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Foraging behaviour and flower handling routine of insect visitors indicate amphiphilous pollination strategy in *Mimusops elengi*

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Abstract

Mimusops elengi L., commonly known as bakul, from the family Sapotaceae, is a well-known avenue tree. Previous studies have classified the tree as wind-pollinated, but there have also been reports of *M. elengi* flowers being foraged by honeybees and other insects. Historical data on these visits are not detailed enough to determine whether they were occasional or regular occurrences. This study aimed to evaluate the performance of floral visitors by indirectly assessing pollen deposition through their foraging activities, such as visitation frequency and duration. During the peak flowering season, we documented 21 species of floral visitors, including bees, wasps, butterflies, and birds, on *M. elengi*. This study highlights the coexistence of different pollination strategies, such as anemophily, entomophily, and amphiphily, in *M. elengi*. However, further research is needed to understand these pollination mutualisms.

Key words: bees, insects, pollinators, *Mimusops elengi*, amphiphilous pollination strategy.

Introduction

The Spanish cherry or bullet wood, *Mimusops elengi* L., is commonly known as bakul. This large evergreen tree, native to India and other tropical regions, can grow up to 15 meters tall. With its attractive foliage and fragrant flowers, it is well-suited for urban landscapes. The tree is resilient to varying soil conditions and moderate air pollution, making it an excellent choice for urban greening projects. Contributing to urban biodiversity, cultural heritage preservation, and attracting to pollinators, *M. elengi* further enhance its suitability for such projects (Jim and Chen, 2008; Escobedo *et al*., 2011).

Chemical analyses reveal tannin, caoutchouc, wax, starch, and ash in the bark, volatile oils in the flowers, and fatty oils in the seeds. Bakul extracts exhibit antibacterial, analgesic, antifungal, anticariogenic, antioxidant properties (Baliga *et al*., 2011). Preclinical studies suggest potential effects, including antimicrobial, antioxidant, and hypotensive effects of *M. elengi* or its phytochemical components (Kadam *et al*., 2012) and also gains reference in Ayurveda.

The bakul tree bears small star-shaped white flowers, emitting a sweet fragrance even when dried. *M. elengi* is functionally unisexual, existing in three types. In the first type, the flowers have functional stamens but do not bear fruit. The second type has only functional ovaries and does bear fruit, while the third type has both stamens and ovaries, allowing it to produce fruit. To prevent self-pollination, a cone formed by inner corolla lobes keeps stamens separated from the stigma. Stigma loses its receptivity before pollen liberation. The species follows xenogamy, relying on pollinating agents for cross-pollination (Reddi and Bai, 1980; Mitra, 1981, Sukri *et al*., 2021).

There is a view that bakul may be wind-pollinated, despite lacking typical wind-pollination traits. The potential production of 159464 pollen grains per flower aligns with a wind pollination strategy (Reddi and Bai, 1980). However, some studies have identified insect pollination syndromes, such as the presence of nectar with high sugar concentration, albeit in low volumes (Sukri *et al*., 2021). Wenzel *et al*. (2020) and Sukri *et al*. (2021) also observed honeybees and other insects foraging on the flowers.

In practice, pollen deposition as a measure of pollinator performance is often modified or replaced by other parameters, such as the duration of pollinator visits to flowers, visit frequency, or pollinator abundance (Ne'eman *et al*., 2010). This study aimed to evaluate the performance of floral visitors by indirectly assessing pollen deposition through their foraging activities. In addition, the diversity and abundance of flower visitors were also investigated.

Materials and methods

Selection of study sites

M. elengi plants from the avenues and parks at Kalyani, West Bengal, India (figure 1) were chosen randomly. Data were collected in the flowering season during April to June, 2021. The geo-coordinates were recorded by GPS (Garmin e-trex). Two types of plants, i.e., one with only flower and another bearing both fruit and flower were considered for the study as both of them produce pollen.

The study was categorized in three steps as follows: (1) focal observation of floral visitor, (2) focal observation to study the foraging behaviour of flower visitors, (3) flower handling routine (FHR).

