

## Nectar feeding behavior in the short-nosed fruit bat *Cynopterus sphinx* (Pteropodidae)

VADAMALAI ELANGOVA<sup>1</sup>, GANAPATHY MARIMUTHU<sup>1</sup>, and THOMAS H. KUNZ<sup>2</sup>

<sup>1</sup>Department of Animal Behaviour and Physiology, School of Biological Sciences, Madurai Kamaraj University, Madurai 625 021, India; E-mail of GM: gmarimuthu@usa.net

<sup>2</sup>Center for Ecology and Conservation Biology, Department of Biology, Boston University, Boston, MA 02215, USA

Nectar feeding behavior of the short-nosed bat, *Cynopterus sphinx*, was observed under natural conditions in South India. Nectar production of 'steady-state' flowers of *Musa × paradisiaca* and 'big-bang' flowers of *Bassia latifolia* was quantified. *Cynopterus sphinx* typically foraged alone on flowers of *M. × paradisiaca* and as groups on *B. latifolia*, largely in response to the availability of these floral resources. Peak visits on flowers of *M. × paradisiaca* by *C. sphinx* occurred at 2000 h and on *B. latifolia* at 2100 h. Peak visits coincided with the maximum nectar production and sugar concentration of these floral resources. In addition to feeding on nectar early in the evening, *C. sphinx* acquired additional energy by feeding on carbohydrate-rich fruit. In return for these food resources, *C. sphinx* provides important pollination and seed-dispersal services to the plants that they visit nightly, and thus can profoundly influence the co-evolution of plants and bats.

**Key words:** *Cynopterus sphinx*, nectar-feeding, plant-visiting, group foraging, solitary foraging, co-evolution

### INTRODUCTION

Almost 30 percent of all living bat species wholly or partially depend on plants for food (Fleming, 1982). These bats gain access to nectar, pollen, and/or fruit in exchange for pollination and seed-dispersal services. These interactions range from highly coupled to diffuse mutualistic relationships that have profoundly influenced the co-evolution of bats and plants (Heithaus, 1982). When selecting food resources, plant-visiting bats make at least four choices: (1) the kind of plant foods that are available, (2) how much of each food type is available, (3) where the food is located, and (4) how long the food is available.

Gentry (1974) recognized four basic flowering strategies, including 'big bang,' the production of large numbers of flowers over a short period, and 'steady state,' the production of a small number of flowers over an extended period. The other two strategies include 'cornucopia,' in which a large number of flowers are produced over a month's time, and 'multiple bang,' in which several widely spaced, large flower crops are produced annually.

In the present study, we chose the cultivated variety of banana tree (*Musa × paradisiaca*), a 'steady-state' species, and the butter tree (*Bassia latifolia*), a 'big-bang' strategist to investigate the nectar feeding behavior of the short-nosed fruit bat,

*Cynopterus sphinx*. This bat typically roosts in small groups in the foliage of the palmyra palm (*Borassus flabellifer*), the kitul palm (*Caryota urens*) (Bhat and Kunz, 1995; Storz and Kunz, 1999), mast trees (*Polyalthia longifolia*), and in vines of the curtain creeper (*Vernonia scandens*) (Balasingh *et al.*, 1993, 1995; Storz and Kunz, 1999). *Cynopterus sphinx* feeds on fruits of at least 23 plant species, leaves of eight species, and flowers of at least two species (Bhat, 1994; Ruby *et al.*, In press). Based on the quantity of floral resources available on a given night, we predicted that individual *C. sphinx* would feed on the steady-state flowers of *M. × paradisiaca* and that groups would feed on 'big-bang' flowers of *Bassia latifolia*.

