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Bat pollination of kapok tree, *Ceiba pentandra*

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Two species of pteropodid bats *Cynopterus sphinx* and *Pteropus giganteus* visited inflorescences of kapok trees, *Ceiba pentandra* through the night. A third species, *Rousettus leschenaulti* infrequently visited the inflorescences. Both *C. sphinx* and *P. giganteus* foraged in groups and there were temporal variations in their visits to the trees. The ventral body surfaces of the bats were covered with pollen grains when they landed on the inflorescences to lap up the nectar. In addition to bats, moths also visited the inflorescences. Bat and insect-exclusion experiments were performed to study their pollination efficiency. Bats were more efficient in pollinating flowers of *C. pentandra* than other pollinators like insects.

ECOLOGICAL interactions between bats and plants are mutualistic, because they yield a direct positive gain in fitness to both. Bats obtain a source of nutrition from plants and in turn transport pollen and disperse seeds of plants¹. Frugivorous and nectarivorous bats are found in two of the

18 families: Phyllostomidae of the New World and Pteropodidae of the Old World tropical regions. Bats belonging to these families pollinate and disperse seeds of hundreds of species of plants, including many economically important species such as *Ceiba pentandra* (kapok), *Durio zibethinus* (durian), *Ficus* sp. (fig), *Mangifera indica* (mango), *Manilkara zapota* (chicle), *Musa* sp. (wild banana), *Ochroma lagopus* (balsa), *Eucalyptus* sp., *Careya arborea* and *Cullenia exarillata*^{2–5}.

Kapok trees *C. pentandra* are cultivated as well as found naturally in the evergreen forests of South India. They bloom at night and flowers emit a strong odour that attracts nocturnal pollinators⁶. The silky fibres of this plant are used in bedding and cushion materials. Kapok seed oil is a useful raw material in the soap industry⁷. *C. pentandra* produces thousands of flowers within a short period annually^{8,9}. In the New World tropics, marsupials (*Caluromys philander* and *Didelphis marsupialis*) and monkeys (*Saimiri sciureus*, *Cebus apella*, *Ateles paniscus* and *Aotus* sp.) pollinate *C. pentandra*¹⁰, whereas in the Old World, bats are the main pollinators of this plant^{11–13}. However, occasional occurrence of self-fertility in *C. pentandra* has been reported^{14,15}. Apart from bats, insects visit the flowers of *C. pentandra* both during night (moths) and day (bees and wasps). The aim of the present study is to investigate the pollination efficiency of pteropodid bats compared to insects.

The study was carried out in a small orchard containing 30 trees of *C. pentandra* that were surrounded by 25 coconut trees at Achampathu (site 1), located in the outskirts of Madurai city (9°58'N, 78°10'E). Additional observations were made on three more trees in the residential area of the Madurai Kamaraj University campus (site 2). The study was conducted from January to February 2004, when this species flowered. Bat species visiting these trees were captured for four nights from dusk to dawn (1800 to 0600 h) with nylon mist nets of 9 m length and 2 m wide with a mesh size of 38 mm (Avinet-Dryden, USA).

Sixty inflorescences (with only buds) were chosen from four trees – three at site 1 and one at site 2. The first set of twenty inflorescences (set 1/control) was covered with transparent polythene bags (40 × 30 cm) containing six holes, each with a diameter of 2 mm to allow only air circulation, but exclude both insect and bat-visits. The second set of twenty inflorescences (set 2) was covered with similar kind of bags containing four holes, each with a diameter of 2 cm to allow insect-visits, but exclude bat-visits. The remaining twenty inflorescences (set 3) were left untouched, and were exposed to both bat and insect-visits. All bags were numbered using 'permanent marker' pen for individual recognition. The bags were gently removed, soon after fruit set. The number of fruits produced from each inflorescence was noted to calculate fruit set index, by dividing the total number of fruits formed with the total number of flowers present in the respective inflorescence¹⁶. The fruit set index is 1, if all the flowers were developed into fruits, and it is 0 if no fruit was formed from any of the flowers. The total

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number of young fruits that were ultimately developed into mature pods was also recorded.

During the flowering season, *C. pentandra* sheds leaves. As most of the branches bore inflorescences at their terminal ends, the flowers were well exposed to pollinators. A single inflorescence consisted of 12.6 ± 7.4 flowers ($n = 60$). Anthesis occurred at 1920 to 1930 h ($n = 28$) and the petals remained open throughout the nights. The petals either began to close or the flowers dropped at 0615 to 0630 h ($n = 28$).