Focal observation of floral visitor

Focal observation of floral visitors was conducted around 14 *M. elengi* plants, each with three different transects (10 m × 2 m), at a steady speed of 1 km/h in a random direction that included the central *M. elengi* plant (figure 2). This study was replicated three times a day,

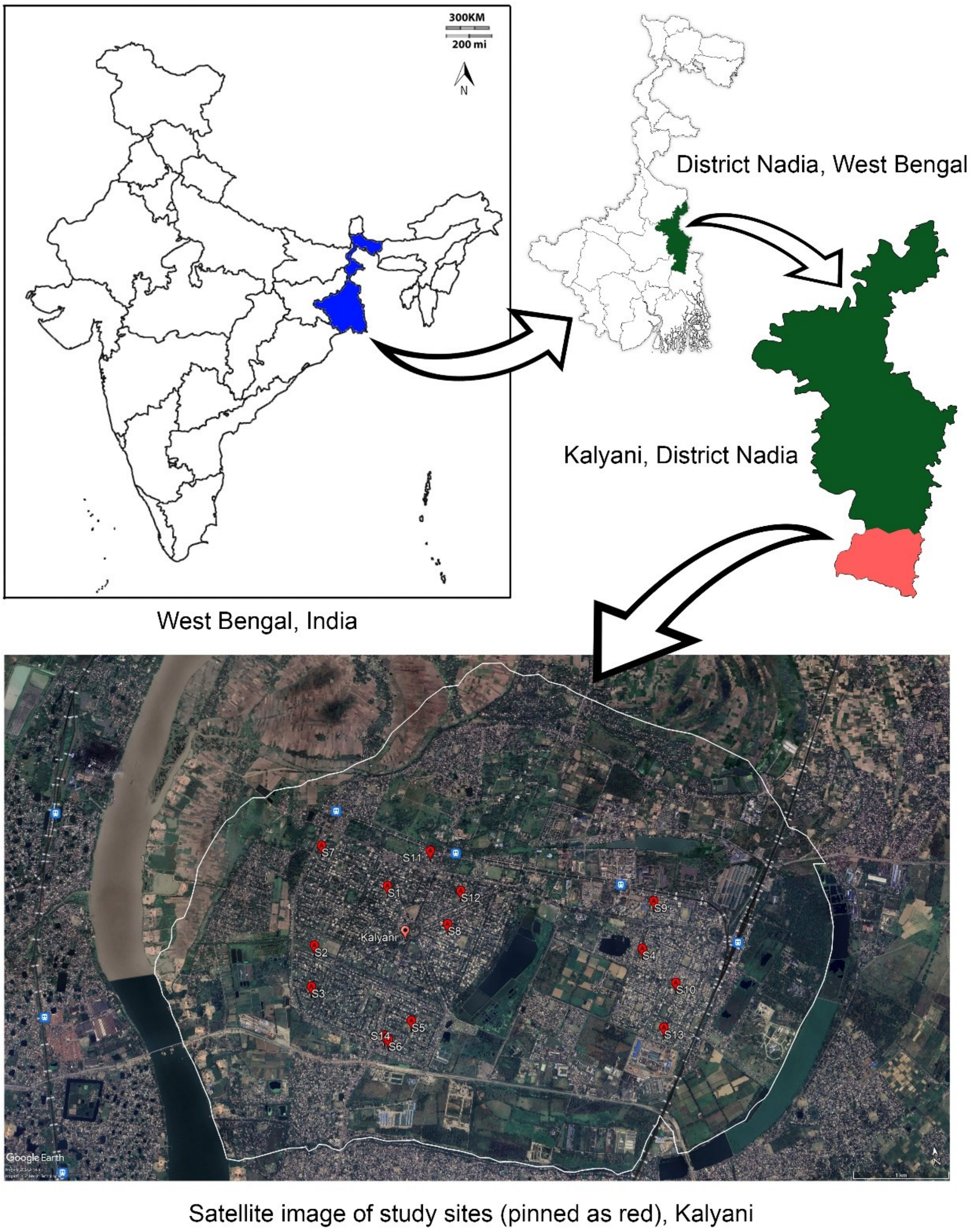

Figure 1. Study sites and relative positions along with satellite image.

from 8:00 to 14:00, on sunny days with moderate wind. The discriminate sweeping method (Prado *et al*., 2017) was used to collect insects visiting *M. elengi* flowers for taxonomic identification when needed. A sweep net with a telescopic handle adjustable from 55 cm to 180 cm was used. Floral visitors encountered along the transect were recorded, identified to the species level whenever possible. The average number of flower visitors observed around 14 distinct *M. elengi* trees was determined by combining data from three repeated transects conducted around each tree. The collected insect specimens were preserved in absolute alcohol.

There were only a few weed plants and grasses present around the central *M. elengi* plant. However, both focal observations and sweep netting were confined to the canopy of the *M. elengi* trees, which were located along the road.

