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Nesting Behaviour and Ecology of a Common Disjunct Bee, *Megachile disjuncta* (Fabricius, 1781) (Hymenoptera: Megachilidae) from India

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Abstract

Megachile disjuncta is a common solitary bee widely distributed and has been reported as an effective pollinator of legume crops in India. A study was conducted using the trap-nest methodology during 2023, and the new information on nesting behaviour and ecology of *M. disjuncta* is presented here. The species successfully occupied artificial nests provided in the form of hollow reeds of *Ipomoea* and bamboo canes. Bees exhibited a clear and significant preference for nesting in bamboo canes compared to *Ipomoea* reeds (χ^2 = 19.572, df = 1; P-value: <0.0001). *M. disjuncta* remained active from March to September, with activity peaking in April. Artificial nests were modified using the mud and resin collected from different plants. The resin was used to construct partition walls between the cells, and mud was used to plug the nest entrance. The average number of brood cells observed was 6.1 ± 2.42, with an average nest length of 10.83 ± 3.05 cm. There is no significant difference in the observed sex ratio [F: M = 1:1.66; χ^2 = 0.23, Critical value (α = 0.05, df = 1) = 3.84], and protandry was observed in the adult emergence pattern. Approximately 49-56 per cent of bees failed to complete their nests due to the high incidence of natural enemies. Reported here for the first time, *M. disjuncta* nest infestation by the clepto-parasitic megachilid bees, ectoparasitic leucospid wasps, and parasitisation by the bombyliid fly. The success of colonising trap nests makes it an interesting and potentially valuable opportunity to utilise the same to pollinate cultivated crops.

Introduction

Megachilids are solitary bee species, often referred to as leafcutter bees, mason bees, and resin bees. Unlike honey bees, these megachilids do not construct their hives using wax; instead, they create their own nests or utilise pre-existing cavities/burrows found in wood, walls, man-made structures, and uncultivated fields (Eickwort et al., 1981; Morato & Martins, 2006; MacIvor & Packer, 2015; Ascher et al., 2016). Leafcutter bees derive their name from their unique behaviour of cutting plant materials, particularly leaves, to construct nests for their brood (Litman et al., 2011). However, not all megachilids use leaves for the construction of nests. Some species use resin, soil, or mixtures of these materials. Blue-orchard bees and other species of the *Osmia* use a combination of mud and chewed leaves; hence, they are often referred to as mason bees rather than leafcutter bees. In India, the family Megachilidae is represented by 240 species, of which the genus *Megachile* is the most diverse and widely distributed, comprising a total of 96 species (Ascher & Pickering, 2024).

Megachilid bees are renowned pollinators and play a significant role in pollinating various cultivated and wild flora (Garantonakis et al., 2016). In many countries, *M. rotundata* is

recognised for its role as a key pollinator of alfalfa (Michener, 2007; Pitts-Singer & Cane, 2011) and *Osmia* species for almond (Artz et al., 2013; Haider et al., 2014). Because of their importance in pollinating commercial crops, several trap-nesting solitary bees, *viz.,* alfalfa leafcutter bee, *Megachile rotundata*, the mason bees, *Osmia cornifrons*, *O. lignaria*, *O. cornuta,* and *O. bicornis* in the family Megachilidae, are now reared on a large scale using artificial traps (Gruber et al., 2011; Torretta et al., 2012; Kunjwal & Khan, 2023). In India, *M. lanata*, *M. disjuncta,* and other species in the genus *Megachile* are considered as effective pollinators of red gram and many other legumes (Abrol & Kapil, 1986; Singh, 2016). Though these are recorded as important pollinators, insufficient knowledge about their nesting biology and ecology is the main obstacle for utilising the megachilid bees as a management tool for pollination services of the legumes and other cultivated crops.

M. disjuncta is most commonly distributed and one of the dominant pollinators on legume crops in India (Padhy et al., 2018; Udayakumar & Shivalingaswamy, 2022). Like other resin bees in this genus, *M. disjuncta* uses resin and mud for nest construction (Sachin, 2016; Pradeep & Belavadi, 2022). Kunjwal & Khan (2023) studied the trap-nesting behavior of six species of the genus *Megachile,* and some aspects of the nesting biology of *M. disjuncta* have been investigated. However, still very little is known about seasonal activity, nesting architecture, emergence pattern, and natural enemies of this species in India. To address such knowledge gaps, we have followed bees visiting artificial nests in a bee hotel throughout the year to investigate and record detailed information on the nest architecture and seasonal activity. In addition, we also recorded various natural enemies affecting their nests.

Material and Methods

Study site

The present study was conducted in 2023 at the College of Sericulture, Chintamani, situated at an altitude of 865 m above sea level, with a latitude of 13.16° N and a longitude of 78.12° E. Seasonal activity patterns, details on nest structure, and observations on natural enemies were recorded. Chintamani lies in the tropical semi-arid climatic region of India, belonging to the Chikkaballapur district of Karnataka state. Meteorological data indicated that the dry climate here is characterized by a hot, dry summer and a mild winter. The study area comprised various crops like Guava (*Psidium guajava* L.), Mango (*Mangifera indica* L.), Sapota (*Manilkara zapota* L.), Jamun (*Syzygium cumini* L.), Tamarind (*Tamarindus indica* L.), Cashew (*Anacardium occidentale* L.), Coconut (*Cocos nucifera* L.), Jackfruit (*Artocarpus heterophyllus* Lam.), Sunhemp (*Crotalaria juncea* L.), Sunflower (*Helianthus annuus* L.), Safflower (*Carthamus tinctorius* L.), and many weed species.

Trap Nests and Nest Sampling

For the present study, trap nests made of hollow bamboo canes and hollow reeds of *Ipomoea carnea* Jacq. (commonly known as the pink morning glory) with lengths of 10 cm to 25 cm and varying diameters were installed. The diameter of the hollow region for bamboo canes ranged from 1.3 cm to 2.5 cm, whereas for *Ipomoea* reeds, it ranged from 0.6 cm to 1.5 cm. These nests were placed in groups in the artificial shelter called the Bee Hotel at the College of Sericulture, Chintamani (Fig 1A & B). The bee Hotel in the present investigation was made of iron and is divided into two blocks – upper and lower [the total height of the bee hotel is 1.73 m, where the lower block (*Ipomoea* block) is 0.72 m above the ground level and the upper block (Bamboo block) is 1.22 m above the ground]. The upper block contains 379 bamboo canes (Fig 1E & F), while the lower block contains 1456 reeds of *Ipomoea carnea* Jacq. (Fig 1C & D). The Bee hotel is oriented with its front facing the south-west direction and its back facing the north-east direction. The nesting substrates (*i.e.,* Bamboo canes and *Ipomoea* reeds) are selected such that they have a hollow opening from both ends, allowing bees to choose and construct their nest from either the south-west direction or the north-east direction. Trap nests were monitored daily during 2023 to record bee activity and nest occupancy.

The nest selection and construction by the selected megachilid bees were observed and marked during 2023. Data on the number of nests occupied during each month, diurnal activity, and foraging activity were recorded. Soon after the completion of the nest-making activity, completed nests were marked with the nest completion date, brought to the laboratory, and kept in emergence cages. Observations were made to know the selection of the nesting structures (material, diameter of reeds/canes, etc.). Ten nests were cut open carefully and data on the number of cells, type of nesting substrate used inside the nest, length of each cell, the diameter of each cell, thickness of partition wall between two cells, thickness of mud wall used for the closing the nest entrance and total number of trap nests occupied, total number of adults emerged and sex ratio was recorded. Contents of the nests were also recorded (e.g., number of immature stages, presence of pollen masses). To observe developmental stages, trap nests were carefully dissected, and the developmental period from egg to adult within each cell was documented.

