

TEMPORAL PATTERNS OF RESOURCE USE BY THE
SHORT-NOSED FRUIT BAT, *CYNOPTERUS SPHINX*
(MEGACHIROPTERA: PTEROPODIDAE)

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The short-nosed fruit bat, *Cynopterus sphinx* (Megachiroptera: Pteropodidae), is a common plant-visiting bat that is widely distributed throughout the Indomalayan region. We quantified foraging behavior of *C. sphinx* as individuals fed on fruits of *Annona squamosa*, leaves of *Cassia fistula* and *Mimusops elengi*, and fruits and leaves of *Coccinia indica*. After making several circling flights and engaging in brief hovering bouts, bats typically land directly on a single fruit and remove all or part of it with the mouth. In contrast, individuals remove leaves from trees during flight, without landing or hovering. *C. sphinx* typically transports fruits and leaves to feeding roosts where it extracts soluble contents and expels fibrous spats beneath day and feeding roosts. This bat consumes mostly fruits upon emergence from day roosts and feeds on leaves later in the night. These temporal differences in nightly foraging behavior may reflect the higher water and carbohydrate (energy) contents of fruits, compared with leaves, and help sustain flight activity throughout the night.

Key words: *Cynopterus sphinx*, folivory, frugivory, India, Old World fruit bats, temporal patterns

Plant-visiting bats in the Neotropics and Paleotropics feed mostly on fruit and nectar (e.g., Banack 1998; Fleming 1993; Gardner 1977; Law 1992; Richards 1995; Tan et al. 1998). Some plant-visiting species also supplement their diet of fruit and nectar with insects (Courts 1998; Gardner 1977) or extract soluble contents of leaves (Banack 1998; Elangovan et al. 1999; Kunz and Diaz 1995; Kunz and Ingalls 1994; Richards and Provic 1984; Ruby et al. 2000; Tan et al. 1998; Zortea and Mendes 1993).

Fruits of many tropical plants are patchily distributed in space and time (Fleming 1992; Howe and Wesley 1988; Terborgh 1986), and few studies have examined how and when plant-visiting bats exploit these

resources. In part, this reflects the difficulty of directly observing behavior of free-ranging bats as they forage. Several observations have been made on Old World fruit bats feeding on fruits, nectar, and pollen (Banack 1998; Gould 1977, 1978; Law 1992), but knowledge of temporal patterns of resource use is limited. By quantifying temporal patterns of food availability, we should be better able to explain foraging patterns of bats that consume these resources.

Many species of tropical plants produce flowers that open only after sunset, and these and other species produce fruits that may ripen over several days. In contrast, leaves of most tropical species are produced year-round but do not exhibit the spatial or

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temporal variation observed in flowers and fruits. Thus, we postulated that temporal patterns of visitation to plants by nectarivorous and frugivorous bats should reflect temporal patterns of nectar and fruit production.

Nectar and ripe fruits also vary widely in nutritional quality (Herrera 1987; O'Brien et al. 1998), and thus we would expect plant-visiting animals to first seek foods that yield the highest net energy return (Fleming 1993; Howe and Wesley 1988; Richards 1995). Moreover, competition for these valued resources may be manifested through differential use of space and time, defensive behaviors at feeding trees, and specialization on different foods. Some nectar-feeding bats vigorously defend floral resources against conspecifics (Law 1992), and some fruit-eating bats reportedly defend specific sites in fruiting trees (Gould 1977; Richards 1995).

We report observations on temporal patterns of resource use by short-nosed fruit bats, *Cynopterus sphinx*. We predicted that plant-visiting bats should first feed on floral and fruit resources that provide an immediate benefit. Because nectar and ripe fruits have a high content of carbohydrate and water, we predicted that plant-visiting bats would first exploit these resources. That prediction was consistent with observations that carbohydrate-rich foods provide the highest net energy return for an animal's foraging effort. Moreover, because bats are maximally dehydrated after their roosting period each day (Kurta et al. 1989), replenishment of total body water should be beneficial. Because leaves contain comparatively little water and carbohydrate, plant-visiting bats would not be expected to forage on those items until after their energy and water demands have been met.

