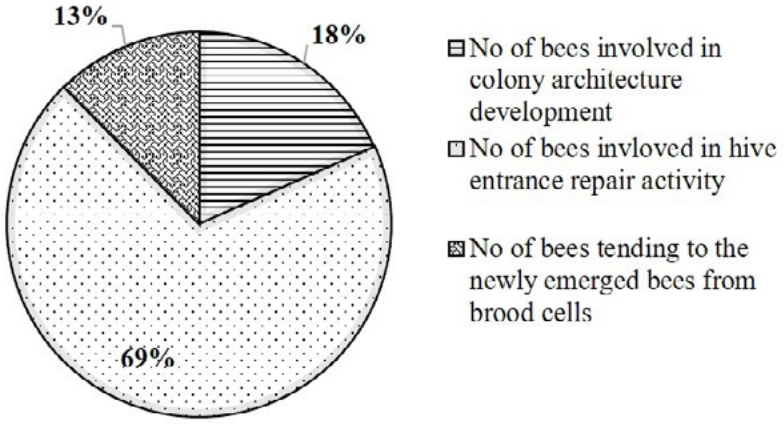


Fig. 5. Task allocation of the bees during initial stages of colony division.

brood cells (Fig. 6). In divided hives where natural defence strategies were excluded, ants were seen consuming the brood in large numbers, negatively impacting the brood emergence rate. The rate of emergence for the brood varied significantly between the newly divided colonies with intact natural defence and the colonies with excluded defence ($F_{1,14}$=55.20; P<0.0001). The percentage of emergence for the brood in the divided colony that exhibits its defence mechanism and the colonies where the natural defence mechanism was excluded were 100 and 10.1%, respectively. Ants were also observed to rob the honey pots leaving the pollen pots intact. A significant difference in the percentage of ants' robbery of honey

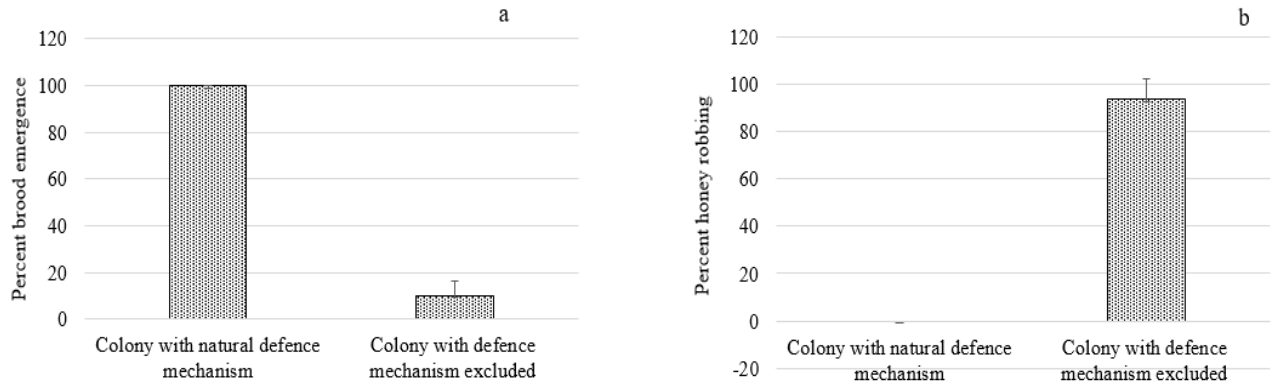


Fig. 6. Damage caused by intruders in newly divided colonies.

pots was recorded between newly divided colonies with intact natural defence mechanisms and colonies with excluded natural defence ($F_{1,14}$=108.12; P<0.0001). We did not observe any robbing of honey pots in the colonies with intact natural defence mechanisms whereas, in natural defence-excluded colonies, a significantly high rate of resin robbing (94%) was recorded. A newly divided colony invaded by ants could be clearly seen by the movement of ants at the entry and exit points of the colony. In the colonies excluded from the defence mechanism, the resin bees were found to have completely robbed the resin material but leaving the brood cells and storage pots intact. No initial hive-building activity was observed in such invaded colonies. Spiders were seen to form a web inside fully damaged colonies two weeks after division in the colony devoid of resources, namely honey and live brood cells.

DISCUSSION

The newly divided stingless-bee colonies during the initial phase of establishment and development were prone to attacks from several natural enemies. Solitary bees *M. disjuncta* and *Megachile cephalotes* were observed to rob the resin applied at the nest entrance. Gopinatha & Basavarajappa (2022) reported that *M. disjuncta* collects wax and cerumen, especially from pollen cells and brood cells in the nest of stingless bees. The allocation of tasks for colony defence might occur appropriately after substantial development of the colony with a sufficient number of foragers allotted as guard bees to defend against intruders. The colony's defence against intruders depends on the colony's size, age and better the better defence (Roubik 2006). The resin carried by the guard bees inside the hive was used to build a complex nest entrance that would obstruct further intruders inside the colony. There were relatively fewer resin-bee invasions a few weeks after colony division coinciding with the established nest entrance and nest architecture in the colony. The material used to seal the entrance of the nest resembled the cerumen layer with which the bees constructed the honey pots. The nest closure behaviour exhibited by the colonies warded off intruders in the current study. Grüter et al. (2010) reported that *Tetragonisca angustula* guarded the nest by closing the entrance against intruders from sunrise to sunset (32% and 56% of the colonies). However, in the present study nest closure was observed during both daylight and night hours.