The study also recorded the data on the natural enemies of megachilids, which infest their nests and broods. All natural enemies that visited the nests were collected, pinned, and identified (the second author did the identification of all hymenopteran parasitoids) during the study, including cleptoparasitic megachilid bees that kill the broods of other megachilids. For external morphological studies of bees and natural enemies, a Nikon SMZ 800N microscope was used. Digital colour images of the nest parameters were taken using a Leica SAPO stereomicroscope with a Flexacam C3 camera

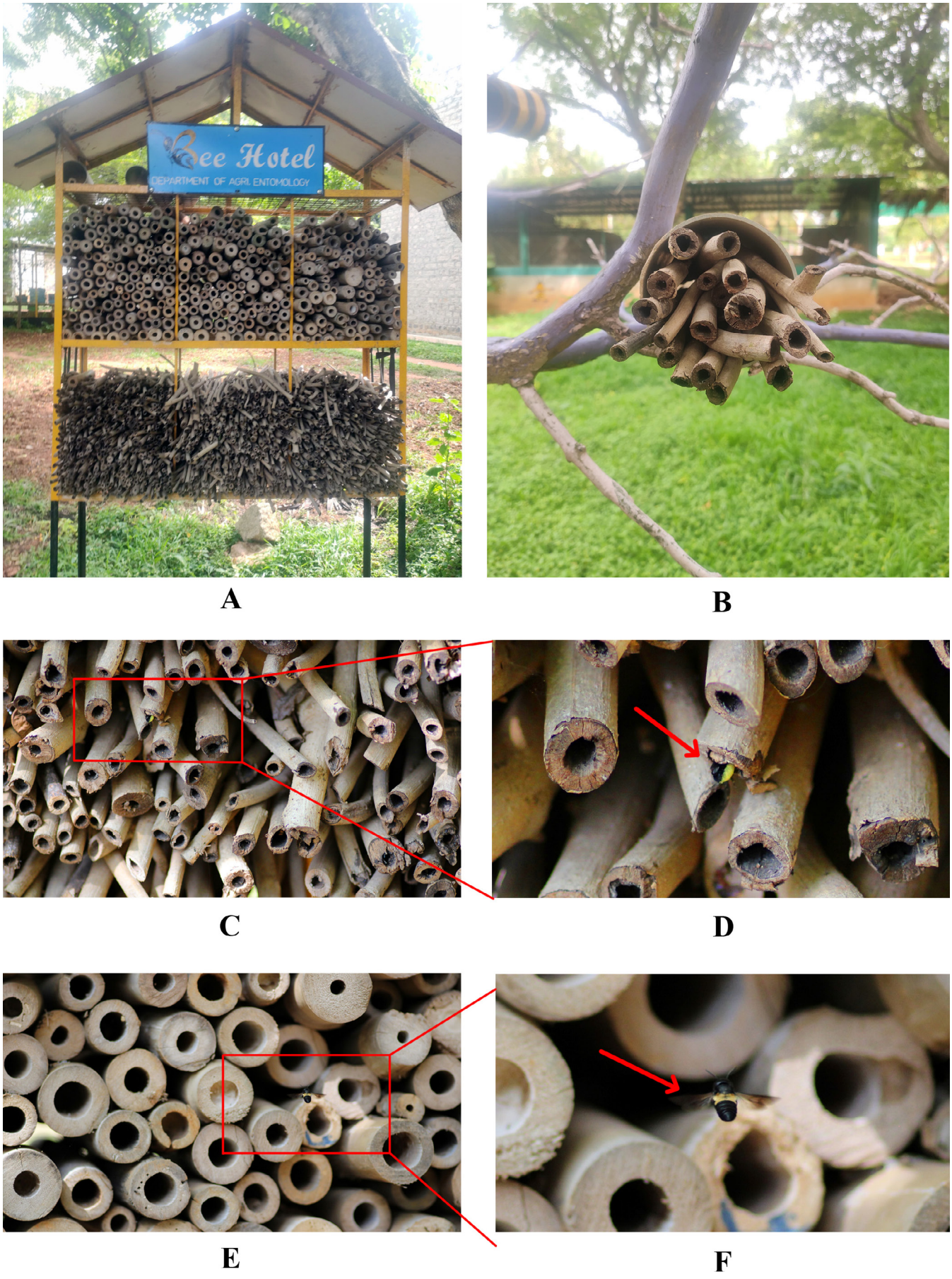

Fig 1. Artificial nesting structures. **A**- Bee hotel; **B**- Artificial nesting reeds in PVC pipes; **C**- *Ipomoea* reeds; **D**- *M. disjuncta* entering *Ipomoea* reeds; **E**- Bamboo canes; **F**- *M. disjuncta* near bamboo canes.

attachment. Field photographs and habitus of species were taken with a Sony DSC 160 digital camera. Images were edited with Adobe Photoshop CS (Version 9.0). Additionally, some miscellaneous observations on the megachilid behaviour were also recorded.

Statistical analysis

We used a Chi-square test for independence with a 2×2 table to examine the association between bamboo canes and *Ipomoea* reeds as nesting substrates. The same test was also used to compare nest completion rates between these two materials, and analyses were performed using GraphPad software. Additionally, a Chi-square goodness-of-fit test was employed to analyse the effect of nest orientation or direction on nesting activity, as well as to check for variations in the sex ratio.

Results

Description and physical features of ***Megachile disjuncta*** *(Fabricius, 1781)*

M. disjuncta is a solitary, medium-sized bee, measuring around 10 to 15 mm in body length. The entire body is robust and shiny black with an off-white/yellowish band at the junction of the thorax and abdomen (especially on the portion of the propodeum and first tergite of the metasoma). The wings are black-tinted. These bees possess very powerful mandibles for cutting and shaping plant materials like resin during nest construction. Females are usually larger (Fig 2D), scopa present on the metasomal sternum (scopa is black), they have 10 flagellar segments in the antenna, and the abdomen is triangular. Whereas males are usually smaller in size (Fig 2E), without scopa at the metasomal sternum and have 11 flagellar segments in the antenna with a rounded abdomen (Michener, 2007; Pampareddy, 2023).

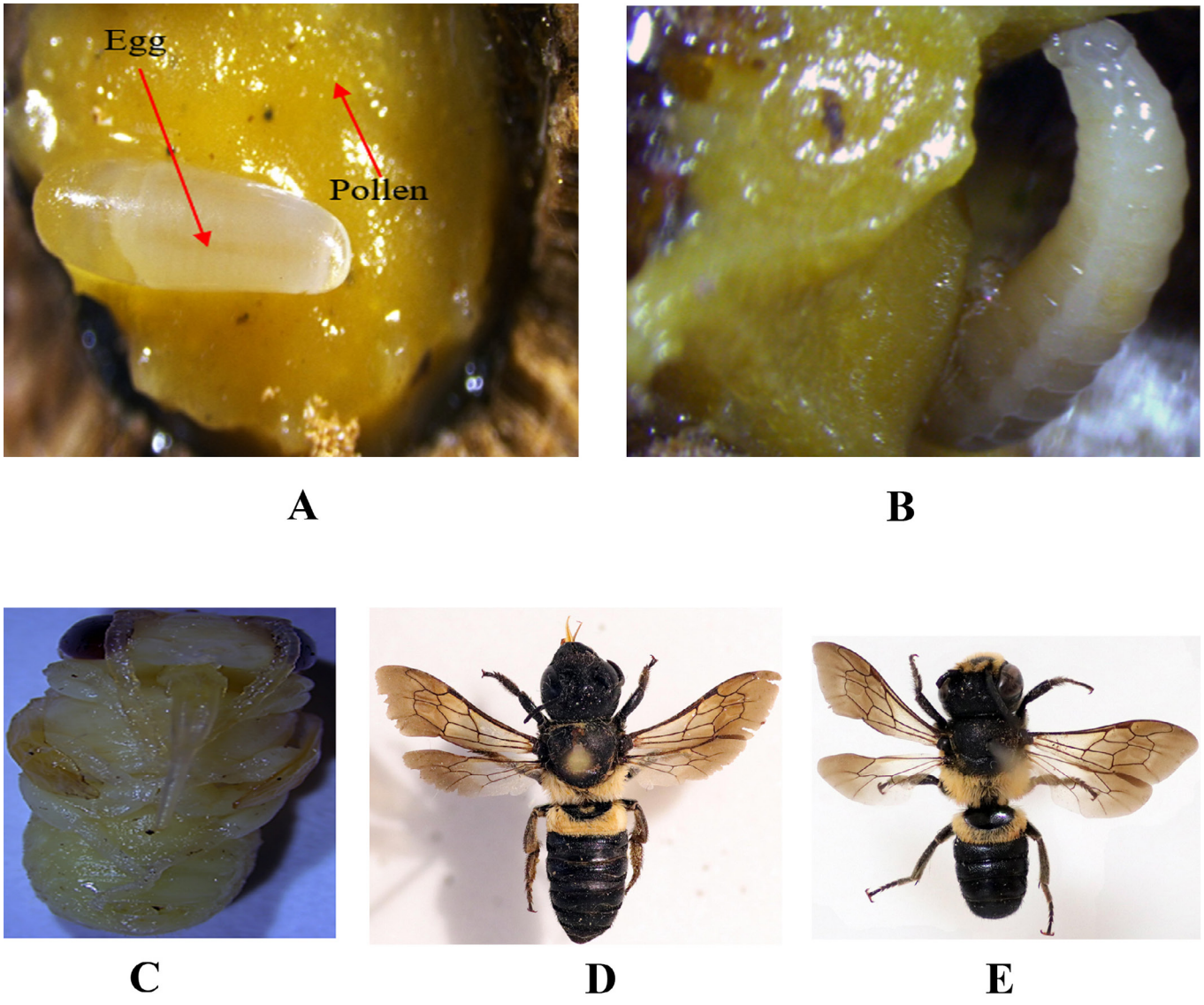

Fig 2. Biology of *Megachile disjuncta* (Fabricius, 1781). **A**- Egg laid on top of pollen food; **B**- Grub; **C**- Pupa; **D** - Adult Female and **E**- Male emerged from the nest.