Focal observation to study the foraging behaviour of flower visitors

Total 30 plants were selected from different avenues and parks. Each plant was observed for 30 minutes, at a go, thrice a day after Altmann, 1974. The insects were followed by sight through active searching and direct observation as in Sutherland, 2006 using Nikon Aculon A211 10×50 Binoculars and photographed with Nikon

Figure 2. Transect design (10 × 2 meters) represented in a white line in a study site.

p900 digital camera when possible. Data collected is mentioned in tables 1 and 2. The floral visitors were identified to the lowest possible taxonomic resolution. The information on time taken was normalized by employing an electronic stopwatch. Unique behaviour traits of the flower visiting insects were defined by modifying after (Giovanetti and Aronne, 2011) (table 2). A total of 11 unique foraging behavioural traits were observed (table 2). With the help of a stopwatch and a voice-recorder, behavioural traits of flower visitors were noted. Total observation time was 242 minutes.

Unmarked floral visitors were followed by sight while they were foraging among flowers. All flowers approached by these visitors within a distance less than 1 cm from the flower, were recorded (Giovanetti and Aronne, 2011). No insects or birds were marked during the study.

Flower handling routine (FHR)

FHR was established using behavioural traits of 5 major insect visitors, grouped as approaching / landing, flower handling time for resource collection, approaching to next flower / leaving (as shown in figure 3A, 3B and 3C). All the visits were legitimate involved active foraging or direct contact with stigmas.

Table 1. Flower handling routine (FHR) of flower visiting insects of *M. elengi* (mean ± standard error).

Flower visitor	Average duration (seconds) of each behavioural trait			Number of flower visit per visitor	Only pollen collection (%)	Pollen and nectar collection (%)	Total time observed (minute)	Total number of individuals observed	Frequency of visitor (visitor per minute)
	Approach/ landing time	Flower handling time	Approach/ leaving time						
A. dorsata	9.96 ± 1.44	23.44 ± 4.30	1.73 ± 0.21	1.31	38.81	61.19	124	67	0.83
Xylocopa sp. 1	0.9 ± 0.12	13.32 ± 0.78	0.46 ± 0.17	2.81	0	100	39	42	1.08
Xylocopa sp. 2	2.15 ± 0.15	8.5 ± 0.7	1.75 ± 0.35	3.80	0	100	45	10	0.11
C. collaris collaris	3.17 ± 0.15	21.2 ± 1.69	1 ± 0.12	0.91	100	0	25	32	0.68
D. conoideum	3.4 ± 0.6	24.15 ± 11.65	1.6 ± 0.6	0.57	25	75	30	14	0.47

Table 2. Unique behaviour traits of flower visiting insects received by *M. elengi* flower.

Behavioural unit code (BUC)	Description of behaviour
BU1	Preference for fresh flowers
BU2	Collecting nectar from half bloomed flowers
BU3	Visiting old flowers
BU4	Scratching flower with forelimbs
BU5	Pollen collection (through rolling the forelimbs)
BU6	Nectar collection (through proboscis extension)
BU7	Assist to open closed flower with their mouth part and pair of fore limbs
BU8	Use of hindlimb to collect pollen
BU9	Gathering pollen on the hind limbs
BU10	Fanning of wings during visitation
BU11	Buzzing

