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Interactions between non-flying mammals and flowers of *Cullenia exarillata* Robyns (Bombacaceae), a canopy tree from the wet forests of Western Ghats, India

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Many non-flying mammals help in the pollination of plant species in tropical forests. However, this remains poorly documented from India. Here we demonstrate with *Cullenia exarillata*, a canopy tree in the Western Ghats, how a wide range of visitors frequent flowers of the tree and how among them a few select mammals are important in pollination. Since *Cullenia* also uses bats as a pollinating vector, we further discuss how the dual strategy of using non-flying mammals and bats could have evolved in the wet forests of the Western Ghats.

Keywords: *Cullenia exarillata*, non-flying mammals, pollination, Western Ghats.

POLLINATION by arboreal non-flying mammals is a rare phenomenon in tropical forests compared to other forms of pollination[1–3]. A recent study conducted in the wet forest of the Western Ghats showed that only 2 out of 89 species of trees were pollinated by mammals[1]. The few instances of non-flying mammal pollination systems that have been observed in tropical forests are interesting for several reasons. First, often flowers are the critical resource for animals during times of food scarcity in the forest and are considered as a keystone resource for them[4–6]. Second, they are often found in areas that are least conducive to other forms of pollination by insects, birds or bats because of cold and wet conditions[7]. Third, they are believed to occur in areas where bats as pollinators are non-existent[8].

Non-flying mammals pollinate trees in Australia, south and central Africa and tropical America[7]. This is not uncommon in countries of the southern hemisphere, mainly because members of the family Proteaceae that are pollinated by many marsupials and rodents apart from birds, are fairly abundant and species-rich[9]. In other parts of the world, families such as Bombacaceae, Combretaceae, Fabaceae and Melastomaceae are also visited by non-flying mammals[7,10,11]. Non-flying mammal pollinators also comprise of many diverse terrestrial mammals ranging from rat to giraffe[9,12–18]. Primates are more often viewed as flower predators because they inflict heavy damage to floral parts while handling flowers. However, Kress *et al.*[19] have

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demonstrated that *Ravenala madagascariensis* was predominantly pollinated by ruffed lemur that is dependent on the nectar of these plants during certain times of the year. *Cullenia exarillata*, an evergreen tree species of the Western Ghats, is reported to be an important keystone species for primates such as the lion-tailed macaque[6,20,21]. However, the reciprocal role of *Cullenia* getting pollinated by primates or other visitors is not understood.

Here we provide evidence of how non-flying mammals are important for *Cullenia*. We also describe the flower and its flowering characteristics of the species, identify the role played by different flower visitors in pollination and flower predation, establish the probable pollinator/s of the species and discuss the evolutionary consequence of non-flying mammal pollination in the wet forests of the Western Ghats.

This study was part of a long-term programme which is in progress since 2000 to understand the role of the dominant canopy tree species, *C. exarillata* on the structural and functional aspects of the wet evergreen forests of the Western Ghats. This is being conducted in the pristine wet evergreen forests at Kakachi (8°33′35″N; 77°22′93″E) of Kalakad–Mundanthurai Tiger Reserve (KMTR), Tamil Nadu, southern India. The wet forests in the reserve occur above 800 m elevation and extend up to around 1600 m. *Cullenia*-dominated forests are more common in the mid elevation wet forests[22] between 900 and 1300 m. The area receives over 3500 mm rainfall annually, spread over 6–7 months in a year.

C. exarillata is a tall (25–30 m) canopy tree. It is an abundant species in the area (119 ha^{-1}) and flowers annually from December to April. The tree is out-crossed and produces anywhere between 300 and 30,000 brownish-yellow tubular flowers in dense clusters around the terminal branches as a classical case of cauliflory[23]. The flowers are tubular and fleshy and are held in a pedicel which is thick and short, and the flowers are borne on numerous woody protuberances on branches. Hundreds and thousands of flowers crowd around the thick woody branch giving an appearance of a giant bottle brush. Nectar is embedded on the inner walls at the basal portion of the sepals as the flowers do not have petals and reproductive parts such as the style and the anthers protrude out of this tube (Figure 1). It is the succulent fleshy base of the flowers soaked with nectar that the visitors prefer and they discard the remaining parts. In the process, they either completely remove the flowers along with the ovary and style or delicately remove the fleshy sepals like a sleeve, leaving the ovary and style intact. An intact style means there is a greater chance of it producing fruits.