Seasonal activity and flight period

The activity of *M. disjuncta* began in mid-March, and the peak activity was observed during the first week of April 2023. The activity was low during June-July and lasted up to September (Fig 3). The highest number of nests closed at Bee Hotel was in May and June, 2023 (Fig 4). During the peak activity of bees, very low rains were received and temperature was slightly higher than average temperature of the year (Fig 5). These bees were diurnal and active during morning hours. The activity of bees was higher during bright sunshine periods. Some of the individuals of this species altogether cease their activity during the afternoon hours when there is intense sunshine or heat. No bees were observed outside the nest or near artificial lights at nighttime.

Nesting behaviour and nest architecture

M. disjuncta built their nests in artificial nesting structures like hollow reeds of *Ipomoea* and bamboo canes. In addition, they were also observed to build their nests in cracks found in walls, hollow iron rods, hollow cavities of wooden windows and doors, bamboo roofing structures, and crevices in tree trunks.

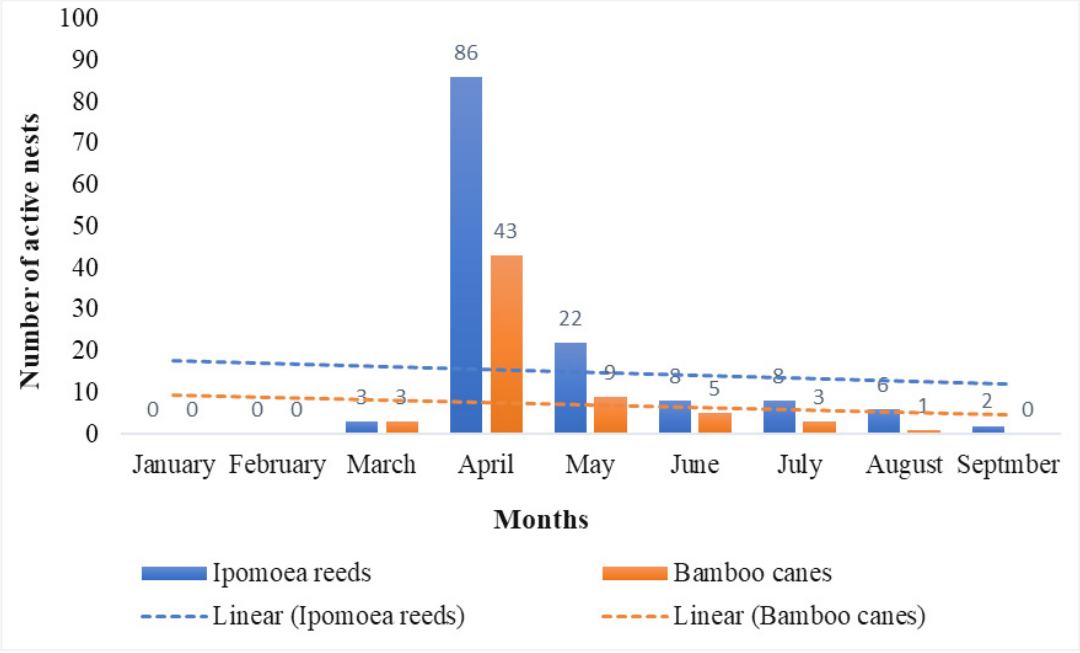

Fig 3. Activity of *M. disjuncta* in trap nests at Bee Hotel in 2023.

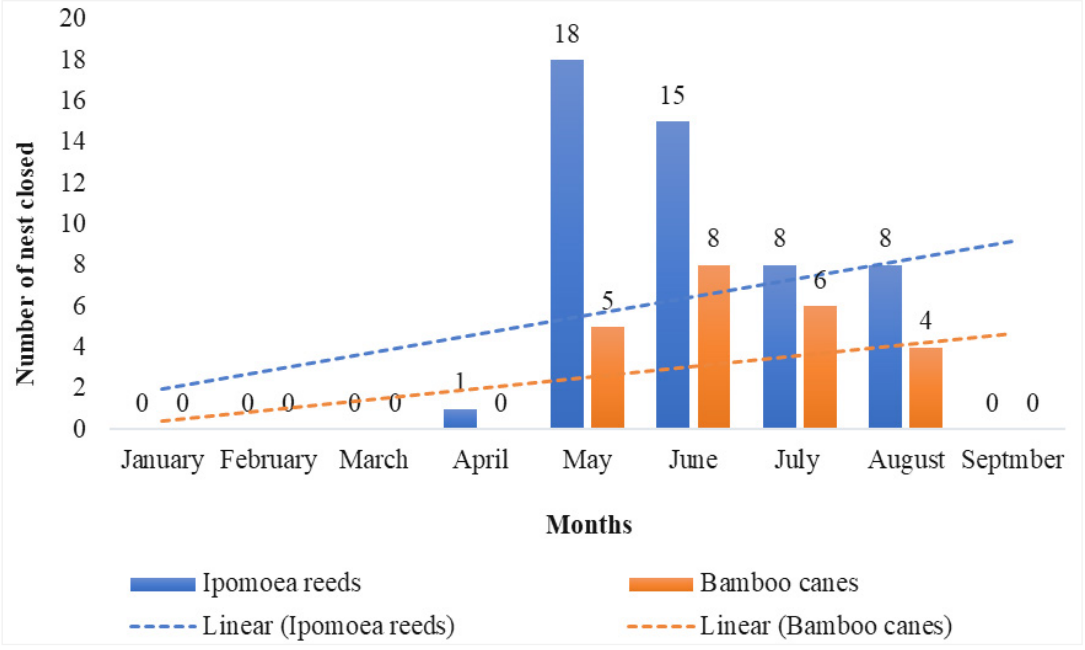

Fig 4. Number of *M. disjuncta* nests closed in each month at the Bee Hotel in 2023.

During the study period, a total of 1456 *Ipomoea* reeds and 379 bamboo reeds were placed in an artificial nesting structure. Among 1456 *Ipomoea* reeds, bee activity was observed in 98 traps (6.73% of the total trap-nests available) (Fig 1F), and only 50 nests were closed completely (51% of total active nests). Out of 379 bamboo reeds, bee activity was observed in 52 reeds (13.72% of total reeds available) (Fig 1D), and only 23 (44.23 % of total active nests) could complete the nests in 2023. In general, the bees significantly preferred bamboo canes for nesting over *Ipomoea* reeds ($\chi^2 = 19.572$, df = 1, P-value < 0.0001). However, there is no significant difference in the success rate of completion of nests between *Ipomoea* reeds and bamboo canes ($\chi^2 = 0.627$, df = 1, P-value = 0.4285, $\alpha = 5\%$) (Fig 4). Interestingly, significantly a greater number of nests were closed in south-west direction in case of both, *Ipomoea* reeds [$\chi^2 = 23.12$, critical value (df = 1 and $\alpha = 0.05$) = 3.841] and bamboo canes [$\chi^2 = 9.78$, critical value (df = 1 and $\alpha = 0.05$) = 3.841] compared to north-east direction. Nesting success also depends on pressure from natural enemies. About 49-56 per cent of active nests failed to close completely because of the heavy incidence of natural enemies during the peak activity period (discussed in the natural enemies of *M. disjuncta*).

The nest construction behaviour shown by the female bees was as follows: At first, female *M. disjuncta* located the cavities, cracks, and hollow reeds of the *Ipomoea* and bamboo canes for nesting, then these bees entered into the hollow reeds by putting their head inside and confirmed the suitability of the surrounding environment for the nest construction. Once the site was found suitable, the bees fly around the artificial nesting structure in a zig-zag manner to memorise the area or site. The female bees go foraging to collect the materials essential for constructing a nest. The bees collected resin from plants and then brought it to the nesting site by holding it between the mandibles (Fig 6A and B). The resin was used to plaster the inner walls of hollow reeds and also for the construction of partition walls between the cells (Fig 6D). The bees mix the resin with a small amount of saliva or with other liquid secretions for ease of handling. Unlike other species, *M. disjuncta* does not use cut pieces of leaves or flower petals in nest construction. Initially, the resinous material was semi-solid, but it acquired a hard, rubber-like consistency after being deposited inside the nest. After constructing a single cell, the bees collected pollen and deposited it on the inner side of the cell. Then, the female bee deposits a single egg on top of the pollen, which develops into an adult (Fig 2A & 6C).