## MATERIALS AND METHODS

We conducted our study on the campus of Madurai Kamaraj University (09°58'N, 78°10'E) from May 1996 to June 1997. Visual observations of bats were made continuously each hour from 1800 to 0600 h for ten nights at a single tree of *B. latifolia*, and for 83 nights at eight trees of *M. × paradisiaca*, for a total of 1,116 h of observation. Bats were captured near the source trees using mist nets, marked individually with collars, and fitted with aluminum bands that were covered with reflective tape. In addition, a chemiluminescent tag (Cormoron Mini Knichlicht, 3.0 mm × 2.5 mm) was attached to the collar with cyanoacrylic adhesive. The collar, together with the tags, weighed less than 5% of the animal's body mass; thus, we assumed that this additional mass did not alter the foraging behavior of the bats (Aldridge and Brigham, 1988). The duration of time that bats spent feeding on nectar during each visit was recorded using a stopwatch.

The volume of nectar produced by the entire male inflorescence of *M. × paradisiaca* was measured each hour between 1800 h and 0600 h on five trees, for a total of 552 hourly samples and 46 collection-nights. To prevent bats from visiting these flowers, each was covered with a nylon-mesh bag before the bracts opened. Samples of nectar were collected from each flower using a 1-ml syringe (without a needle) and transferred to 1.5 ml Eppendorf tubes. Because the flowers of *B. latifolia*

began to drop from the tree at 2100 h, we measured nectar production for 10 fresh flowers before this time. These flowers were not covered. Since each initial visit of *C. sphinx* to a fresh flower of *B. latifolia* was always accompanied by removal of the flower, we presumed that these 10 flowers were untouched by *C. sphinx*. The volume of each sample was quantified using a 200 µl Gilson pipetman. To estimate total sugar present in the nectar, we collected 500 µl from each hourly sample from two or three trees. Total sugar concentration was estimated after Dubois *et al.* (1956).

Differences in temporal patterns of foraging bouts and nectar production were examined using one-way ANOVA to independently compare the number of foraging bouts on flowers for each hour of the night. A Bonferroni procedure was used to correct for multiple tests (Sokal and Rohlf, 1995). One-way ANOVA and a Tukey's test were used to estimate the hours of peak foraging on flowers. The Kolmogorov-Smirnov test was applied to determine whether these data were normally distributed, and Levene's test was used to confirm homogeneity of variances (Sokal and Rohlf, 1995). All assumptions were met after the data were transformed to natural logs.

## RESULTS

The bracts covering the inflorescence of *M. × paradisiaca* began to open about 30 min after sunset. The number of creamy-white flowers ranged from 10 to 11, and each mature inflorescence lasted for only one night. *Cynopterus sphinx* began to visit banana flowers at the same time the bracts were sufficiently opened, and single bats made all visits. Each bat made two to three circling flights around the tree before landing on the bract. The bats hovered over the flowers, landed on the cone of the unopened bract and immediately crawled toward the inflorescence. Each bat inserted its rostrum into a flower and began lapping nectar, moving around the inflorescence and lapping nectar from two to three flowers before flying away. The duration of each visit averaged 46.4 s ± 40.9 SD (range 15 to 180 s, *n* = 688). Thus, each visit indicates that an individual *C. sphinx* landed on

a bract of *M. × paradisiaca* or a group of bats that removed flowers from *B. latifolia* (see below), followed by feeding on nectar. One-way ANOVA indicates that the peak visit of bats to *M. × paradisiaca* flowers occurred near 2000 h ( $F_{10, 44} = 3.5$ ,  $P < 0.01$ ; Fig. 1a).

Nectar production from flowers of *M. × paradisiaca* showed a steady increase beginning at 1900 h and peaked at 2100 h ( $F_{10, 44} = 2.94$ ,  $P < 0.05$ ). The average volume of nectar produced by a single inflorescence ranged from  $361.5 \mu\text{l} \pm 223.9 \text{ SD}$  ( $n = 46$ ) at 2100 h to  $24.5 \mu\text{l} \pm 0.3 \text{ SD}$  ( $n = 46$ ) at 0500 h. (Fig. 1b). The average volume of nectar produced per flower was  $2,520 \mu\text{l} \pm 817.6 \text{ SD}$  (range = 1,550 to 4,315  $\mu\text{l}$ ,  $n = 46$ ). Total sugar concentration in nectar from *M. × paradisiaca* collected between 1900 and 2400 was relatively constant, ranging from 235.3 to 224.0 mg/ml. By contrast, the minimum sugar concentration of nectar was 157.0 mg/ml at 0500 h (Fig. 1c).

