

FLOWER USE BY ARBOREAL MAMMALS AND POLLINATION OF A RAIN FOREST TREE IN SOUTH WESTERN GHATS, INDIA

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ABSTRACT. *Cullenia exarillata* (Bombacaceae), a common tree of south Western Ghats, flowers during times of fruit scarcity in the rain forest and thus attracts the entire diurnal and nocturnal frugivore community. In addition to bats, the frugivores include many non-volant mammals and birds. Little information exists on the pollination mechanism of *C. exarillata* or on the major pollinators among its visitors. All mammal visitors to the tree eat the flowers, and a study was conducted from 1996 to 1998 on the role of these mammalian vectors in pollination of *C. exarillata* at Kakachi, a rain forest site in the Kalakad Mundanthurai Tiger Reserve of south India. Data suggest that *C. exarillata* may represent the first documented case of a predator-pollinator system for a mammal-pollinated tree species.

Key words: rain forest, flowers, mammals, pollination, India

INTRODUCTION

Flower characteristics of tree species in the tropics have evolved and diversified in response to flower-visiting animals (Knudsen & Tollsten 1995). These phenotypic traits of flowers along with their corresponding pollinators have been categorized broadly into several pollination syndromes (Faegri & van der Pijl 1979). Some flower-pollination systems, however, do not fit any of the syndromes described, especially in the Old World tropics where fewer pollination studies have been carried out compared to the New World tropics (Appanah 1990, Bawa 1990, Kress 1993, Devy 1998). Pollination by arboreal mammals, which is yet to be studied intensively, needs to be explored, because flowers provide flower-visiting animals with critical resources during periods of fruit scarcity in some forests (Terborgh 1986, Bawa 1990, Menon 1993). Thus a study was made of flower characteristics and the pollination mechanism of a tree species in the rain forest of Western Ghats, India—a tree whose flowers are visited by a variety of mammals and birds.

Flowers of *Cullenia exarillata* (Bombacaceae), a common tree of south Western Ghats, are visited by bats, many non-volant mammals, and birds. At the study site, the trees flower during times of fruit scarcity, which results in the convergence of the entire diurnal and nocturnal frugivore community on them (Menon 1993, Ganesh & Davidar 1997). Little information exists on the pollination mechanism of *C. exarillata* or on the major pollinators among its visi-

tors. Because all of the mammal species that visit this tree eat the flowers (Ganesh & Davidar 1997), we chose to investigate the role of mammalian vectors in pollination of *C. exarillata*. The study site was Kakachi, a mid-elevation (ca. 1250 m) rain forest with more than 3500 mm of annual rainfall in the Kalakad Mundanthurai Tiger reserve of south India. The study was conducted from 1996 to 1998. *Cullenia exarillata* is the dominant species in the area, with 65 individuals per ha (Ganesh et al. 1996).

METHODS

Anthesis (the harvestable stage), nectar levels, and sucrose concentration of nectar were determined by observing 30 tagged mature buds at 2-hour intervals. Observations continued until the perianths dried up. Stigma receptivity was determined by pollinating the flowers with cross pollen at various stages; and fruit set was followed after 2 weeks. Observations on flower visitors, carried out from vantage points and canopy rafts, were made from 6.30 to 12.30 hours for diurnal visitors and 18.00 to 22.00 hours for nocturnal visitors. Observations were replicated on a minimum of five trees. During each observation period, we recorded the number and species of visitors, the way flowers were handled by each species, and the stage at which the flowers were harvested. Where direct observations did not yield sufficient data, indirect observations were made of discarded flowers. Flowers that fell to the ground below the trees were distinguished broadly as having being partly eaten by primates, squirrels, birds, or bats (Ganesh & Davidar 1997). We sampled fallen

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FIGURE 1. Cauliflory exhibited by *Cullenia exarillata* requires whole branches to be bagged for pollination experiments.



FIGURE 2. Equipment used to access flowers of *Cullenia exarillata*.

flowers from five trees to estimate the damage inflicted on the flowers by the various visitors.