The nutrition provided for the maturing larvae within the nest consisted of a mixture of pollen and nectar (Fig 2B & 6C), and the pupa observed was exarate type (Fig 2C). Female bees were observed gathering pollen, predominantly from pongamia (*Millettia pinnata* (L.)), sun hemp (*Crotalaria juncea* L.), and pigeon pea (*Cajanus cajan* (L.) Millsp.) plants to nurture the brood. The transportation of pollen was facilitated by the scopa located on the metasomal sternum. In the process of depositing pollen inside the cell, the bees employed a method involving rubbing their hind legs against the scopa before placing it within the cell.

During the optimum sunshine period, females made 2–6 foraging trips per hour to collect nesting materials and pollen. On average, they spent a total of 25–34 minutes per hour in foraging activity, with the duration of individual trips ranging from 4 min 08 s to 13 min 56 s. Within the same hour, females also spent 24–33 minutes inside the nest, where they engaged in activities such as sealing the inner walls,

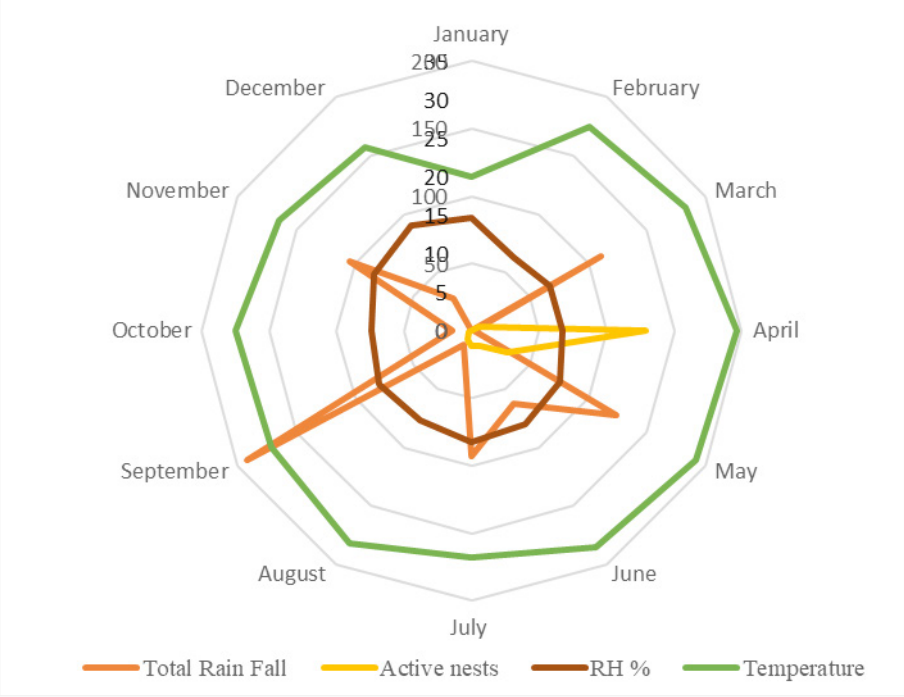

Fig 5. Pattern of rainfall (mm), temperature (º C), RH (%) and activity of *M. disjuncta* during 2023 at the study site.

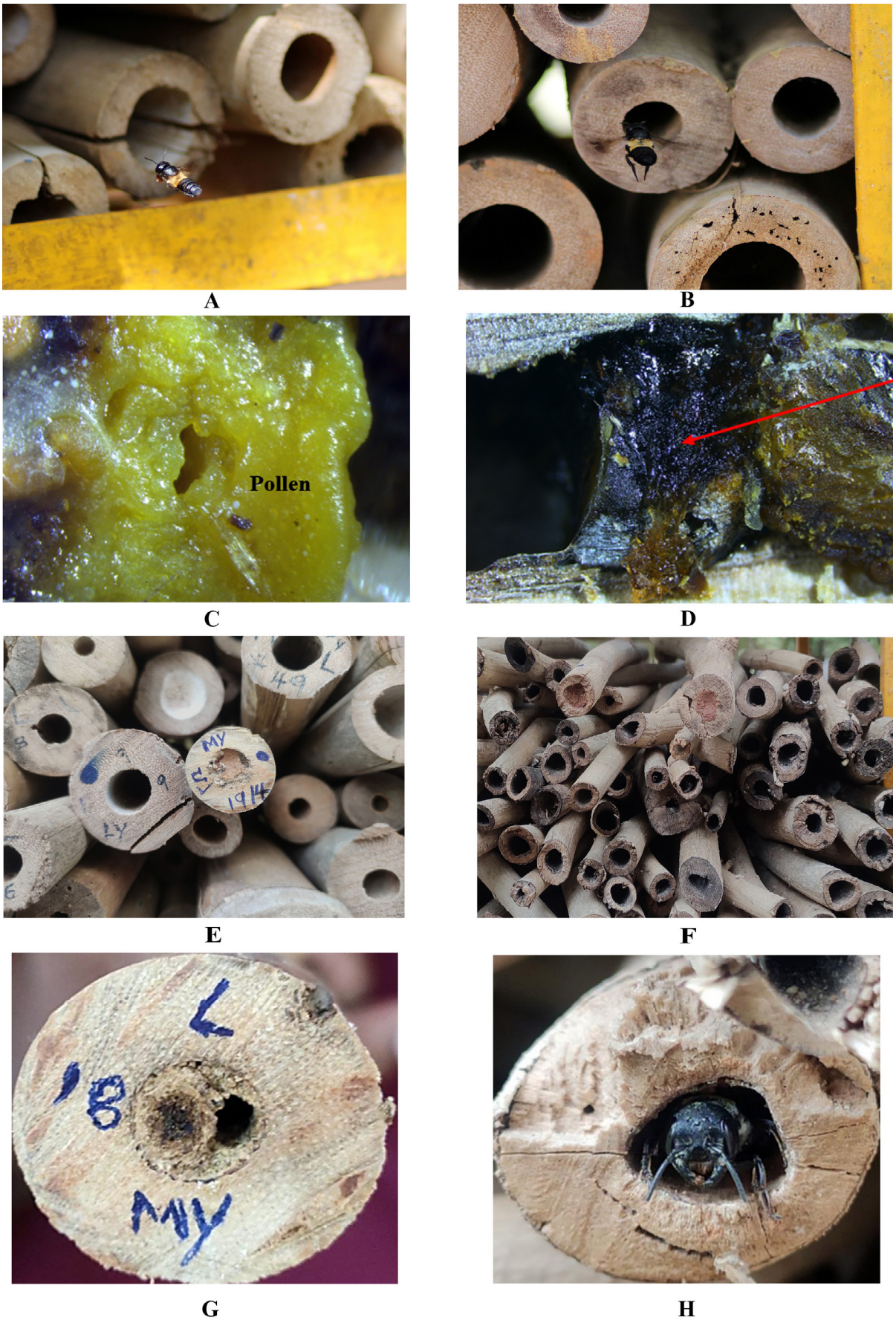

Fig 6. Nesting behaviours of *Megachile disjuncta.* A & B- Female disjunct bee carrying nesting materials; C- Pollen deposits at cell; D- Resinous partition wall; E & F- Nest entrance closed with mud; G- Exit hole created by adult bee during emergence; H- Female taking shelter inside the nest during intense heat.

constructing partition walls, depositing pollen, or oviposition. The time spent inside the nest after each foraging trip ranged from 3 min 28 s to 14 min 49 s. However, no nest construction activity was noticed during very hot sunshine hours or in rainy weather. Only a few bees were engaged in foraging or nest-building activity during cloudy weather. The bees were not active in the nest construction activity during the night hours.

The nest was constructed from the inner side of the hollow reed and reached to the outer end of the reed. In some nests, empty cells (intercalary cells) were observed between adjacent cells. There were no pollen or eggs noticed in those cells (Fig 7). In most of the nests (> 90%), vestibular cells were present (the first cell from the entrance was empty and referred to as vestibular cells). After filling the hollow reeds with cells, the entrance to the nest was sealed with mud (Fig 6E & F). The mud was initially wet due to the mixing of saliva, but later on dried up. Mud was transported and manipulated by its mandibles.

The overall count of cells within the nest exhibited variability, ranging from 6.1 ± 2.42, with a maximum recorded at 11 cells and a minimum at 03 cells. The average length of the nest measured was 10.83 ± 3.05 cm, with the longest nest recorded at 18.50 cm and the shortest at 8.45 cm. Notably, the initial or first cell in most nests remained unoccupied (Vestibular cell), measured 1.37 ± 0.53 cm. The mean dimensions of the cells within the nests were 1.44 ± 0.40 cm in length and 0.54 ± 0.076 cm in diameter. The thickness of the partition wall, constructed using resin, measured 0.37 ± 0.03 cm, while the mud wall employed to seal the nest entrance had a thickness of 0.65 ± 0.07 cm (Table 1).