*Cynopterus sphinx* began to visit flowers of *B. latifolia* about 30 min after sunset. A group of five to 25 bats visited the tree, where approximately 10,000 flowers of *B. latifolia* were available for bats each night. The flowers were small (mean mass = 240 mg) and white and located about 5 m above the ground. Each bat typically made circling flights around the flowering tree, briefly hovered over the flowers, landed on a branch with wings spread, picked up an entire flower using its mouth, sucked the nectar while in flight and dropped the flowers. One-way ANOVA showed that the peak visit to the *B. latifolia* flowers occurred at 2100 h ( $F_{10, 44} = 19.8$ ,  $P < 0.01$ ; Fig. 2). Once the flowers began to drop, visits to them also declined. The mean volume of nectar per *B. latifolia* flower was 179  $\mu\text{l}$  ( $n = 20$ ).

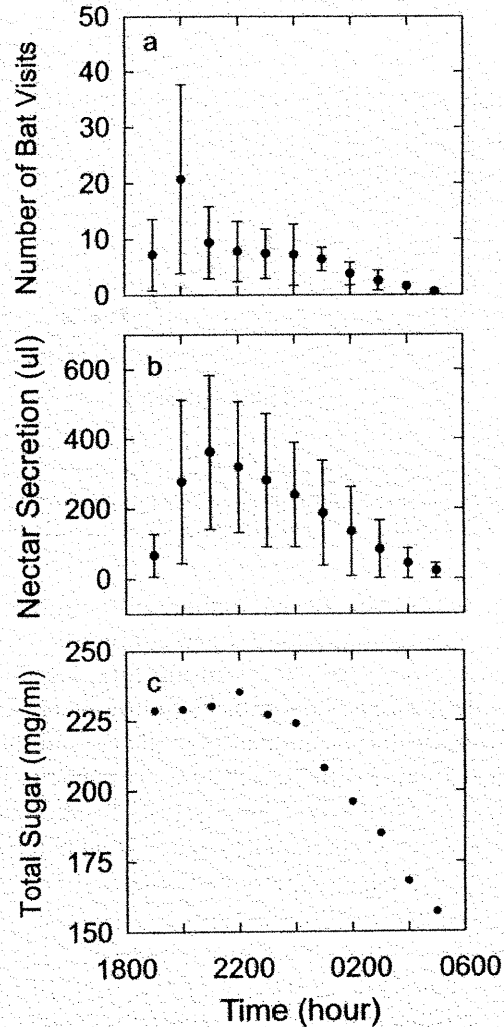


FIG. 1. Temporal pattern of (a) the number of visits made by *C. sphinx* while feeding on the nectar from flowers of *Musa × paradisiaca*, (b) volume of nectar produced by bagged flowers, and (c) concentration of sugar in nectar. Data for numbers of visits and nectar production are expressed as means  $\pm$  SD

## DISCUSSION

As predicted, *C. sphinx* foraged on steady-state flowers of *M. × paradisiaca* as singles and on big bang flowers of *B. latifolia* in groups. These results are consistent with the foraging patterns of other nectarivorous bats based on the availability of floral resources (Sazima and Sazima, 1977; Fleming, 1982; Heithaus, 1982). Solitary