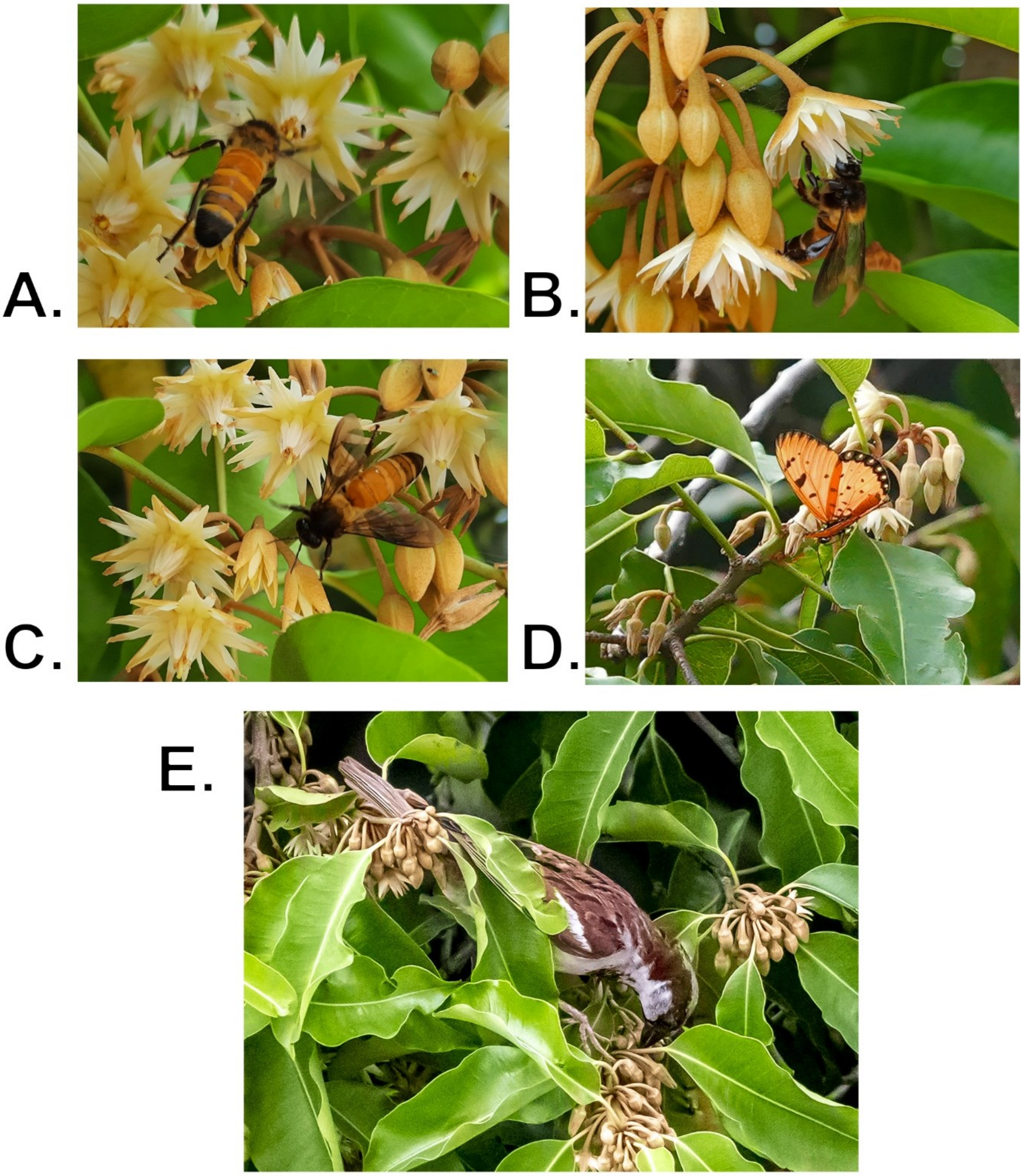

Figure 3. Foraging floral visitors of *M. elengi*. (**A**) Approaching or landing by *A. dorsata*, (**B**) flower handling by *A. dorsata*, (**C**) approach or leaving by *A. dorsata*, (**D**) *A. terpsicore* taking nectar, (**E**) foraging of *P. domesticus*.

Statistical analysis

Statistical analysis was done in *R- version* 4.2.1 and M.S. Excel 2016.

The study area map was created using ArcGIS 10.1, and the satellite imagery was sourced from Google Earth Pro.

Results

A total of 21 species of floral visitors were documented on *M. elengi* during the peak flowering season, as shown in table 3 and figure 4. Of these 21 species, 14 were regular visitors, frequently recorded with a higher visitor frequency and spending ample time handling the flowers (marked with * in table 3) during focal observation of floral visitor.

In total, 160 flower-visiting insects were observed on 262 *M. elengi* flowers, including 114 bees and 46 wasps during the FHR observations (table 1).

To determine the species diversity of the floral visitor community, Simpson's diversity index, species richness and species evenness were calculated to be 0.7224, 14 and 0.0989 respectively, based on legitimate visits.

A comparison was conducted between the number of

Table 3. List of flower visitors of *M. elengi* (* regular visitors).

Order	Family	Species
Hymenoptera (bees)	Apoidea	*Apis dorsata**, *Apis cerana*, *Xylocopa* sp. 1 (with yellow thoracic hair)*, *Xylocopa* sp. 2 (with black thoracic hair)*
Hymenoptera (wasps)	Scoliidae	*Campsomeriella collaris collaris**
	Vespidae	*Delta conoideum**, *Polistes flavus*
Lepidoptera (butterflies)	Pieridae	*Catopsilia pomona**, *Delias eucharis**, *Leptosia nina**, *Pieris canidia*
	Lycaenidae	*Zizula hylax**
	Nymphalidae	*Junonia almanac**, *Junonia lemonias*, *Danaus chrysippus*, *Acraea terpsicore*
Piciformes (birds)	Megalaimidae	*Psilopogon asiaticus*
	Muscicapidae	*Copsychus saularis**
	Pycnonotidae	*Pycnonotus cafer**
	Nectariniidae	*Leptocoma zeylonica**
	Passeridae	*Passer domesticus*