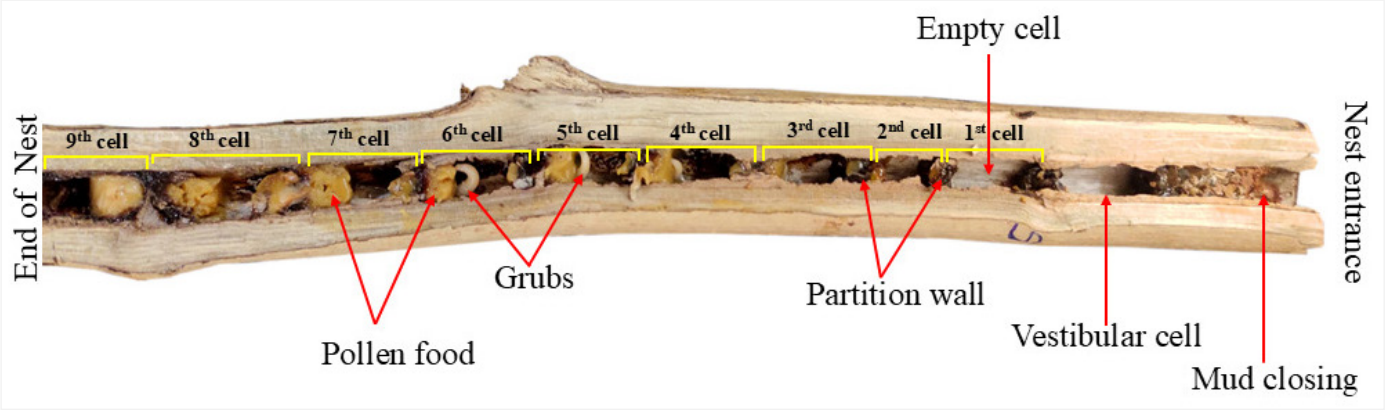

Fig 7. Internal nest architecture of *Megachile disjuncta*

Table 1. Nest dimensions and measurements of *Megachile disjuncta.*

Sl. No.	No. of cells	Nest length (cm)	Vestibular cell length (cm)	Mean cell length (cm)	Mean cell diameter (cm)	Mean thickness of the resin wall (cm)	Thickness of mud wall (cm)
1	05	10.01	0.00	1.49	0.56	0.42	0.70
2	06	11.63	1.30	1.45	0.64	0.43	0.75
3	04	08.50	1.60	1.52	0.65	0.31	0.65
4	11	18.50	1.10	1.20	0.41	0.41	0.50
5	09	13.20	1.50	1.19	0.59	0.34	0.74
6	03	09.35	1.90	2.48	0.55	0.37	0.66
7	06	09.35	1.60	1.25	0.44	0.39	0.68
8	06	09.28	1.70	1.22	0.52	0.36	0.71
9	04	08.45	1.30	1.61	0.55	0.36	0.55
10	07	10.05	1.70	1.02	0.58	0.35	0.65
Mean ± SD	6.1 ± 2.42	10.832 ± 3.05	1.37 ± 0.53	1.44 ± 0.40	0.54 ± 0.076	0.37 ± 0.03	0.65 ± 0.07

The number of brood cells per nest increased with increasing nest length (Fig 8) and mean brood cell length decreased with increasing number of brood cells (Fig 9). While mean cell length and vestibular cell length were not dependent on nest length (Fig 10A & B), however, the thickness of the mud wall decreased with increasing nest length (Fig 10C).

Adult emergence pattern and sex ratio

Protandry manifested in the adult emergence dynamics of *M. disjuncta*, with male cells strategically positioned at the outer periphery of the nest, enabling the initial emergence of male bees. In contrast, female cells were situated toward the inner side of the nest, resulting in their emergence following that of males. Interestingly, in 7 out of 8 nests observed, it was the male that emerged first, followed by the females. Despite individuals from the inner cells maturing earlier than their counterparts in the outer cells, it was observed that they tended to await specific stimuli from the peripheral individuals before emerging from the nest.

The duration necessary to finalize the construction of an individual nest, involving sealing one hollow reed, spanned from 12.4 ± 3.89 days. The first adult emergence occurred approximately 28.30 ± 1.82 days after the nest entrance was closed. Across a sample of 10 nests, 21 males and 18 females emerged. The gender distribution exhibited no significant difference in the sex ratio, with females to males at 1:1.66 [$\chi^2 = 0.23$, $P > 0.05$, Critical value ($\alpha = 0.05$, $df = 1$) = 3.84] (Table 2).

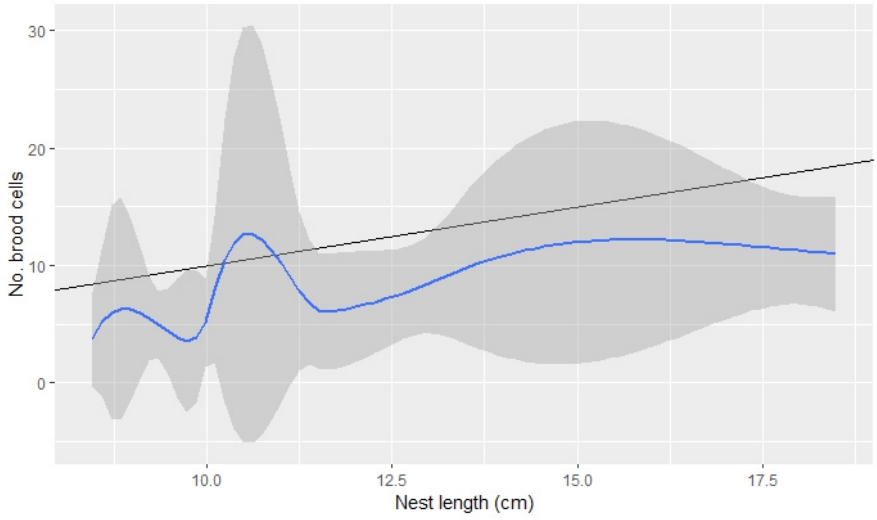

Fig 8. Positive relationship between nest length (cm) and the number of brood cells constructed by females in 10 nests examined in 2023.

Table 2. Nest closing and adult emergence pattern.

Sl. No.	Time taken to close the nest (days)	Time taken for first adult emergence (days)	Total Number of males emerged	Total Number of females emerged
1	14	30	03	02
2	07	28	02	01
3	09	30	01	01
4	13	31	02	02
5	10	27	01	02
6	16	29	03	01
7	17	25	06	04
8	14	27	01	01
9	17	27	01	02
10	07	29	01	02
Total			21	18
Mean ± SD	12.4 ± 3.89	28.30 ± 1.82	2.1 ± 1.59	1.80 ± 0.92

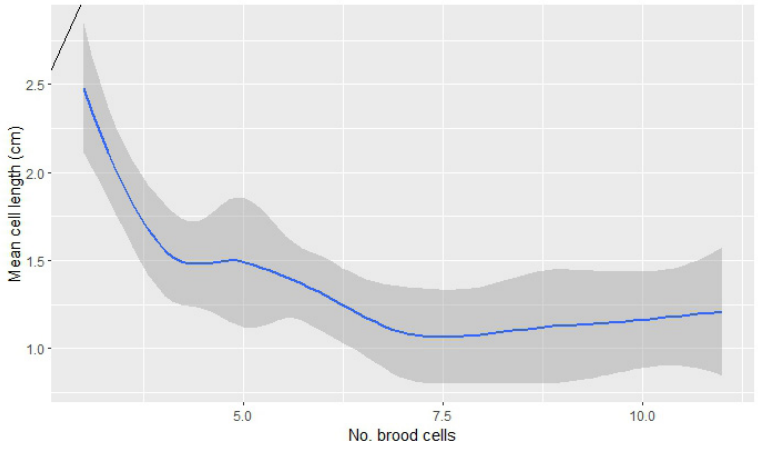

Fig 9. Negative relationship between number of brood cells and mean cell length (cm) in the 10 nests examined in 2023.