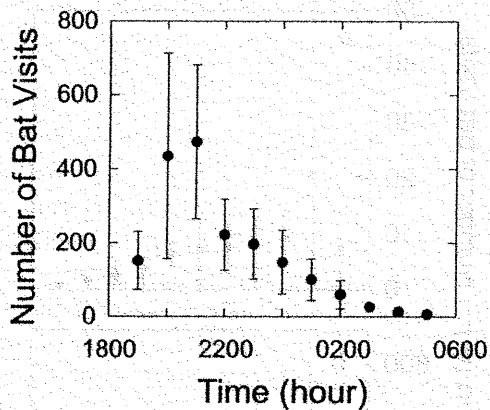


FIG. 2. Temporal pattern of flower visitations by *C. sphinx* while feeding on the nectar from flowers of *Bassia latifolia*. Data are expressed as means  $\pm$  SD.

foragers benefit by reduced interference while feeding, and reduced competition for food (Fleming, 1982). Group foraging provides three advantages, including increased protection from predators while commuting and foraging, increased sensory capacity to locate patchily distributed food, and increased knowledge of which food patches to visit by conspecifics (Howell, 1979).

*Cynopterus sphinx* feeds primarily on nectar (this study), fruits (Bhat, 1994; Marimuthu *et al.*, 1998), and leaves (Elangovan *et al.*, In press; Ruby *et al.*, In press). In addition it also feeds on flowers (Bhat, 1994) that probably include pollen. Pollen is an important protein source for megachiropterans (Law, 1992). The banana trees on which *C. sphinx* foraged in the present study were the cultivated variety and hence did not produce pollen (Start and Marshall, 1976). Nectar and fruits provide important sources of carbohydrates and water, and leaves provide important sources of protein and minerals (Ruby *et al.*, In press). The peak visitation times of *C. sphinx* on flowers of *B. latifolia* and *M.  $\times$  paradisiaca* by *C. sphinx* correspond to the periods of peak nectar production and sugar concentration. These observations are consistent with the

timing of visitations of nectar feeding bats (*Glossophaga longirostris* and *Leptonycteris curasoae*) to columnar cacti (Nassar *et al.*, 1997). When *C. sphinx* visits flowers of *B. latifolia* this bat possibly provides an important pollination service (Subramanya and Radhamani, 1993).

Plant characteristics that define pollination syndromes include time of anthesis, nectar secretion, color, odor, morphology, position of flowers, amount and protein content of pollen, volume of nectar, and concentration of sugar (Faegri and van der Pijl, 1979). The nightly emergence activity of *C. sphinx* coincides with the timing of bract opening, nectar production, and the faintly musty, sweet odor of *M.  $\times$  paradisiaca*. A conical bract covers the inflorescence of *Musa*, and this structure permits only a single bat to land and lap nectar from its flowers. With such remarkable suitability for bat-pollination, sterility of the cultivated variety of these bananas is surprising. Perhaps a study on a naturally occurring wild species of banana will exemplify the need for bat-pollination. By contrast, the small flowers of *B. latifolia* encourage *C. sphinx* to remove and transport them in flight. Removal of entire flowers by the bats to gain access to nectar suggests destructive foraging. However, we cannot rule out the possibility that when a flying bat detaches a flower, its pollen grains may be carried by the wind or even by the bat to nearby intact flowers. That the flowers of *B. latifolia* are dropped before midnight suggests that this species is pollinated exclusively by nocturnal visitors.

#### ACKNOWLEDGMENTS

We thank two anonymous reviewers for their suggestions. This study was supported by a Senior Research Fellowship to VE, and grants from the CSIR (No. 37/861) to GM and The Lube Foundation, Inc. to THK. This paper is contribution No. 69 of The Lube Foundation, Inc.