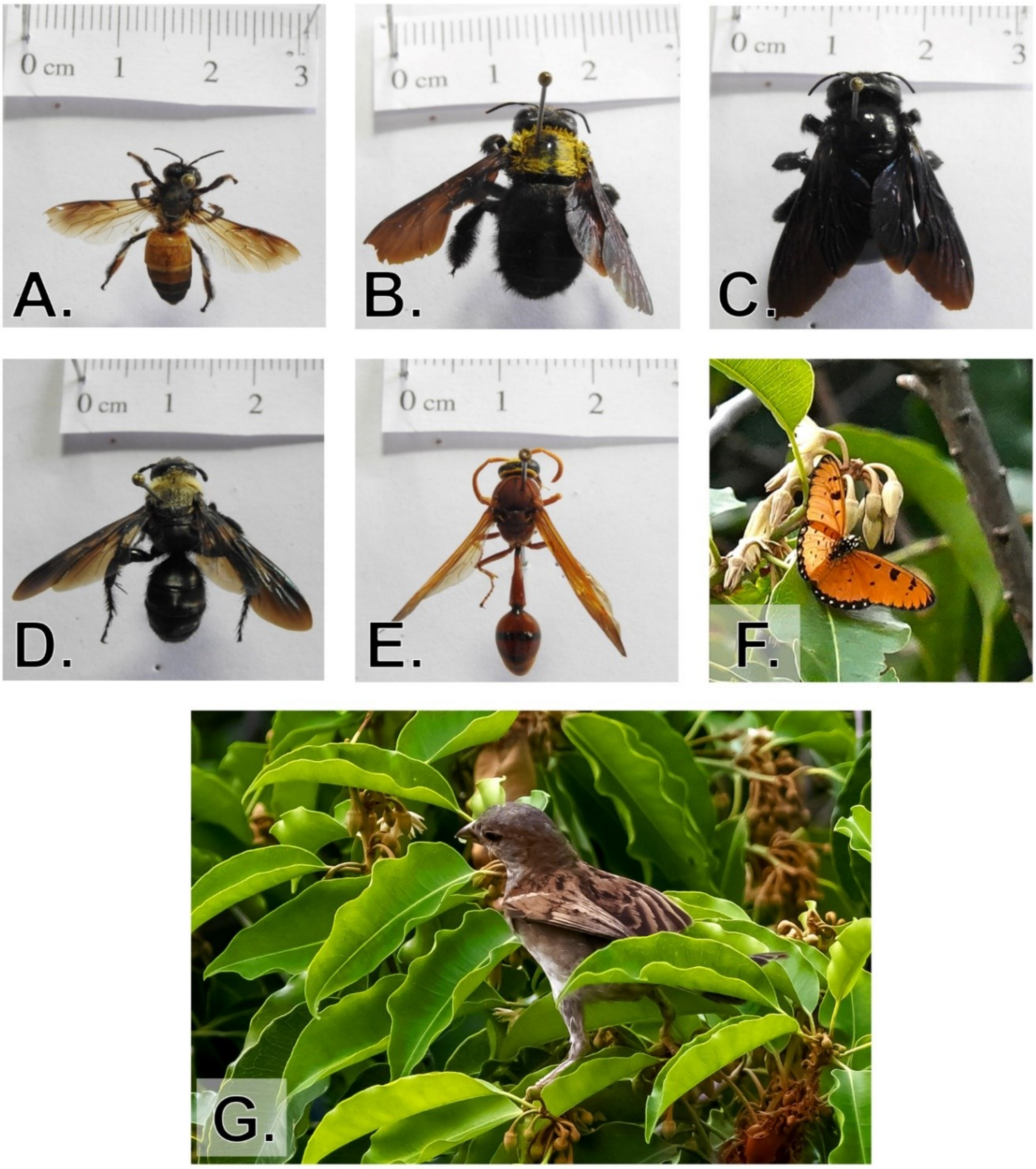

Figure 4. Visitors of *M. elengi*. (**A**) *A. dorsata*, (**B**) *Xylocopa* sp. 1, (**C**) Xylocopa sp. 2, (**D**) *C. collaris collaris*, (**E**) *D. conoideum*, (**F**) *A. terpsicore*, (**G**) *P. domesticus*.

Figure 5. (**A**) Fresh and bright, white coloured (potential pollen and nectar source) flowers, (**B**) brownish, partly dried flowers.

floral visitors observed on freshly bloomed white flowers rich in nectar and pollen and on old brown flowers lacking floral resources (figure 5). Since the data did not meet parametric assumptions, a Mann-Whitney U-test was performed, showing statistical significance (p-value 1.672×10^{-5}) between the number of floral visitors on freshly bloomed versus old flowers. Floral visitors tended to prefer fresh, bright white flowers, indicating these as potential sources of pollen and nectar. Specifically, honey bees such as *A. dorsata* spent significantly more time visiting freshly bloomed flowers compared to old ones (p-value 2.2×10^{-16}).