The flowers are visited by a variety of animals. We used different techniques to document these visitors and the flower-handling behaviour. To document and record the frequency of visitors to the flowers, we set infrared-based passive camera traps in the canopy during *Cullenia* flowering from 2001 to 2004. The cameras were strapped around vertical branches, 20–25 m above ground facing the flowering branch. The tree was accessed using a single rope climbing gear used in canopy studies. The camera recorded the time of visit of various visitors to the flowers and captured a picture of the visitor each time the animal visited the branch. This enabled us to work out the frequency of visits by various visitors. We carried out camera trap observations on 11 trees, each spanning over seven continuous days and nights and over a three-year period.

Since camera traps could only record frequency of visits and not how animals handle the flowers, supplemental direct observations of the visitors were also made for several hours (368 h). Nocturnal animals were observed using a torchlight with a red cellophane paper wrapped over the bulb, as the animals are less sensitive to red light. Dense foliage and overall shyness of the animals made observations difficult. Flower processing by nocturnal visitors was often difficult and we had to resort to indirect methods like collecting fallen flowers to identify species and how it is processed. Initially for both the nocturnal and diurnal visitors, the falling flower parts, as the animals processed, were collected and examined. This helped us determine what parts are eaten by various visitors even after the animals had left the trees. This was especially ideal to record bat visits to the tree, as they sometimes devour the flowers at the tree itself. These flowers were also observed for traces of predation. Fallen flowers with style were considered predated and those where only the sepals were discarded, were assumed to have left the style and ovary intact on the tree, allowing for fruit formation. We also made observations in the canopy over temporary platforms with binoculars to check this and found it to be true in most cases (T. Ganesh, unpublished data). Over 20 flower traps of 1 m × 1 m were set under 40 trees for this purpose and each trap was visited in the morning and again in the evening to record visitors to the tree. Bats were captured using mist nets in the canopy of the flowering trees to identify the species. Multiple year observations carried out over a period of four years from 2001 to 2004 generated adequate data on animal foraging on *Cullenia* flowers.

The cameras and observers recorded seven species of mammals visiting the flowers. These include the lion-tailed macaque (*Macaca silenus*), Nilgiri langur (*Trachypithecus johnii*), giant squirrel (*Ratufa indica*), giant flying squirrel (*Petaurista petaurista*), Malabar spiny dormouse (*Platacanthomys lasiurus*), dusky striped squirrel (*Funambulus sublineatus*) and the brown palm civet (*Paradoxurus jerdonii*) (Figure 1) and two species of bats. Apart from these, over 16 species of birds, two species of social bees, few butterfly species and few other insects such as ants, beetles and moths were also encountered.