MATERIALS AND METHODS

This study was conducted on the campus of Madurai Kamaraj University, Madurai, India (9°58'N, 78°10'E) from May 1996 to June 1997, where *C. sphinx* commonly roosts in small

groups beneath altered leaves of palms, stems and leaves of mast trees, stems of a vine, and beneath eaves, awnings, and similar man-made structures (Storz and Kunz 1999). Plants that dominate the diet of *C. sphinx* in India include fruits of ≥ 23 plant species, leaves from 8 species, and flowers from 2 other species (Bhat 1994). We observed *C. sphinx* foraging on fruits of *Annona squamosa* ($n = 9$ nights), leaves of *Cassia fistula* ($n = 28$ nights) and *Mimusops elengi* ($n = 27$ nights), and fruits and leaves of *Coccinia indica* ($n = 14$ nights). Partly chewed leaves, expelled leaf pellets (spats), rejected fruit parts, and expelled spats from masticated fruits (including small seeds) were collected from beneath feeding and day roosts. Numbers of foraging bouts were recorded continuously from 1800 to 0500 h, resulting in 848 h of observation. A foraging bout was recorded when a bat collected part or all of a fruit or leaf with or without landing on a tree. Most observations were made at night using diffuse illumination from nearby street lamps, but in dark areas our observations were aided by a red-filtered light.

Bats also were captured using mist nets as they foraged near trees. Selected individuals were marked with plastic collars and aluminum bands that were covered with colored reflective tape to assess behavior of individuals. A light tag (3.0 by 2.5 mm; Mini Knicklicht, Cormoron, Munich, Germany) was attached to the plastic collars. The collar, together with the light tag, weighed $<5\%$ of an adult's body mass, thus we assumed that this additional mass did not influence foraging behavior (Aldridge and Brigham 1988). Numbers of foraging bouts on fruits and leaves of selected tree species (pooled for each hour of the night) were analyzed using 2-way analysis of variance. Presence of a significant ($P \leq 0.05$) interaction between time and food (fruit or leaves) was considered evidence of a difference in temporal feeding patterns between fruits and leaves. Differences in temporal patterns were examined using 1-way analysis of variance to compare independently the number of foraging bouts on fruits and leaves at each hour of the night. A Bonferroni procedure was used to correct for multiple tests (Sokal and Rohlf 1995). One-way analysis of variance and Tukey's test were used to estimate the hours of peak foraging on fruits and leaves. The Kolmogorov-Smirnov test was used to determine whether those data were normally distributed,

and Levene's test was used to confirm homogeneity of variances (Sokal and Rohlf 1995). All assumptions were met after data were transformed to natural logarithms.

RESULTS

Cynopterus sphinx began to forage each night about 30 min after sunset. Individual bats typically made circling flights around trees before attempting to remove fruits or leaves. After a brief hovering bout, an individual bat typically landed directly on a ripe fruit and removed all (*C. indica*) or part (*A. squamosa*) of it with its mouth. In contrast, bats removed leaves while they were in flight, without landing or hovering. Individuals seldom, if ever, remained in source trees to feed on fruits or leaves. Instead, they carried food to feeding or day roosts where they chewed, expelled, discarded, or ingested selected parts. Feeding bouts were followed by periods of roosting of 5–30 min.

Nightly feeding activity of *C. sphinx* began about 1800 h and peaked near 2200 h (Fig. 1), at which time individuals fed mostly on the ripened fruits of *A. squamosa* ($F = 7.6$, $d.f. = 10$, 143, $P < 0.001$; Fig. 1a). Temporal foraging patterns differed when that bat fed on fruits and leaves of *C. indica* ($F = 2.1$, $d.f. = 10$, 286, $P < 0.01$). *C. sphinx* began to feed on leaves of *C. indica* at about 1930 h, with peak activity occurring at about 0200 h; $F = 11.6$, $d.f. = 10$, 55, $P < 0.02$; Fig. 1b). When bats fed on leaves of *C. fistula* and *M. elengi*, foraging activity peaked about 0100 h and 0200 h (Fig. 2). A peak of feeding activity ($F = 1.5$, $d.f. = 10$, 33, $P = 0.05$) was evident when individuals fed on leaves of *C. fistula* but not when feeding on leaves of *M. elengi* ($F = 1.5$, $d.f. = 10$, 33, $P = 0.19$).

DISCUSSION

Temporal patterns of nightly foraging activity indicate that *C. sphinx* feeds predominantly on fruits during the early hours of the night and later feeds on leaves. This bat also feeds on nectar from flowers of banana