Foraging behaviour

The study could observe profuse pollinator visit in flower bearing plants. The foraging activity and flower handling routine were observed in 5 major flower visitor insects during focal observation. All of them were legitimate visitors with pollen dispersal potential.

Pollinator performance was assessed using parameters such as pollinator behaviour within the flower, including visit duration and visit frequency, as pollen deposition is often influenced by these factors (Ne'eman *et al*., 2010). In this study, the 'quantity' of visits was defined by the frequency of visitors (visitors per minute), the number of flowers visited per visitor, and the flower handling time, which serve as indirect methods to measure the success of pollen deposition.

The following observations substantiate that all the 5 insects (table 1) are actively involved in the collection of flower resources and their dispersal.

Flower handling routine (FHR)

We recorded the FHR (table 1) and foraging behaviours, such as landing position, orientation in flowers, and resource collection. In this study, flower handling time (seconds) represents the time spent on the flower collecting resources, which potentially aids in pollen dispersal. The mason wasp *Delta conoideum* (Gmelin) had the longest visitation duration (24.15 ± 11.65 seconds), followed by the giant honey bee *Apis dorsata* F. (23.44 ± 4.30 seconds) and the flower wasp *Campsomeriella collaris collaris* (F.) (21.2 ± 1.69 seconds). The carpenter bee *Xylocopa* sp. had moderately shorter times (13.32 ± 0.78 seconds and 8.5 ± 0.7 seconds). *A. dorsata* took the longest to approach or land on a flower (9.96 ± 1.44 seconds), followed by *D. conoideum*, *C. collaris collaris*, and *Xylocopa* sp. 2 (3.4 ± 0.6 seconds, 3.4 ± 0.6 seconds, and 2.15 ± 0.15 seconds, respectively). Notably, *Xylocopa* sp. 1 spent the least time (0.9 ± 0.12 seconds) on this activity before moving to the next flower. The time taken to approach subsequent flowers or leave a flower was similar among all visitors except *Xylocopa* sp. 1. Despite its low flower handling time, *Xylocopa* sp. 2 visited the most flowers per visitor (3.80), while *D. conoideum* visited the least (0.57). *Xylocopa* sp. 1 was the most frequent visitor (visitors per minute visiting a flower = 1.08), followed by *A. dorsata* and *C. collaris collaris*. *A. dorsata* and *Xylocopa* sp. collected 61.19% and 100% of available resources (pollen and nectar), respectively. *C. collaris collaris* carried numerous pollen grains on their body hairs but did not forage for nectar. *Xylocopa* sp. 1, *A. dorsata*, and *C. collaris collaris* had higher flower visitation rates per minute (1.08, 0.83, and 0.68, respectively), while *Xylocopa* sp. 2 and *D. conoideum* had lower rates (0.11 and 0.47, respectively). Visitation rate serves as a measure of pollinator quantity and helps assess pollinator effectiveness (Herrera, 1987).

Unique foraging behavioural traits

In addition to FHR, 11 behavioural traits related to foraging were observed in the study (table 2). We calculated species-specific individual behaviour traits or units (BU) exhibited by flower-visiting insects on *M. elengi* flowers (figure 6). A total of 110 records were collected. A bar diagram (figure 6) illustrating species-wise behavioural traits on *M. elengi* flowers showed that traits like preference for fresh flowers (BU1), pollen collection (BU5), and using fore and hind limbs to collect pollen (BU8) were the most frequently observed. Among the five insect taxa studied, nectar collection behaviour (BU6) was observed in all except *C. collaris collaris*. Scratching flowers with forelimbs (BU4) was a common behavioural trait noted in four of the flower-visiting insect taxa.