The pattern of mammal visits to the flowers based on canopy camera trap data shows a late morning peak, unlike the usual early morning peak, observed for most vertebrate visited flowers. Nocturnal visits peak at dusk
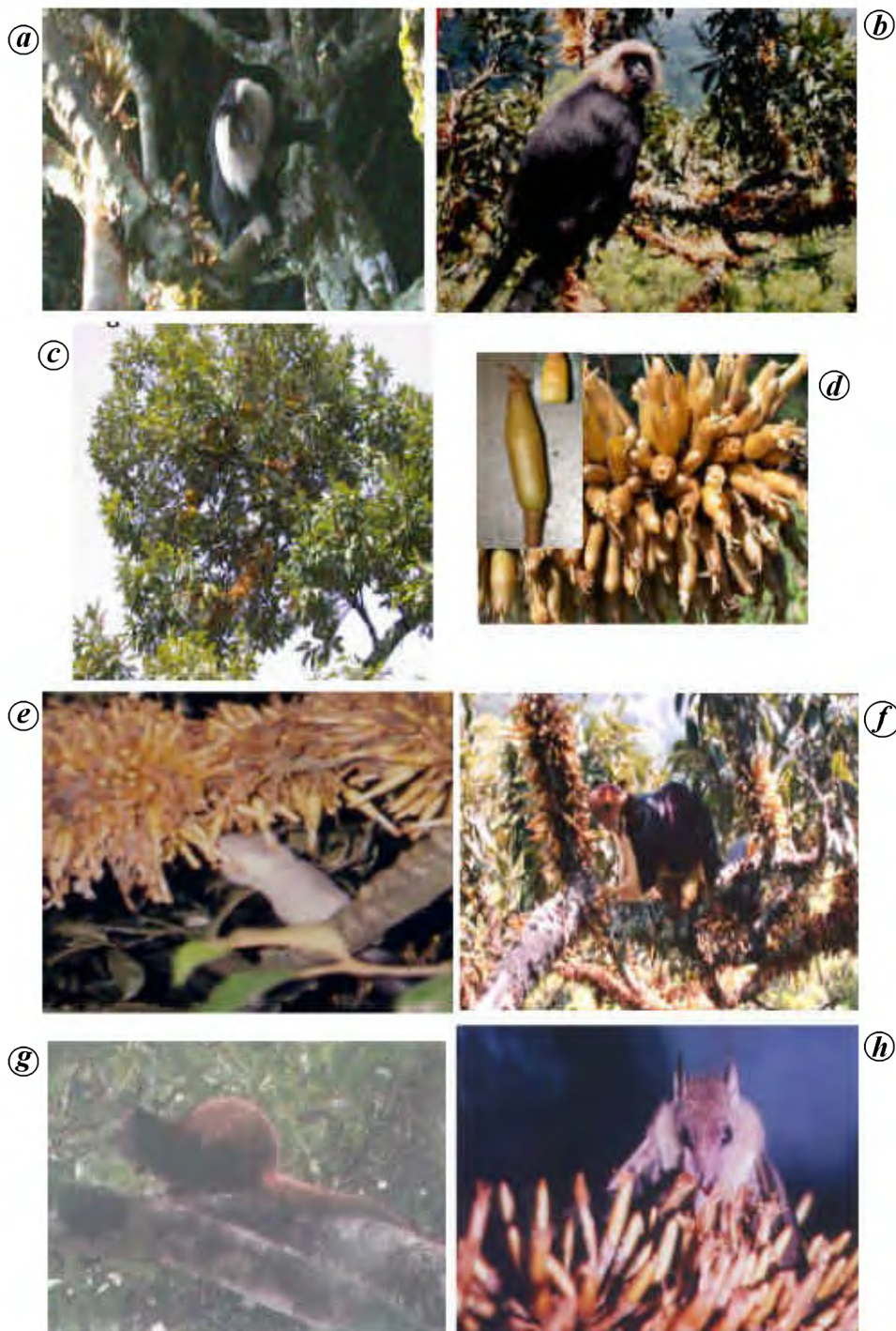
Figure 1. *Cullenia exarillata* is a large canopy tree whose flowers and fruits are eaten by a variety of animals in the forests. *a*, *Macaca silenus*, *b*, *Trachypitecus johnii*, *c*, Cullenia tree, *d*, Nectar embedded in the tissue and sepal has to be chewed (inset) for extraction, *e*, *Platacanthomys lasiurus*, *f*, *Ratufa indica*, *g*, *Paradoxurus jerdonii*, *h*, *Rousettus leschenaultia*.

followed by few sporadic visits at night (Figure 2). The frequency of visitors to the flowers is more from diurnal flower visitors than by nocturnal visitors. Between 6.30 am and 6.30 pm the tree received a total of 25 visits over a period of 7 days. During the same period night visits between 6.30 pm and 6.30 am was 21. This difference is ex-

pected as two of the three common visitors during the day are primates. They come in troops that comprise 10–15 individuals. The nocturnal visits are entirely by solitary foragers such as flying squirrel and palm civets. Bats visited only certain individual trees heavily and this comprised a small proportion of total individuals present in the forest.
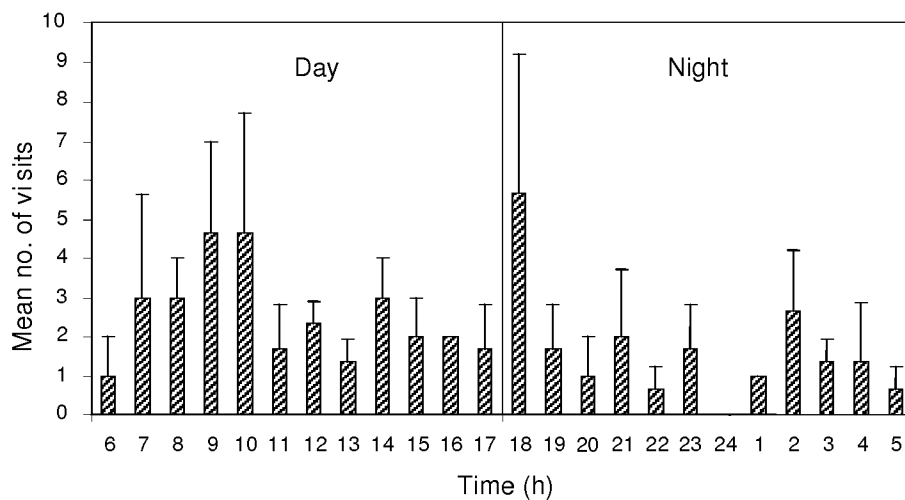
Figure 2. Diurnal and nocturnal visitation by non-flying mammals to flowers of *Cullenia exarillata* in the wet evergreen forests of Kalakad–Mundanthurai Tiger Reserve (mean ± SD, $n = 1680$ h).