Mist-netting and visual observations revealed that two species of fruit bats, namely *Cynopterus sphinx* and *Pteropus giganteus* visited *C. pentandra* all through the night. Another species, *Rousettus leschenaulti* made infrequent visits. Although the visits of both *C. sphinx* and *P. giganteus* showed a bimodal pattern, there was a distinct temporal partition among their visits. The primary and secondary peaks on the visits of *C. sphinx* occurred at 1900 and 2300 h respectively. Whereas the corresponding peaks on the visits of *P. giganteus* occurred during 2200 and 0200 h respectively (Figure 1). Both species visited *C. pentandra* trees in groups. We observed that a maximum of eight individuals of (5.6 ± 1.35 , $n = 20$) *C. sphinx* fed upon nectar simultaneously from different inflorescences in a single tree without showing any intra-specific interference. Foraging activity of *C. sphinx* included hovering over the inflorescences, landing on them directly and lapping on nectar (Figure 2a). It fed a total of six to eight times on a single inflorescence every night and each bout lasted for 0.08 ± 0.04 min ($n = 10$). Similarly, 7–9 *P. giganteus* visited a single tree. There were aggressive interactions during foraging. Such intra-specific conflicts in *P. giganteus* were prominent between 1900 and 2000 h and lasted for a maximum period of 1.6 ± 0.8 min ($n = 20$). Unlike *C. sphinx*, *P. giganteus* neither hovered over the inflorescences nor landed on them directly. Instead, they landed on branches at a distance of 30–50 cm away from the inflorescences and then reached the latter with bipedal and quadrupedal movements. When close to the inflorescences they stretched one of their wings, slowly turned the flowers towards their mouths and started lapping the nectar. While feeding on nectar, they remained hanging upside down (Figure 2b). In a single feeding bout, *P. giganteus* lapped up nectar from 3 to 8 inflorescences for 3.8 ± 1.7 min ($n = 16$). On completion of feeding, *P. giganteus* stayed in the trees without showing much movement for 11.3 ± 8.1 min ($n = 6$) and then flew away.

Other than bats, some unidentified species of moths also visited the flowers of *C. pentandra* and consumed the nectar from both second and third sets of marked inflorescences. The activity of the insects was not observed throughout the night. However, their maximum visits occurred between 1800 and 2000 h (131.1 ± 38.8 , $n = 10$). A single inflorescence was visited by 4–6 moths at night. Bees (*Apis florea*, *Melipona iridipennis*) and wasps (*Ropalidia cyathiformis*) were observed in these trees during daytime (0700–1100 h).

However, during daytime the flowers were completely closed and these insects mainly fed on the honey left over on the inflorescence. A palm squirrel (*Funambulus palmarum*) was also observed ($n = 11$) in these trees in the evening hours (1500–1700 h), but it consumed about 3–4 entire flowers.

After 32.8 ± 3.6 days ($n = 60$), fruits were formed in all the three sets of inflorescences. Total numbers of fruit set and pod formation in each inflorescence are given in Table 1. We observed 81% fruit set from the uncovered inflorescences that were visited by both bats and insects. Fruit set in the inflorescences to which only insects visited was 56%, whereas it was only 41% in the control set of inflorescences. However, not all the young fruits were converted into mature pods. From the uncovered inflorescences 50% pods were produced. Insect visitation resulted in 22% pods compared to 14% in control. One-way ANOVA ($F_{2,57} = 15.96$, $P < 0.001$) showed that there is a significant difference in the fruit set among set 1 (control), set 2 (only insect-visits), and set 3 (both insect and bat-visits). Further analyses with Tukey multiple comparison test showed that differences between set 1 and set 2 were not significant ($t = 1.77$, $P > 0.05$), but it was significant between set 2 and set 3 ($t = 3.76$, $P < 0.01$) and highly significant between set 1 and set 3 ($t = 5.53$, $P < 0.001$). Out of a total of 355 visits made by *P. giganteus* in the entire study, we observed that on 24 occasions it fed upon the tender fruits of *C. pentandra*. However, *C. sphinx* never fed upon such tender fruits.