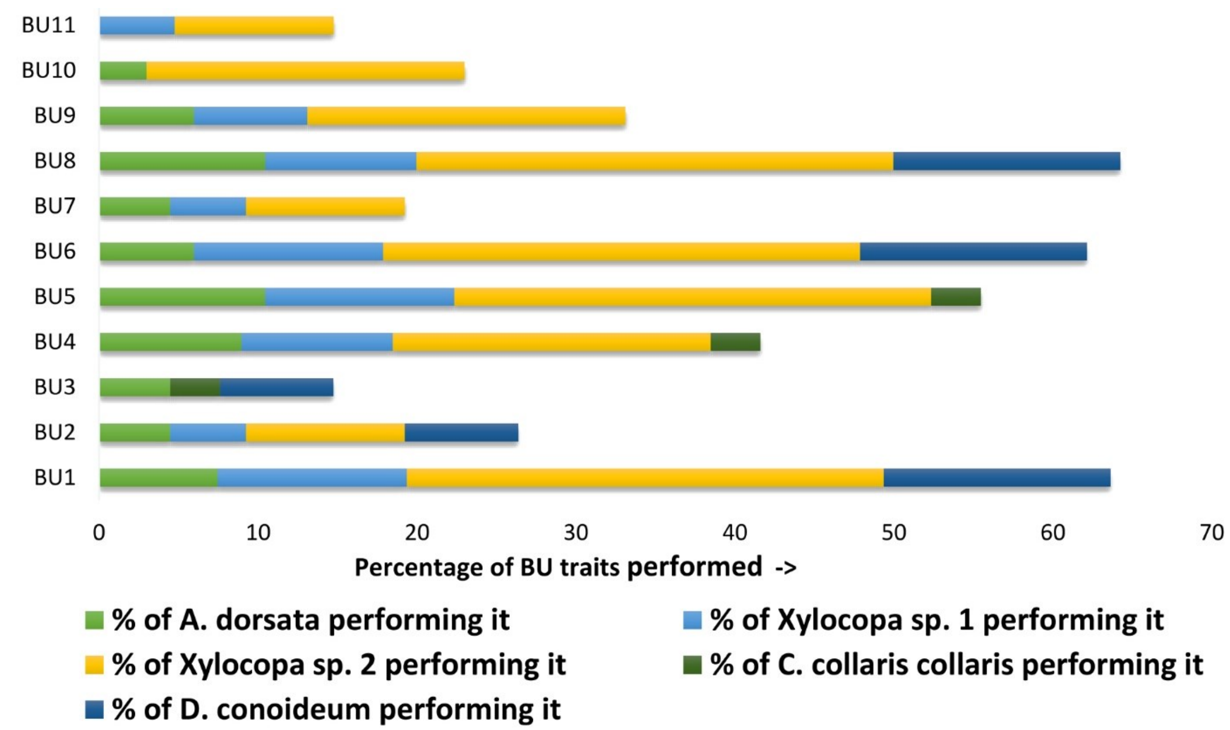

Figure 6. Percentage of behavioural traits of flower visiting hymenopteran insects on *M. elengi* flowers.

Comparison of major traits aiding in pollen collection exhibited by the five insect taxa studied:

- *Xylocopa* spp. led in BU5 (pollen collection by rolling the forelimbs), followed by *A. dorsata*.
- *A. dorsata* exhibited traits such as pollen collection through forelimb rolling (BU5) and the use of hind limbs to collect pollen (BU8) at the highest frequency (10.45%) and frequently scratched flowers with forelimbs (BU4) (8.96%).
- Both *Xylocopa* sp. 1 and *Xylocopa* sp. 2 showed a preference for visiting fresh flowers (BU1) and collecting pollen (BU5) and nectar through proboscis extension while also using fore and hind limbs to collect pollen (BU8).

Some additional observations

Other interesting observations on the behavioural study, not included in the analysis, being:

- When present in large numbers *C. collaris collaris* outcompeted other insect visitors, like *A. dorsata* (in a focal observation of 25 minutes, 32 *C. collaris collaris* individuals were noted. They visited approximatively 4-5 flowers per minute).
- *Xylocopa* sp. buzzed the flowers almost in every visit selecting mostly the freshly bloomed flowers over the old flowers.
- The pierid, lycaenid and nymphalid butterflies were observed to forage for relatively shorter durations (1-3.5 seconds' visit on a single flower), but several flowers were visited in a short time.
- Tawny coaster butterflies were also found to visit several flower clusters, one after the other.
- Small flocks of sparrows were found visiting several panicles of *M. elengi* flower daily.
- Apart from the above, 4 bird species were also found to visit *M. elengi* (table 3). All of them were local resident birds and fall under the IUCN least-concern species category.

Discussion

Evolutionarily, traits like the presence of pollen, nectar and fragrance, serve to attract pollinators. Flowers that are scented and with sugary rewards are often insect pollinated (Momose *et al.*, 1998). *M. elengi* flowers are fragrant and are good resources for pollen and nectar (Wenzel *et al.*, 2020), attracting several groups of flower visitors.