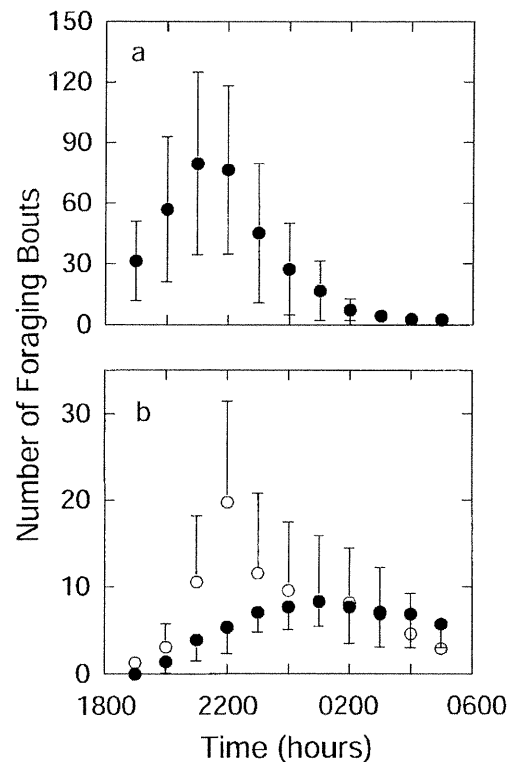


FIG. 1.—Temporal pattern of the number of foraging bouts ($\bar{X} \pm SD$) by *Cynopterus sphinx* when feeding on a) fruits of *Annona squamosa* and b) fruits and leaves of *Coccinia indica*; solid and hollow circles indicate fruits and leaves, respectively.

(*Musa × paradisiaca*) and butter trees (*Bassia latifolia*) early in the night, which begin to open shortly after sunset (Elangovan et al. 2000). Nectar and ripe fruits are generally rich in carbohydrates and water, but low in protein and fats (Corlett 1996; Herrera 1987; Martinez de Rio and Restrepo 1993; Mattson 1980; Ruby et al. 2000). Carbohydrates and water should be preferred by bats following a prolonged day-roosting period, during which they have no access to these resources. Leaves are ubiquitous and are relatively low in carbohydrates and water compared to fruit and nectar. Consequently, no a priori reason exists to expect bats to feed on leaves until their requirements for energy and water are met.

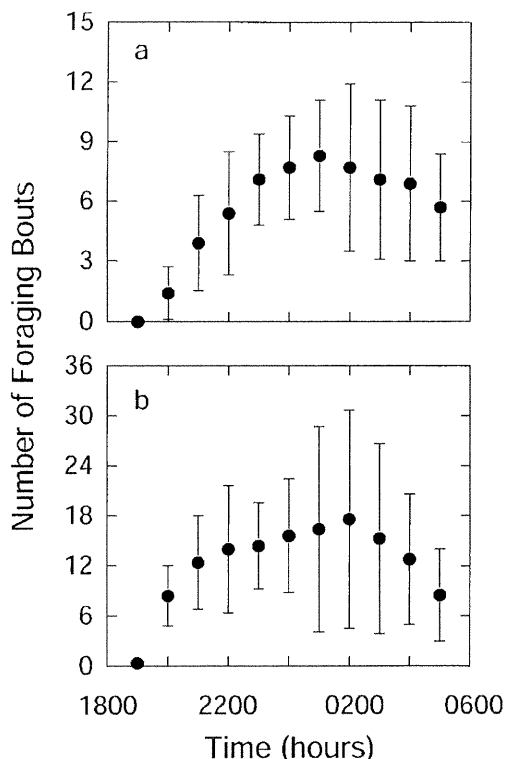


FIG. 2.—Temporal pattern of the number of foraging bouts ($\bar{X} \pm SD$) by *Cynopterus sphinx* when feeding on leaves of a) *Cassia fistula* and b) *Mimosa elengi*.

If fruits or flowers used by *C. sphinx* are limited temporally or spatially, we would expect individuals to compete for these resources most intensely immediately after the onset of nightly foraging activity (Elangovan et al. 1999; Fleming 1979) and exploit the abundant and ubiquitous leaves at other times. Our observations are consistent with these predictions.

In contrast to most fruits, leaves of several plant species are rich in protein (Kunz and Diaz 1995; Ruby et al. 2000; Telek and Martin 1983), calcium, and other minerals (Rajamani et al. 2000; Ruby et al. 2000). Our observations that individuals of *C. sphinx* remove entire leaves from certain tree species and carry them to both day and feeding roosts where they extract the soluble contents provides additional support

that leaves are important dietary items. If other plant-visiting bat species regularly ingest enough of the liquid fraction of leaves high in protein (Kunz and Diaz 1995; Richards and Provic 1984; Ruby et al. 2000; Tan et al. 1998; Zortea and Mendes 1993) or a sufficient quantity of insects (Courts 1998; Thomas 1984b), these bats should be able to meet their requirements for protein without overingesting fruits rich in carbohydrates (Thomas 1984a). By extracting soluble contents of leaves, plant-visiting bats are able to exploit a ubiquitous, abundant, and rich source of protein, minerals (e.g., calcium), and other nutrients important for their maintenance and reproduction.

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