Pollination experiments such as geitonogamy, autogamy, and xenogamy were conducted using previously bagged flowers. Because *Cullenia exarillata* exhibits cauliflory, whole branches need to be bagged (FIGURE 1). On five trees, branches with mature buds were bagged for exposure to diurnal and nocturnal visitors, with both exposures made on each tree. All the experiments were carried out from tree rafts erected at the canopy and accessed by ladders (FIGURE 2). Fruit set was scored after 15 days.

RESULTS AND DISCUSSION

Cullenia exarillata exhibits cauliflory with flowers clustering on woody knobs in the branches. Each flower is 4–5 cm long and pinkish brown in color. The sepal is modified to a long tubular form that envelops the staminal tube, inside of which are the ovary and a long wiry style (Gamble 1928). Nectar, held between the sepal and the staminal tube at the base of the flower, is accessible only by removing the sepal. Pollination is thus not possible by any species with long proboscides or beaks.

Another distinct feature of *Cullenia exarillata* flowers is their slow flower growth, which requires more than 60 hours for complete maturation. In contrast, other mammal-pollinated flowers last 24–48 hours (Sazima & Sazima 1978, Kress et al. 1994). The stigma appeared

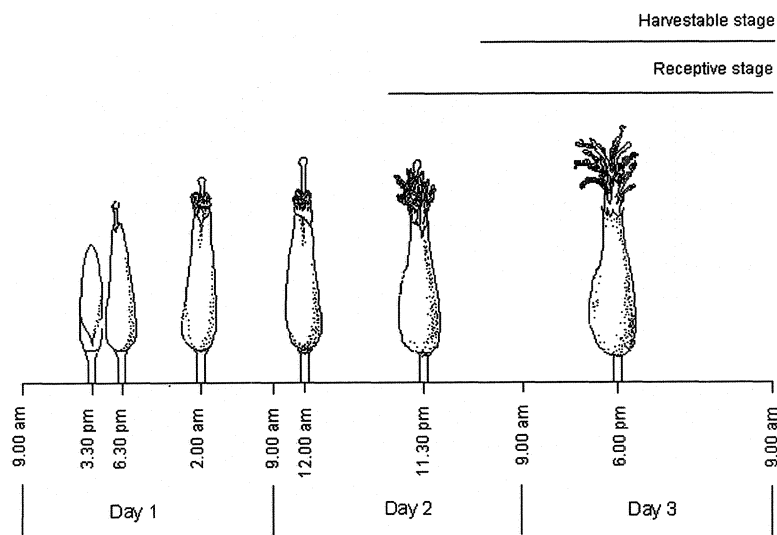


FIGURE 3. Extended anthesis of *Cullenia exarillata*, showing stages of flower maturation and the receptive and harvestable stages of the flower.

first at 15.00–16.00 hours, and the style grew to ca. 8 mm. The anther lobes appeared later in whorls, as a result of the staminal tube growth. In all, five such whorls appeared sequentially during the next 30 hours. The base of the flowers swelled as nectar accumulated. The whole sepal (which is fleshy) also softened, swelled, and became detachable (similar to a loose sleeve) from the pedicel at the final stages of anthesis, inflicting little damage to the stigma or ovary (FIGURE 3).

In bat-pollinated *Freycinetia* (Cox et al. 1991) and *Madhuca indica* (Fageri & van der Pijl 1979), nectar is the reward; but in *Cullenia exarillata*, the sepal embedded with nectaries is the prize. *Cullenia exarillata* produced exceptionally low levels of nectar (2–10 μl , $x = 5.5 \pm 3.2 \mu\text{l}$, $n = 20$), compared to other mammal-pollinated flowers. The tree, however, produced comparable percentages (10–13%, $x = 11.1 \pm 1.6\%$) of sugar concentration (Baker 1973, Howell 1976, Sussman & Raven 1978, Sazima & Sazima 1978, Lumer 1980, Scogin 1980, Janson et al. 1981). Concurrent with nectar accumulation, an appreciable amount of fragrance was released by the flowers in the evenings. Flower fragrance was not apparent at other times of the day. These characteristics make *C. exarillata* distinct from other mammal-pollinated flowering trees.