Table 1. Flower visitors and their role in the pollination of *Cullenia exarillata*

Species	Pollinator/predator	Frequency	Diurnal (D)/nocturnal (N)	Possible pollinator
Lion-tailed macaque (*Macaca silenus*)	Pollinator and predator	+++	D	#
Nilgiri langur (*Trachypithecus johnii*)	Pollinator and predator	++++	D	#
Giant squirrel (*Ratufa indica*)	Predator	++++	D	–
Dusky striped squirrel (*Funambulus sublineatus*)	Predator	+	D	–
Brown palm civet (*Paradoxurus jerdonii*)	Predator	++	N	–
Malabar spiny dormouse (*Platacanthomys lasiurus*)	Predator	++	N	–
Giant flying squirrel (*Petaurista petaurista*)	Predator	+++	N	–
Short-nosed fruit bat (*Cynopterus sphinx*)	Pollinator and predator	+	N	#
Fulvous fruit-bat (*Rousettus leschenaultia*)	Pollinator and predator	+	N	#
Birds	Predator/pollinator	++	D	–
Arthropods	Pollen robbers	+	D/N	–

++++, Daily visits; +++, Not daily; ++, Occasional; +, Rare.
#This is based on fallen flower collection that indicated escape from total predation. It was not possible to indicate how much is the escape from each species, but put together primates and bat-eaten flowers only showed escape from total predation.

Visitation by bats was rare in most sites except along the forest edges.

Not all visitors to the flowers were pollinators but invariably all visitors predated the flowers. Based on direct observations and flowers processed by foragers, the amount of damage done to the flowers was quantified for each visitor. Almost all visitors help in transferring pollen between (geitnogamy) and within a flower (autogamy), and in the process predate on the floral tissues. Rodents (squirrel and dormouse) and palm civet eat the flowers and are considered as predators. Primates also predate, but leave behind a few flowers intact or remove only the sepals. These subsequently lead to fruit set (Table 1). Bats were observed choosing the right phase of the flowers, removing them like a loose sleeve and leaving the style and ovary intact, which resulted in fruit set. Nearly 50% of the bat-processed flowers collected from the flower traps did not have the style, and these can be considered

Table 2. Comparison of the characteristics of bat and non-flying mammal pollinated flowering systems with those of *C. exarillata*

Flowering characteristics	Bats	Non-flying mammals	*Cullenia exarillata*
Size	Medium to large	Large	Small
Shape	Solitary/infloresence/ clustered/tubular	Cup-shaped	Tubular, large number
Display	Not much	Good	Good
Anthesis	Late in the day	Day/night	Day
Firm construction	Yes	Yes	Yes
Borne on robust/short branches	Yes	Yes	Yes
Colour	White, creamish	Dull	Dull brown
Nectar volume	Large (ml)	Large (ml)	Very small (μl)
Nectar concentration	Dilute	Concentrated	Concentrated
Sucrose-rich nectar	Yes	Yes	?
Odour	Musty	Musty	Musty
Quantity of pollen	Plenty	Not much	Plenty
Flowers exposed	Yes	Yes	Yes
Longevity	Short (few hours)	Long (several hours)	Long (several hours)
Prolonged flowering	Short (couple of weeks)	Short (couple of weeks)	Long (a month or more)

as not predated. Bats were also documented eating the style at times, as noticed from chewed flowers found below their temporary night feeding roost sites.

Birds probed the flowers sideways and few species such as black bulbul (*Hypsipetes madagascariensis*) and white-cheeked barbet (*Megaliama viridis*) probed from top, damaged the reproductive parts and sometimes completely devoured the flowers. None of the bird-visited flowers results in fruit set. Insects such as bees and beetles visited the flowers for pollen. The frequency of their visits was low and they did not manage to completely remove the pollen from the flowers. Insects could be transferring pollen to adjacent flowers and selfing a few flowers, but these also did not result in fruit set (T. Ganesh, unpublished data).