## LITERATURE CITED

- ADLRIDGE, H. D. J. N., and R. M. BRIGHAM. 1988. Load carrying and maneuverability in an insectivorous bat — a test of the 5% "rule" of radio-telemetry. *Journal of Mammalogy*, 69: 379–382.
- BALASINGH, J., S. S. ISAAC, and R. SUBBARAJ. 1993. Tent roosting by the frugivorous bat *Cynopterus sphinx* (Vahl 1797) in South India. *Current Science*, 65: 418.
- BALASINGH, J., A. J. KOILRAJ, and T. H. KUNZ. 1995. Tent construction by the short-nosed fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae) in Southern India. *Ethology*, 100: 210–229.
- BHAT, H. R. 1994. Observations on the food and feeding behavior of *Cynopterus sphinx* (Vahl) (Chiroptera, Pteropodidae) at Pune, India. *Mammalia*, 58: 363–370.
- BHAT, H. R., and T. H. KUNZ. 1995. Altered flower/fruit clusters of the kitul palm used as roosts by the short-tailed fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae). *Journal of Zoology (London)*, 234: 597–604.
- DUBOIS, M., K. A. GILLES, P. A. ROBERTS, and F. SMITH. 1956. Calorimetric method for determination of sugars and related substances. *Analytical Chemistry*, 25: 350–356.
- ÉLANGOVAN, V., G. MARIMUTHU, and T. H. KUNZ. In press. Temporal patterns of resource use by the short-nosed fruit bat *Cynopterus sphinx* (Megachiroptera: Pteropodidae). *Journal of Mammalogy*.
- FAEGRI, K., and L. VAN DER PIJL. 1979. The principles of pollination ecology. 3rd ed. Pergamon Press, Oxford, 244 pp.
- FLEMING, T. H. 1982. Foraging strategies of plant-visiting bats. Pp. 287–325, in *Ecology of bats* (T. H. KUNZ, ed.). Plenum Press, New York, xviii + 425 pp.
- GENTRY, A. H. 1974. Flowering phenology and diversity in tropical Bignoniaceae. *Biotropica*, 6: 64–68.
- HEITHAUS, E. R. 1982. Coevolution between bats and plants. Pp. 327–367, in *Ecology of bats* (T. H. KUNZ, ed.). Plenum Press, New York, xviii + 425 pp.
- HOWELL, D. J. 1979. Flock foraging in nectar-feeding bats: advantages to the bats and to the host plants. *The American Naturalist*, 114: 23–49.
- LAW, B. S. 1992. The maintenance of nitrogen requirements of the Queensland blossom bat (*Syconycteris australis*). *Physiological Zoology*, 65: 634–648.
- MARIMUTHU, G., K. E. RAJAN, A. J. KOILRAJ, S. S. ISAAC, and J. BALASINGH. 1998. Observations on the foraging behavior of a tent-roosting megachiropteran *Cynopterus sphinx*. *Biotropica*, 3: 321–324.
- NASSAR, J. M., N. RAMIREZ, and O. LINARES. 1997. Comparative pollination biology of Venezuelan columnar cacti and the role of nectar-feeding bats in their sexual reproduction. *American Journal of Botany*, 84: 918–927.
- RUBY, J., P. T. NATHAN, J. BALASINGH, and T. H. KUNZ. In press. Chemical composition of fruits and leaves eaten by the short-nosed fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae). *Journal of Chemical Ecology*.
- SAZIMA, I., and M. SAZIMA. 1977. Solitary and group foraging: two flower-visiting patterns of the lesser spear-nosed bat, *Phyllostomus discolor*. *Biotropica*, 9: 213–215.
- SOKAL, R. R., and F. J. ROHLF. 1995. *Biometry*. 3rd ed. W. H. Freeman and Company, New York, 887 pp.
- START, A. N., and A. G. MARSHALL. 1976. Nectarivorous bats as pollinators of trees in W. Malaysia. Pp. 141–149, in *Tropical trees: variation, breeding and conservation* (J. BURLEY and B. T. STYLES, eds.). Academic Press, London, 243 pp.
- STORZ, J., and T. H. KUNZ. 1999. *Cynopterus sphinx*. *Mammalian Species*, 613: 1–8.
- SUBRAMANYA, S., and T. R. RADHAMANI. 1993. Pollination by birds and bats. *Current Science*, 65: 201–209.

Received 1 May 2000, accepted 17 June 2000