Table 1. Fruit set index (% fruits/flowers) in the control and treated inflorescences of *Ceiba pentandra*

Set	Types of inflorescence	No. of buds	No. of fruits	No. of mature pods	Fruit set index
1	Bagged flowers	229	94	33	0.41
2	Insect-visits	236	132	51	0.56
3	Open pollination	254	205	128	0.80

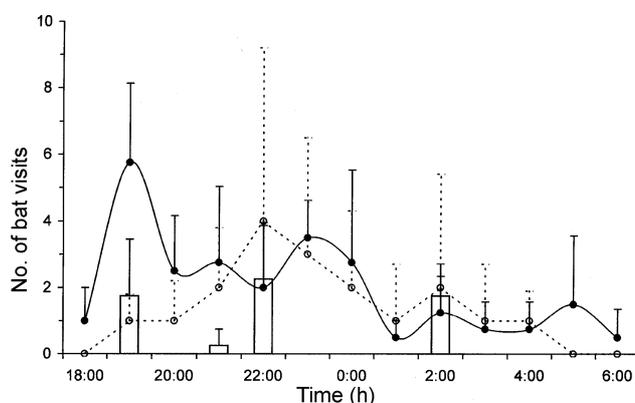


Figure 1. Nectar feeding visit patterns of three sympatric fruit bats during blooming period of *Ceiba pentandra*. Closed circle, *C. sphinx*; open circle, *P. giganteus*; vertical bar, *R. leschenaulti*; values are given as mean \pm SD.

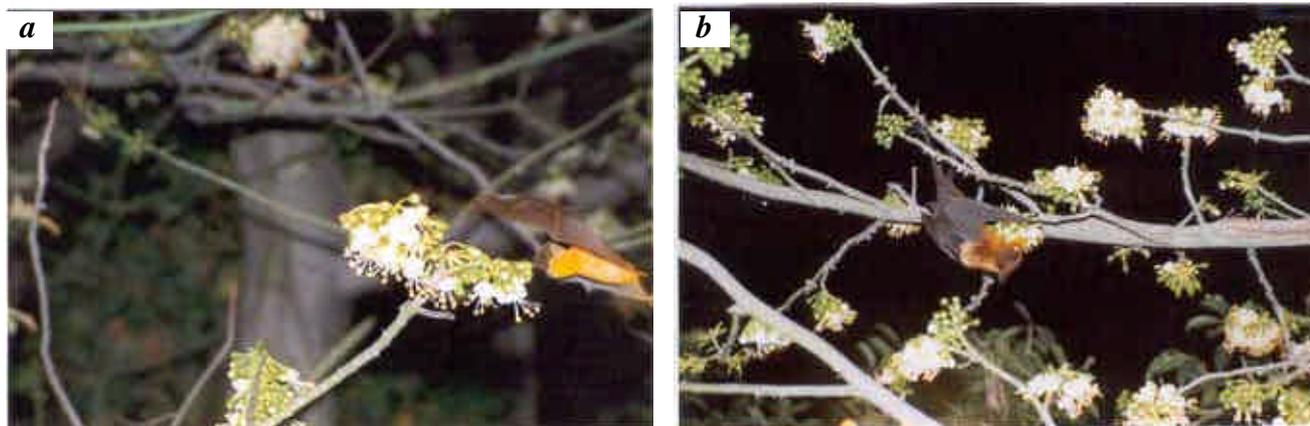


Figure 2. *a*, The Indian short-nosed fruit bat *Cynopteris sphinx* approaching *Ceiba pentandra* to feed on nectar (note the ventral body surface of the hovering bat is covered with pollen). *b*, The Indian flying fox *Pteropus giganteus* lapping nectar from the inflorescence of *C. pentandra*.

Our study supports a recent report¹⁷ describing pteropodid bats visiting inflorescences of *C. pentandra*. We demonstrate that both *C. sphinx* and *P. giganteus* were the principal visitors of *C. pentandra*, but *R. leschenaulti*, was visited rarely. However, in contrast to the earlier report¹⁷, *C. sphinx* and *P. giganteus* foraged in groups in our study. Usually in mass flowering plants such as *Ficus* species and *Bassia latifolia*, group foraging by bats is common¹⁸. Our study shows a similar pattern. The solitary foraging by bats on the nectar of *C. pentandra* in the previous study¹⁷ may be presumably due to variations in the area of canopy and lesser availability of bats in nearby habitats. The significantly greater duration of feeding bouts of *P. giganteus* and its lesser number of feeding visits compared to that of *C. sphinx* facilitate to conserve its energy that is needed to exhibit commuting flights, since flight cost increases with increase in body mass of bats¹⁹. The scanty visits of *R. leschenaulti* suggest that nectar of *C. pentandra* may be one of its less preferable food items. Alternatively, population size of *R. leschenaulti* was low around our study areas. Our study clearly shows that bats such as *P. giganteus* and *C. sphinx* are important pollinators of *C. pentandra*.

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