Flowers pollinated by non-flying mammals usually possess large flower heads with copious nectar and inflorescence, with mechanically strengthened tissues (particularly the style) that could accommodate a large mammal without undue damage to the floral tissues. In case of *Cullenia*, there are no big flowers with copious nectar. Nectar levels in *Cullenia* are usually a few microlitres. Most of the nectar is embedded in the inner wall of sepals and is not filled up to the brim[23], but flowers are held strongly by the short and thick stalk to the branch and cannot be easily dislocated. A large number of flowers produced in the tree compensates for the low quantity of nectar per flower. Anthesis of *Cullenia* is prolonged, but flowers provide nectar only for a day or two after the anthers dehisce. This is not common with non-flying mammal pollination, where most of the nectar and pollen are removed during the night or over the following day. This makes the flowering phenology of *Cullenia* interesting as it does not have a parallel in both non-flying mammal and bat-pollinated flowers reported earlier[7]. The two characteristics most similar with bat-pollinated flowers are the large amount of pollen produced per flower and the fermented,

musty odour found in *Cullenia* flowers (Table 2). All three have strong pedicels supported on branches. In short, 7 out of 12 flower characters are common with non-flying mammal pollination syndrome and 6 out of 12 with bat characters (Table 2). *Cullenia*, therefore, not only seems to share the characters of non-flying mammal and bat pollination systems, but has certain unique traits.

Now the question arises as to why *Cullenia* has evolved floral traits that overlap between the bat and non-flying mammal syndromes which attract a contrasting kind of pollinator, one a social animal and another largely a solitary forager. The ability to have a dual pollination strategy by night or day is not entirely new. Several species do have this strategy as a back-up mechanism to compensate if one of them fails[24]. Such strategies evolve in systems where there is uncertainty in pollinator visits. In Kakachi forest, primates are reliable visitors compared to bats. Occurrence of fruit bats in the site is highly seasonal (T. Ganesh, pers. obs.) and patchy, more often restricted to the edges of the forest. This could lead to poor fruit set in the forest interior. Some preliminary evidence does show that this is true. The need to have a reliable but not a very efficient pollinator which is diurnal (primates), is a means to buffer from complete failure at times when bats become unavailable.

Flowers of *Cullenia* are densely packed along branches and it takes a week to 10 days for a branch to complete flowering. Primates and squirrels visit trees regularly and harvest a considerable number of flowers. It was also observed that trees which were not visited on a regular basis by them were infected by fungus and subsequently no fruit set was observed. Selective thinning of the dense clusters by diurnal mammals appeared to increase the probability of flowers setting fruits (T. Ganesh, unpublished data). The tree seems to have adapted to rely heavily on mammal visitors by producing a large number of flowers and at the same time kept its odour to attract bats.

Many Bombacaceae species are pollinated by a diversity of animals ranging from insects, birds, bats and arboreal mammals[10,25]. Most of the other Bombacaceae species reported from India are either pollinated by birds or bats[26]. *Cullenia* does not have a typical flower with free flowing nectar, which could by utilized by birds. It offers soft floral parts (basal part of sepal) with embedded nectaries soaked with nectar as reward, which is best suited for mammal-handling.

Non-flying mammal pollination system is considered as a relatively primitive form of pollination system[8,19]. The dual strategy of *Cullenia* is a helpful clue to understand the evolution of such systems. Sussman and Raven[8] highlight the importance of bats in the evolution of non-flying mammal pollination. They stress the fact that non-flying mammals evolved in areas where bats are few or non existent. In Kakachi, this is not entirely applicable because both primates and bats co-occur. However, differential visits to the trees based on habitat characteristics do indicate the importance of primates as well as bats in the pollination of *Cullenia*. In this site, primates are reliable visitors of *Cullenia* and bats are not. In the closed undisturbed forest, primates are the major pollinators of the species. Bats visits were few and far apart. In contrast, *Cullenia* trees in the disturbed forests and along the edges of the forests attracted bats in large numbers. This points to the fact that *Cullenia* is a non-volant, mammal-pollinated species that benefits from bat visits in disturbed environments.

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Palmar dermatoglyphics of the scheduled caste Madigas in Andhra Pradesh

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The study reports on bilateral palm prints among 400 unrelated individuals (200 males and 200 females) of Madigas in two revenue districts of Cuddapah and Chittoor in Andhra Pradesh were collected and analysed. The principal mainline formula is frequently occurring modal type in either sex. The highest incidences of Mainline D, Mainline C, Mainline B and Mainline A endings were commonly observed in types 11, 9, 7 and 3 respectively. Majority of the individuals possess axial triradius at t irrespective of sex difference. A general trend of the prevalence of the true patterns in decreasing order can be seen as IV interdigital area > III interdigital area > hypothenar area > thenar/I interdigital area > II interdigital area. The above values of the present study compared to other populations reveal the values are within the range of AP caste populations.

Keywords: Axial triradus, Madigas, mainline endings, principal mainline formula, true patterns.

HUMAN populations are known to differ in terms of a number of characteristics of anthropological significance.

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