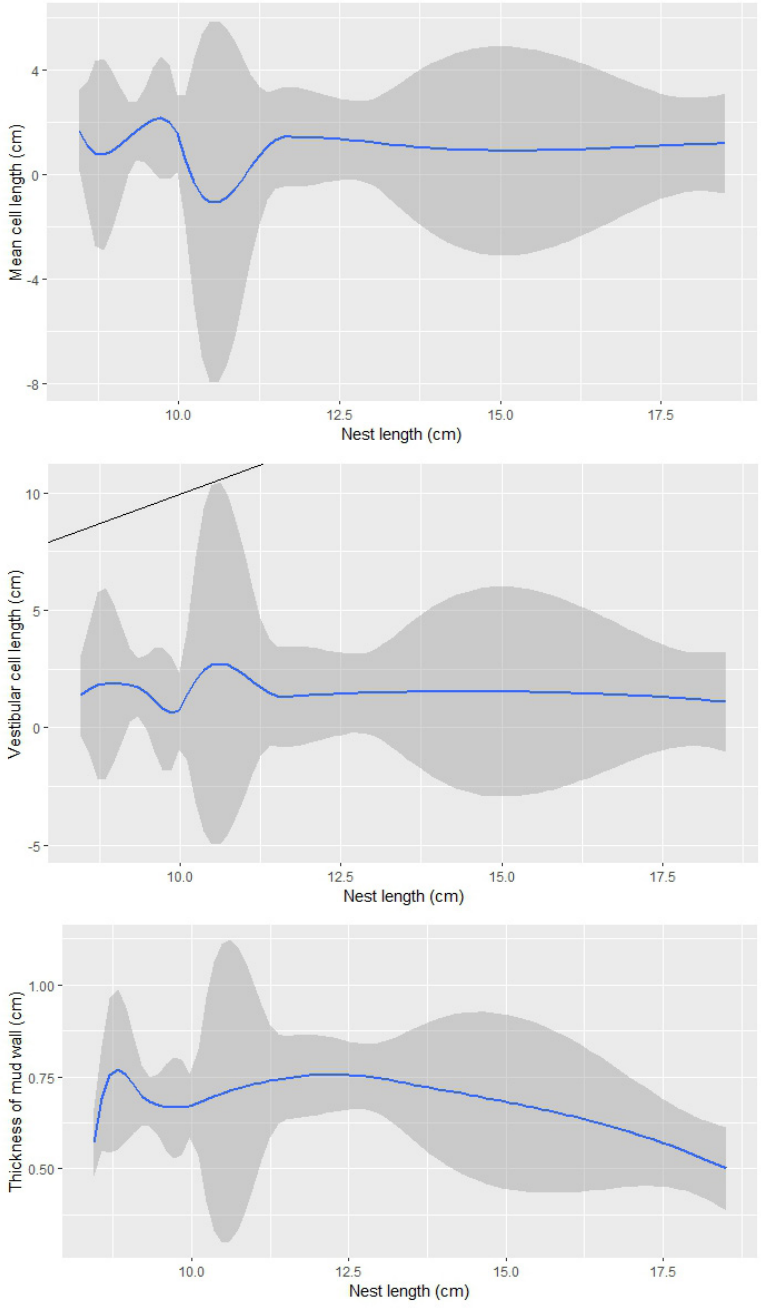

Fig 10. A & B -No relationship between nest length (cm) and mean cell length (cm) and vestibular cell length (cm). C- Negative relationship between nest length (cm) and thickness of mud wall (cm) in 10 nests examined in 2023.

Miscellaneous behaviour

The construction of nests was solely undertaken by female bees, with no participation observed from males in the nest-building process. During peak sunlight hours, when the intensity of sunshine was high, females were observed resting inside the nest, positioning their heads toward the entrance (Fig 6H). Conversely, during nighttime, females were found inside the nest facing their heads towards the inner side and their backs towards the entrance. Notably, no aggressive behaviour was observed in any of the circumstances during the nest-making activity. In a few instances, some females deposited excessive resin in a single location within the cell, impeding their movement. In some instances, females were trapped within the accumulated resinous material, leading to their death. The shaping of resin was accomplished with the aid of mandibles. After completing their larval period within the nest, the emerging adults created a circular opening in the mud wall for their exit (Fig 6G).

Natural enemies of ***Megachile disjuncta***

The nests of *M. disjuncta* fell prey to various natural adversaries, notably cleptoparasitic bees of the family Megachilidae (Fig 11). The recorded cleptoparasites were *Coelioxys fuscipennis* Smith, 1854, *Coelioxys confusa* Smith,

Coelioxys basalis Smith

Coelioxys fuscipennis Smith (Female)

Coelioxys fuscipennis Smith (Male)

Coelioxys confusa Smith

Euaspis edentata Baker, 1995 (♀)

Euaspis carbonaria (Smith, 1854) (♀)

Euaspis carbonaria (Smith, 1854) (♂)

Fig 11. Cleptoparasitic megachilids collected in nests of *M. disjuncta.*

1875, and *Coelioxys basalis* Smith, 1875. Additionally, the nest of *M. disjuncta* faced infiltration by other cleptoparasitic megachilids, such as *Euaspis carbonaria* (Smith, 1854) and *Euaspis edentata* Baker, 1995 (Fig 11). These parasitic bees strategically deposited their eggs on the amassed pollen provisions collected by the diligent disjunct bees. Subsequently, the developing progeny of these cleptoparasitic bees within the nest proceeded to eliminate the larvae of *M. disjuncta*, contributing to a complex interplay within the nests. These parasitic hymenopterans were responsible for a considerable infestation of the nests.

The prevalence and parasitic incursion by three distinct species of ectoparasitoid leucospid wasps (Leucospidae: Chalcidoidea), namely *Leucospis guzeratensis* Westwood, 1839, *Leucospis histrio* Maindron, 1878, and *Leucospis petiolata* Fabricius, 1787 (Fig 12), exhibited a pronounced severity throughout the entire period of nest construction. These leucospid wasps laid their eggs on pollen, as well as on the larvae of megachilid bees (Fig 12A). Given their ectoparasitic nature, the sustenance and maturation of these parasitoids were observed to occur at the expense of the larvae of the disjunct bees.