Because *Cullenia exarillata* flowers during times of fruit scarcity at the site, all frugivores converge on its flowers (Ganesh & Davidar 1997). Four diurnal mammal frugivores visited the trees; two were primates, the lion-tailed macaque (*Macaca silenus*) and the Nilgiri langur

(*Trachyopithecus johnii*); and the other two were squirrel species, the Malabar giant squirrel (*Ratufa indica*) and the dusky-striped squirrel (*Funambulus sublineatus*). We also observed four nocturnal species, of which two were rodents, the giant flying squirrel (*Petaurista petaurista*) and the Malabar spiny dormouse (*Platanthomys lasiurus*). The other two night visitors were a brown palm civet (*Paradoxurus jerdoni*) and a fruit bat (*Cynopterus sphynx*) (FIGURE 4). Ten species of birds frequent the flowers: black bulbul (*Hypsipetes madagascariensis*), yellow-browed bulbul (*Lole indica*), red-whiskered bulbul (*Pycnonotus jocosus*), small green barbet (*Megalaima viridis*), spider hunter (*Aracanothra longirostris*), small sunbird (*Nectarinia minima*), white eye (*Zosterops palpebrosa*), quaker babbler (*Alcippe poiocephala*), scmittar babbler (*Pomatorhinus horsfieldi*), and white-breasted laughing thrush (*Garrulax jerdoni*).

Because data were inadequate to calculate systematic visitation rates, we used observations of flower handling to compare damage to flowers caused by the various visitors. Most visitors ate the flowers and damaged the style, resulting in flower predation. The squirrels and the dormouse did the maximum damage, followed by the primates (TABLE 1). Pollen was neglected completely by primates, squirrels, and the dormouse; but civets often swallowed the entire mature flower. In all cases, flowers were damaged. The least damage to the style was noticed in bat-visited flowers, where more than 50% of the flowers handled had intact styles. Although



FIGURE 4. *Cynopteres sphinx*, a bat pollinator of *Cullenia exarillata*, is shown feeding on flowers.

birds do even less damage to the style, flowers abort after birds visit (M.S. Devy unpubl).

Visits by nocturnal mammals resulted in 10 times more fruit set than did visits by diurnal mammals, although this difference is statistically insignificant (Mann Whitney $U = 21$, $N = 11$, $p = 0.11$, all frugivores, TABLE 2). Such differences could be the result of damage inflicted by the visitors. Both diurnal and nocturnal flower visitors, including the bats, inflict heavy damage on the flowers. Diurnal visitors probably inflict more damage, as they include primates and squirrels. With synchronous flowering both along a flowering branch and between flowering branches, a tree does not have many mature flowers per day. Thus visitors, especially diurnal ones, may have been eating immature flowers resulting in predation of the style.

Tight packing of the flowers in *Cullenia exarillata* promotes fungal growth that leads to high levels of flower abortion. Flower harvesting and removal therefore prevent fungal growth. Mammals, especially monkeys, help thin out

flowers by removing many of them during a single visit and by deliberately removing old fungal flowers from branches. Fungus removal by visitors may benefit the species, as the fraction of flowers that escape predation and retain styles and ovary then develop into fruits (M.S. Devy unpubl). Investment in huge floral output may be an adaptation that balances the benefits of attracting reliable pollinators against costs of excessive exploitation. By flowering during annual fruit scarcity, the tree is able to attract frugivorous mammals to the flowers as reliable pollinators (Ganesh & Davidar 1997).

Cullenia exarillata was out-crossed and produced negligible fruit set under geitonogamy and no fruit set under autogamy (TABLE 3). We determined stigma receptivity by cross-pollinating flowers on each of the three days following stigma appearance. Maximum fruit set was observed only during day 2 (TABLE 4). Flowers were receptive from the evening of the first day and almost for the whole of the second day, during day and night hours.

TABLE 1. Flower handling by visitors to *Cullenia exarillata* in a rain forest of south Western Ghats, India, 1996–1998. Percentage is shown in parentheses.

Flower-visiting species	Styles		Flower no.	Tree no.
	Bitten	Intact		
Primates	1458 (69)	653 (31)	2111	16
Squirrels, other rodents	2438 (95)	123 (5)	2561	18
Bats	777 (49)	821 (51)	1598	15
Birds	256 (21)	982 (79)	1208	22
Total	4929 (66)	2549 (34)	7478	

TABLE 2. Fruit set from flowers exposed to diurnal and nocturnal visitors to *Cullenia exarillata*.