The FHR study (table 1), explains the frequent mutualistic interactions between the flowers and insects in terms of resource (nectar and pollen) collection for which they spend sufficient time and effort. Pollinator performance measurement and indirect methods of pollen deposition through foraging behaviour of insect visitors strongly indicates their role in pollen dispersal, similar to the study by Sukri *et al.*, 2021. Pollen collection behaviour was noted as rolling the forelimbs (Giovanetti and Aronne, 2011) and attachment of pollens to the body hairs (Nagasaki, 2021). Nectar collection was through proboscis extension (Giovanetti and Aronne, 2011).

Along with Apidae bees, scoliid wasps were also found as pollen vector of *M. elengi* as plenty of pollen from the flowers were found deposited on their body hairs. Scoliid wasps primarily feed on carbohydrates derived from nectar (Spradbery, 1973) and honeydew (Illingworth, 1921) but have also been observed as pollen vectors in wild grapes, *Ampelopsis glandulosa* (Nagasaki, 2021), likewise this study.

In the present study, it was observed that *A. dorsata* and *Xylocopa* spp. collected pollen (BU5) and gathered it on their hind limbs (BU9), which are typical steps in pollen collection that can often lead to cross-pollination (Hoffman *et al*., 2018).

The brief foraging visits by pierid, lycaenid, and nymphalid butterflies (table 3) suggest that *M. elengi* flowers offer only small quantities of nectar, as noted by Reddi and Bai (1984).

In addition to the aforementioned species, blue-throated barbets (*Psilopogon asiaticus*), oriental magpie-robins (*Copsychus saularis*), red-vented bulbuls (*Pycnonotus cafer*) and purple-rumped sunbirds (*Leptocoma zeylonica*) were observed foraging on *M. elengi* flowers (table 3). Our study also documented house sparrows (*Passer domesticus*) collecting resources from these flowers (figure 3E), although they were noted to mutilate the flowers in the process. House sparrows have previously been reported as occasional nectar feeders on *Aloe arborescens* (Leveau, 2008). Notably, the nectarivorous purple-rumped sunbirds were also observed feeding on nectar from *M. elengi* flowers.

As an adaptation to prevent self-pollination, the stigma loses its receptivity before pollen grains are released, emphasizing the necessity for cross-pollination either by wind (Reddi and Bai, 1980) or by biotic agents (Sukri *et al*., 2021, Rao and Raju, 2022). This can be an instance of proterogyny (Honek, 1997; Buck, 2001). Since the stigmas in partially bloomed *M. elengi* flowers are typically receptive, bees visiting these flowers may transfer pollen from their bodies, thereby facilitating cross-pollination.

M. elengi was initially considered to be wind-pollinated (Reddi and Bai, 1980) despite lacking typical wind-pollination characteristics (Kerner, 1904; Knuth, 1906; Percival, 1965; Whitehead, 1969; Faegri and Pijl, 1971; Ehrendofer, 1973). However, some studies have reported insect pollination syndromes, such as the presence of sweet fragrance, nectar with high sugar concentration, but low volumes (Reddi and Bai, 1980; Sukri *et al*., 2021). This suggests that insect visitors may play a significant role in pollination, particularly under unfavourable weather conditions for airborne pollen dispersal, indicating that *M. elengi* may not be exclusively wind-pollinated.

This study puts light on the possibility of co-existence of different pollination strategies like anemophily and entomophily or amphiphilous (wind + insects) pollination strategy (Giovanetti, 2018; Layek and Karmakar, 2018) in *M. elengi* plants, as in the case of *Fraxinus ornus* and *Castanea sativa* (Giovanetti and Aronne, 2011) and several other seemingly anemophilic plants like *Elaeocarpus* and *Pandanus tectorius* (Corlett, 2004). Amphiphilous pollination refers to a type of pollination that involves the transfer of pollen between flowers by both wind and animals. Birds may aid in pollen dispersals, but insects, especially bees are recorded to be very frequent and regular floral visitors, which may often lead to pollen transfers. Mutualistic benefits of pollinators and *M. elengi* contribute to the sustenance of both the parties of this ecological interaction. The mechanical disturbance by the floral visitors can lead to pollen release thus benefiting the plant, increasing their reproductive success. Amphiphilous pollination strategy as observed in this study reveals underrated costs and benefits in the plant- animal interactions related to *M. elengi*, warranting more studies.

Conclusions

From an evolutionary perspective on pollination strategies, studying insect visits to wind-pollinated species could reveal overlooked advantages and disadvantages in plant-animal interactions. Different pollination strategies in the same plant species promotes reproductive fitness and sustenance. As outcome of this study, the coexistence of diverse pollination strategies and mutual benefits between pollinators and the flowers of *M. elengi* contribute to the survival and well-being of both participants in this ecological interaction. How significant is zoophily to wind pollinated plants, demands further exploration.

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