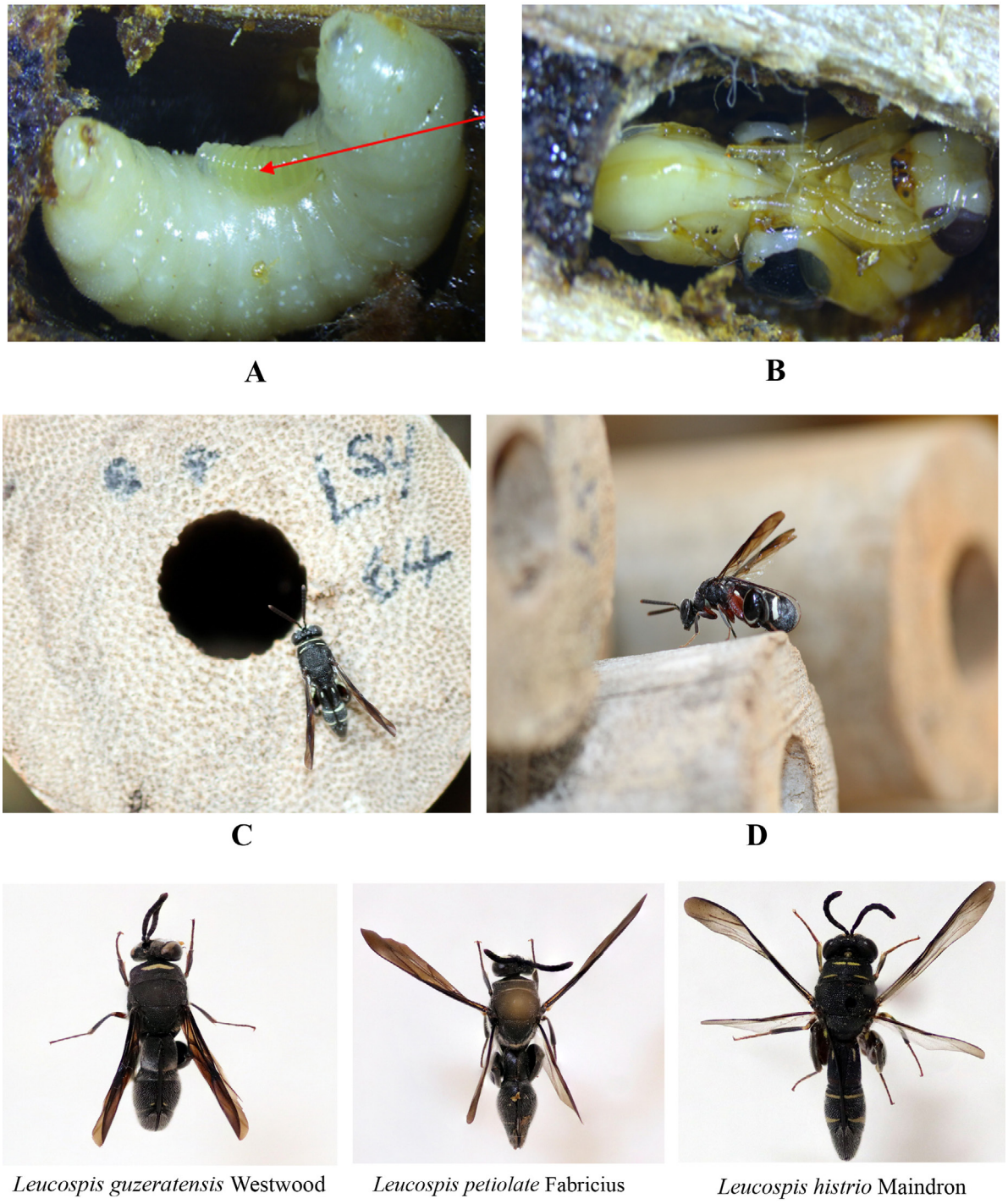

Fig 12. Leucospid parasitoids infesting the nest of *M. disjuncta.*

The ants, specifically of the genus *Tetraponera*, constitute the most pernicious menace to both the nests and developing brood (Fig 13A). These ants exhibited a proclivity for absconding with the pollen-nectar amalgam, the primary sustenance for the larvae, while also demonstrating a proclivity for brood mortality through the expropriation of this alimentary provision. After the ant predation, rodents and lizards induced destruction emerged as the next predominant adversarial force within the artificially constructed nesting site. Rodents, displaying nocturnal tendencies, were implicated in the destruction of 12 nests. Rodents scraped and opened the reeds that housed the megachilid nests (Fig 13B), causing damage to the reeds and the grubs found within. Notably, the damage from rodents was observed in *Ipomoea* reeds rather than bamboo reeds; the bamboo reeds remained untouched, likely due to their robust and hard nature, which made it challenging for the rodents to cut them open.

The dipteran parasitoid *Anthrax* sp. (Diptera: Bombyliidae) was observed in the early days of April, and its parasitic activity targeting megachilids was confirmed when it emerged from a sealed nest of the *M. disjunct* bee (Fig 13C). A total of four nests succumbed to parasitism by *Anthrax* sp. Additionally, Psocids were also recorded within the nests, exhibiting parasitic behaviour towards the larvae and pupae of *M. disjuncta*.

In summary, concerning the hierarchical severity of infestation, ants unequivocally dominated as the preeminent threat (nearly 50%), followed by cleptoparasitic megachilids, leucospid parasitoids, rodents and lizards, poscids, and, lastly, the dipteran *Anthrax* sp. In general, nearly 49–56 per cent of bees failed to complete their nests due to the high incidence of these natural enemies.

Discussion

We describe here in detail the natural history and provide novel information on the trap-nesting characteristics of *M. disjuncta*. The present study shows that *M. disjuncta* remained active from March to September, with peak activity in April and May (during drier periods), consistent with Michener's (2007) observation that summer is a period of particularly active nesting behaviour for leafcutter bees. We observed more activity in the months with low rainfall and slightly high temperatures. This finding is also in agreement with studies by Kunjwal et al. (2016) and Marinho et al. (2018), indicating that foraging peaks of *Megachile* spp. occur in months with lower rainfall. Our results on the flight period are consistent with data collected by Kunjwal and Khan (2023), which show that *M. disjuncta* is present throughout the year, with a peak in April to July. Seasonal activity in megachilids

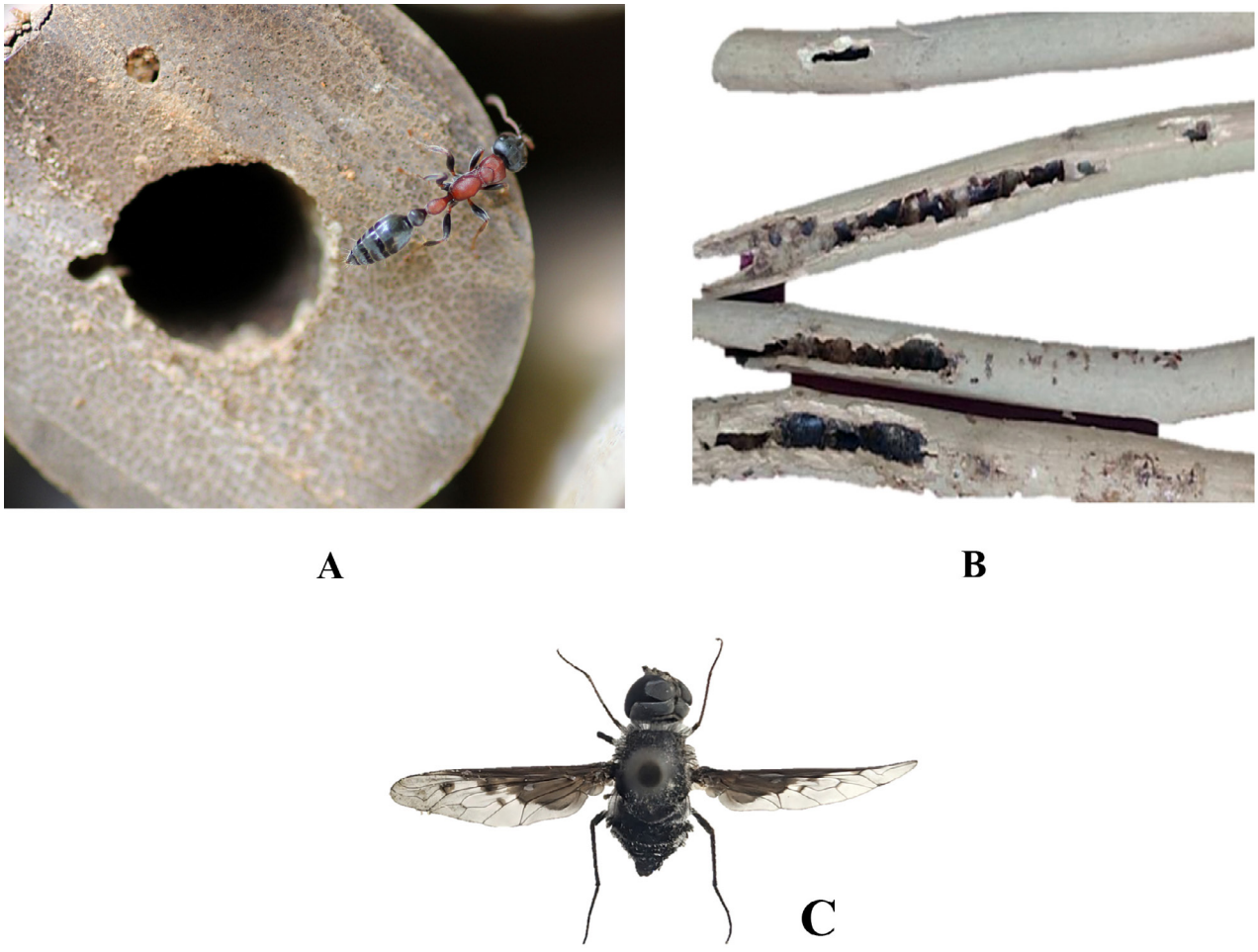

Fig 13. Natural enemies of *M. disjuncta*. A-Ants, B- Damage to nests by rodents and C- Bombyliid (Anthrax sp.).

is influenced by climatic factors such as temperature, rainfall, and the rhythmic activity of predators (Roulston & Goodell, 2011; Vitale et al., 2020).

In this study, bees were observed to build their nests inside the hollow reeds of *Ipomoea* and bamboo canes. Notably, the same bee species tended to establish nests within fissures and apertures in wall crevices, as well as beneath zinc roofing sheets, which were situated close to a sun hemp field. Chaudhary and Jain (1978) reported that the mason bee, *Megachile lanata,* readily accepted and nested in artificial tunnels made from castor leaf stalks, hollow castor stems, and wooden boxes with drilled holes. Sachin (2016) recorded the trap nest preference of megachilid bees and observed that the percentage of nesting by megachilids was high in mixed trap nests (30.77%) and bamboo nests (26.15%), followed by *Ipomoea* reeds (21.74%). More recently, Kunjwal and Khan (2023) studied the nesting habits of six different megachilid bees, and maximum nesting for *M. disjuncta* was recorded in the bamboo sticks, followed by wooden logs. It is important to notice that, in our study, only this species of bee was nesting abundantly in trap nests offered during the research period.