Treatment	Flower no.	Fruit-flower ratio
Diurnal exposure	2164	0.002
Nocturnal exposure	6717	0.024
Control	5230	0.027

A temporal segregation was apparent between the receptivity stage and the harvestable stage of the flowers (FIGURE 1). This timing ensures minimal damage when flowers are harvested, because they are past the receptive stage and may be fertilized. Once flowers are pollinated, the styles are much more virile and can withstand flower handling by mammals, at least to some extent. In addition, the transfer of pollen to the stigma by visitors during the receptive stage occurred inadvertently as pollinators handled neighboring mature flowers. Pollination by visitors is facilitated by flowering asynchrony along a branch, because flowers in varying stages of growth are available for both diurnal and nocturnal visitors (see references in Knudsen & Tolsten 1995).

Many species, even those with floral traits adapted for nocturnal visitors, have had both diurnal and nocturnal visitors observed on them. The flowers of *Cullenia exarillata*, however, were receptive during an exceptionally long period of time, including both day and night hours. Such receptivity ensured pollination either by a diurnal or a nocturnal visitor.

The study considered the rationale for *Cullenia exarillata* attracting both day and night visitors and for its divergent floral traits compared to other bat- and other mammal-pollinated species. *Cullenia exarillata*, a common species in the mid-elevation rain forests of Western Ghats, produces an enormous amount of flowers. Such an outburst of flowering is unlikely to be serviced by a single group of vertebrate pollinators, such as only bats or only monkeys. The species thus depends on a variety of vertebrate visitors, including diurnal and nocturnal ones, for pollination. This dependence may have led to evolution of flower traits such as prolonged availability of flowers on a branch and the obligate removal of the sepal to access nectar. Such flower traits ensure a uniform method of flower manipulation by visitors, all of them frugivores, who become responsible for the tree's pollination. At the same time, the flower traits prevent undue loss of nectar to other visitors, such as insects.

Cullenia exarillata appears to have capitalized on the period of fruit scarcity in the forest

TABLE 3. Pollination experiments conducted on *Cullenia exarillata* using samples from three trees.

Treatment	Flower no.	Fruit no.	Fruit/flower ratio
Autogamy	142	1	0.01
Geitonogamy	246	1	0.00
Cross	266	59	0.22
Open	628	10	0.02

to attract visitors by offering them nutritious floral tissue, because nectar alone may be insufficient to sustain the frugivorous community during such periods. Even the tree structure of the species appears geared to attracting more non-volant heavy mammals than bats. Branches with numerous flowers clustered on woody knobs are exceptionally strong and robust and can bear the weight of visitors such as large monkeys. Usually these flowers occur on branches parallel to the ground that generally serve as walkways for many of the mammal visitors.

Sussman and Raven (1978) hypothesized that bat-pollinated trees were once pollinated by other mammalian flower visitors but that bats out-competed them or that other mammals became extinct before bats evolved. Trees and non-volant mammal pollinators may represent a co-evolved relationship between living fossils. The floral traits of *Cullenia exarillata* are adapted to take advantage of the present contingent of frugivores, including bats and others animals that are largely seed predators. Its pollination system differs from other systems involving non-volant pollinators, because flower predators pollinate the flowers. Similar strategies have been reported, but thus far only in tightly co-evolved insect-pollinated systems, such as figs pollinated by *Agonid* wasps and yucca by *Tegiticula* moths. Although more diffuse than insect systems, the *C. exarillata* relationship with pollinating-predators, which depends on an array of visitors, may be the first case of a predator-pollinator system within a syndrome of mammal-pollinated species.

TABLE 4. Stigma receptivity measured by fruit-set ratio during the 3-day study period. In each treatment, 20 flowers were pollinated daily. Five trees were sampled, three in 1996 and two in 1998.

Treatment	Day 1	Day 2	Day 3
Autogamy	0	0	0
Geitonogamy	0	0	0
Xenogamy	0	0.12 ± 0.09	0

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