The in-hive workers after accepting the hive were seen repairing the hive entrance and engaged in the building of a complex architecture at the nest entrance (Fig. 7A & B). This activity of the in-hive bees could be a proactive measure to prevent the entry of intruders into the colony. The behaviour of building complex long entrance tubes by trigonine stingless bees to defend the colony was reported by Duangphakdee et al. (2009). Bänziger et al. (2011) reported the behaviour of the tear-drinking stingless bee, *Pariotrigona klossi*

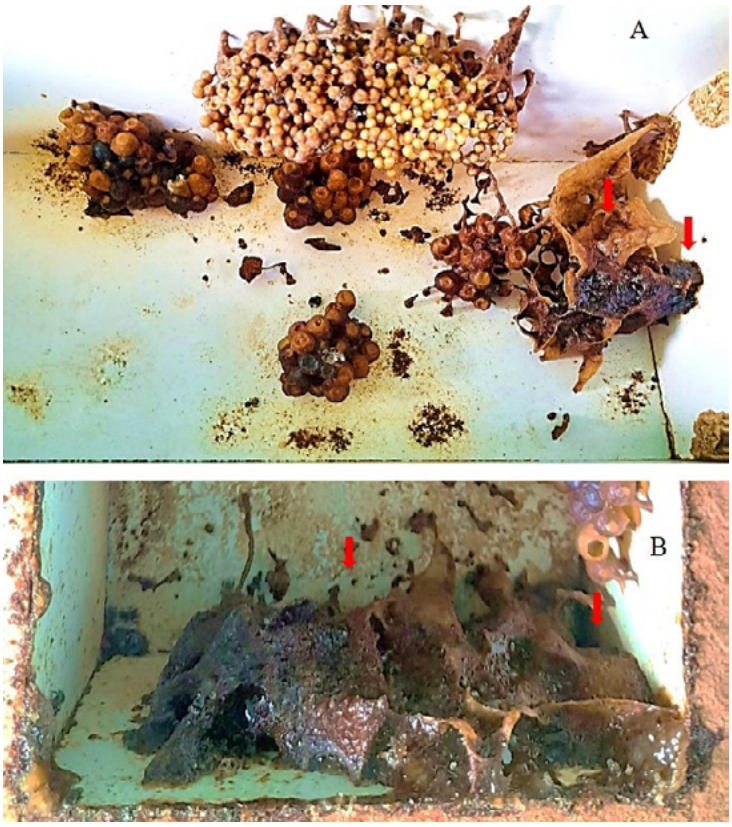


Fig. 7. Complex nest architecture at nest entrance. Red arrow indicates the complex coral like internal nest entrance made by the bees to pose a difficulty for the intruders during their navigation inside the nest.

(Schwarz), in building a complex nest entrance with dozens of coral-like tubelets to trap the intruders. The in-hive workers were observed to constantly coat the inner layer of the complex hive entrance with fresh resin as to prevent intruders from entering the colony. Freshly applied resin at the entrance of nest plays a vital role in protecting the nest against such intruders as ants (Leonhardt & Bluthgen, 2009). Foragers collect resin during the early days after colony division as it is the basic hive-building material for constructing the hive architecture during the initial days of colony establishment (Amala et al., 2021).

The invaders, especially the spiders, were seen to be blocked between layers of thin capping of mud coated with resin before the nest entrance closure. Resin and mud were used to obstruct the entry of spiders into the colony. The ability to defend against adult small hive beetle, *Aethina tumida*, by mummifying it using the resinous substance of the hive by the workers of *Trigona carbonaria* Smith (Hymenoptera: Apidae) was reported by Greco et al. (2010). The application of fresh resin droplets at the entrance to the hive reported by the authors in the present study was consistent with the observations by Wittmann (1989). The behaviour of stingless bees to fortify the nest entrance by applying of fresh resin drops to trap invaders was reported by Shanahan & Spivak (2021).

In our studies, guard bee activity was recorded a week after colony division, as there were negligible or relatively fewer attacks by intruders in the colony from the second week after division. The adaptive defence behaviour exhibited in the newly divided colonies favoured uniform brood emergence with appropriate task allocation of the bees for guarding and foraging with protective nest architecture. Older worker bees (3-4 weeks old) of the colony were reported to be involved in colony guarding activity (Quezada-Euán, 2018). However, in the current study, after the initial hive architecture was established, the deputation of guards at the entrance of the hive showed the typical adaptive strategy followed by bees to protect the colony against intruders. Ants damaged the pupal broods inside the cells negatively impacting the emergence of adult bees from brood cells and both ants and resin bee was involved in the robbing of honey and resin resources in the hive. Ants have been reported to be a major predator in stingless bee colonies (Kumar et al., 2012; Ashari et al., 2019) and are also the major robbers of sugar reserves in managed bee colonies (Payne et al., 2020).

The results of the study emphasised that stingless bees have an adaptive defence behaviour along with a complex nest architecture to protect the colony during earlier stages of its establishment by trapping and killing accidental intruders in the colony. The observations in the study could be used to generate alerts for stingless bee keepers so that they can keep a watch out for invasions on newly divided colonies invaders that may threaten their successful establishment.

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