We reported *M. disjuncta* females preferred bamboo canes over *Ipomoea* reeds, and our findings in line with earlier reports of Gazola and Garofalo (2009) and Rauf et al. (2022), where they found that bamboo placed inside wooden boxes proved to be a better nesting material than cardboard tubes. This preference may be due to the perceived safety they provide for their offspring, as bamboo canes are more durable and naturally water-resistant, and their rigid walls help protect the nests by preventing parasites, predators, and mites from easily entering and infecting the broods (Rubene et al., 2015). The greater thickness of bamboo canes might have also influenced this choice in comparison to *Ipomoea* reeds, coupled with the elevated positioning of bamboo canes (*Ipomoea* reeds placed at 0.72 m above the ground, whereas bamboo canes are placed at 1.2 m above the ground). Similar assertions were made by Sachin (2016), where megachilids selected trap nests installed at higher elevations. According to Medler and Koerber (1958), *Megachile relativa* exhibited a preference for nesting sites located along woodland edges, typically at elevations of 5–7 feet above ground level, as opposed to sites situated closer to the ground. In our investigation, though we did not analyse the direct relationship between the body size of the bees and the diameter of the artificial reeds, we can speculate that the diameter might have significantly influenced the nest preference (Fricke, 1991), because bamboo canes offered the cavities with a diameter in the range of 1.3 cm to 2.5 cm. In contrast, for *Ipomoea* reeds, it was in the range of 0.6 cm to 1.5 cm. The successful occupation of artificial nesting substrates depends not only on the cavity diameter but also on the presence of a suitable and stable microclimate. Female bees tend to choose nests that maintain cooler and more stable temperatures during their foraging periods (Wilson et al., 2020). In our study, bamboo canes may have provided a more stable and suitable microclimate compared to Ipomoea reeds, which may also have influenced bees' preference for bamboo canes over *Ipomoea* reeds.

The direction of the trap nest also influences the nest occupancy rate for the various cavity nesting bees. In the present study, *M. disjuncta* built and completed more nests facing southwest. This may be because of the thick tree plantation in the southwest direction near the Bee Hotel, and the presence of a storehouse in the same direction might have acted as a wind breaker, leading to more nest occupancy in the southwest direction compared to the northeast direction. Interestingly, in our study area, the wind blows from the southwest between June and September, and from the northeast during October to May. Similarly, for instance, the highest number of trap nests were occupied in the south-west direction, followed by south-east, north, north-west, and west direction by the *Osmia* spp. (Yoon et al., 2015). This behaviour is attributed to the wind blowing direction; nests that were oriented towards a non-wind direction preferred more compared to the windward direction, and similar observations were made by Witter et al., 2010; Martins et al., 2012; MacIvor, 2017; Youngsteadt & Favre, 2022; Henry et al., 2023.

Among the different megachilid bees, *M. disjuncta* used both soil and resin for nest construction. In the current investigation, *M. disjuncta* used resin for the construction of partition walls and soil for closing the nest entrance. The nesting material used matches remarkably with the populations assessed by Sachin (2016) and Pradeep & Belavadi (2022). Kunjwal and Khan (2023) recorded that *M. disjuncta* females constructed nests using resin as well as trichomes, plant hair, and fibres mixed with resin in different combinations and distribution patterns. Many species in the subgenus *Callomegachile* use plant resin and mud for the construction of the nest, hence they got their name as resin bees (Michener, 2007; Chatthanabun et al., 2020).

The observations made on nest measurements were on par with the various earlier reports (Sachin, 2016; Pradeep & Belavadi, 2022; Kunjwal & Khan, 2023). However, minor variations in the nest parameters may be due to variations in the diameter of the artificial reeds provided for nesting, length of the reeds, sex ratio of offspring, and age of the female (Akram et al., 2022). In the nests of certain cavity nesting bee species, empty spaces are often found either at the end of the row of brood cells (known as vestibular cells) or between the brood cells (called intercalary cells). These empty sections serve as a protective barrier, reducing the risk of eggs and developing larvae being attacked by predators or parasites (Krombein, 1967; Morato & Martins, 2006). Similarly, in our study also vestibular cells and intercalary cells might have served for the same reason.

Megachilid bees construct cells in a series within the reeds. In our investigations, the male cells were constructed at the exterior side of the nest, and female cells were present at the inner side. A similar pattern was observed by Pradeep & Belavadi (2022), where *M. disjuncta* positioned male cells toward the outer side of the nest, and female cells were

situated more towards the inner side. The mother places male eggs in cells near the entrance, from which the resultant adults can escape without disturbing the slower-developing females. Among the various efforts, the arrangement of female offspring cells towards the inner side of the nest, followed by male offspring cells towards the posterior end, may also be a strategic response to potential threats such as parasitism, predation, and adverse environmental conditions (Michener, 2007). This strategy may restrict the possible threats to the initial few cells, ensuring safety for the inner cells.

Protandry was observed in the adult emergence pattern, and the sex ratio was non-significant (female: male, 1:1.166) in the present study. Pradeep & Belavadi. (2022) also observed protandry in the adult emergence pattern of megachilid bees. The male: female ratio in the spring progeny of *M. disjuncta* was 1.71:1 (Kunjwal & Khan, 2023), which was male-biased. Diaz et al. (2021) recorded a sex ratio strongly biased to males in a megachilid species, *i.e., Megachile sculpturalis* (4.2 males for 1 female). Trap-nesting studies on *Megachile cephalotes* have consistently shown a sex ratio that is significantly biased towards females at all study locations (Akram et al., 2022). Various factors influence the sex ratio in cavity nesting bees, like substrate cavity diameter (Morato & Martins, 2006; MacIvor, 2017; Rauf et al., 2022), and reproductive potential of the female (Rosas-Ramos et al., 2017). Changes in the sex ratio may also occur as a response to unfavourable conditions, such as low genetic diversity, limited food resources, poor climate, or high pressure from parasites, and also the sex ratio is a location-dependent limiting factor for the cavity nesting bee (Kim, 1997; Paini & Bailey, 2002; Akram et al., 2022). Gruber et al. (2011) found that when nests were shorter than 15 cm, more males were produced. This was because male cells near the entrance act as a protective barrier, helping to shield the female brood cells deeper inside from parasites and predators (Seidelmann, 2006). In our study, both bamboo canes and *Ipomoea* reeds provided a variety of diameters. Therefore, the balanced sex ratio we observed cannot be explained by the diameter of the nesting material alone. However, since we only had a small sample size – 39 bees in total (21 males and 18 females) from 10 nests, it is not easy to draw a firm conclusion. Furthermore, we strongly suspect that a male-biased sex ratio would occur if the sample size were increased.

The nests of *Megachile disjuncta* were subjected to egregious predation by an array of natural antagonists, with ants, specifically of the genus *Tetraponera*, constituting the most pernicious menace to developing brood. Following the ants, the subsequent critical threat was posed by cleptoparasitic megachilid bees. Additionally, leucospid parasitoids, rodents, dipteran parasitoids, and poscids were responsible for a considerable infestation of the nests. Udayakumar and Shivalingaswamy (2022) recorded the natural parasitisation by *Melittobia* sp. (53.67%) and parasitisation by *Coelioxys* sp. (6.67%) in the brood cells of megachilid bees. In addition, unidentified mites were observed infesting the neck and body of newly emerged adult *M. disjuncta* (Kunjwal & Khan, 2023). Similarly, Sachin (2016) and Pradeep & Belavadi (2022) observed the parasitisation caused to the artificial nests of megachilid bees and recorded the trap nests infested by *Coelioxys* spp., *Euaspis* spp., Chalcids, *Melittobia* sp., bee fly, and also reported the attack of psocids, ants, and nest damage by rodents.

In the present investigation, nearly 49 – 56 per cent of bees failed to complete the nests because of the hefty incidence of these natural enemies. It was observed that the females of *M. disjuncta*, strategically positioned at the outer periphery of the nest or at the nest entrance, engaged in actively repelling these parasitoids. On occasions, a collective effort involving three or four *M. disjuncta* females was observed, effectively driving away their natural enemies and safeguarding their progeny. This interesting behaviour was also witnessed in the sunhemp field, where a coalition of *M. disjuncta* females even deterred the bee-eater bird *Merops orientalis* Latham (Coraciiformes: Aves).

In the present investigation, *Megachile disjuncta* was found to colonize artificial nesting structures, and the study confirms that *M. disjuncta* can easily adapt to bee hotels, unlike the other resin bees found in the area. This observation highlights a significant opportunity to utilize these bees for enhancing pollination efficacy and rates, particularly in crops such as alfalfa, sun hemp, pigeon pea, and a wide range of vegetables. Placing artificial nesting substrates such as bamboo canes and *Ipomoea* reeds near or within crop fields could significantly improve pollination. However, further research is needed to find ways to increase nest occupancy and regulate natural enemy infestations.

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Authors' Contribution

P: Investigation, data curation, formal analysis, and writing-original draft, writing-review &editing.
AP: Conceptualization, methodology, supervision, investigation, bee specimen identification, writing-original draft, writing-review & editing.
MCN & MKL: Conceptualization, methodology, supervision,
AV: Formal analysis and Software.
All authors have read and approved the manuscript.

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