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Temporal patterns of individual and group foraging behaviour in the short-nosed fruit bat, *Cynopterus sphinx*, in south India

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ABSTRACT. The short-nosed fruit bat, *Cynopterus sphinx*, begins to visit fruit-bearing trees about 30 min after sunset. Individual bats often hover near or land on fruits or on nearby branches to remove whole or parts of fruits with their mouth. These bats seldom remain in the fruit-bearing trees to feed, but instead carry fruits to feeding roosts, repeating this behaviour several times throughout the night. Analysis of the temporal distribution of feeding behaviour has revealed two peaks of activity, one in the pre-midnight hours when bats fed mostly on 'steady state' fruits, and another during the post-midnight hours when bats fed on 'big-bang' fruits. Only solitary bats visited and fed on species with steady state fruiting phenologies, whereas groups of bats regularly visited and fed on species with big-bang fruiting phenologies. Thus, plant species which produce large numbers of fruits appear to promote group foraging during the latter hours of the night. It is suggested that the temporal use of available fruits in south India made it possible for *C. sphinx* to successfully exploit them, and thereby reduced interference competition with conspecifics.

KEY WORDS: Chiroptera, *Cynopterus sphinx*, feeding behaviour, fruiting strategies, interference competition

INTRODUCTION

The short-nosed fruit bat, *Cynopterus sphinx* Vahl, 1797 roosts alone or in small groups in so-called 'tents' created from modified foliage, modified flower and fruit clusters (Bhat & Kunz 1995) and modified mast trees and vines (Balasingh *et al.* 1993, 1995), as well as beneath living and dead palm fronds

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and sometimes in buildings (Bhat & Kunz 1995). This bat feeds on fruits from at least 23 plant species, leaves from eight species, and flowers from two species (Bhat 1994). *C. sphinx* visits fruit-bearing plants which have both 'steady state' (production of a small number of fruits over an extended time period, e.g. *Polyalthia longifolia*) and 'big-bang' (production of a large number of fruits over a short period, e.g. *Ficus religiosa*) phenological patterns (Gentry 1974). Harem males forage relatively close (<1 km) to day roosts, whereas non-harem males and females forage at greater distances from day roosts (Marimuthu *et al.* 1998). The purpose of this study was to test the hypothesis that *C. sphinx* forages both alone and in groups on fruit-bearing trees which have either steady state or big-bang phenological patterns. We predict that since fruits produced by trees with steady state fruiting phenologies are only available in small numbers, bats should feed on these fruits during the early hours of the night. We further predict that since fruits from species with big-bang fruiting strategies are available in greater numbers, bats should feed on these fruits during the later hours of the night.

METHODS

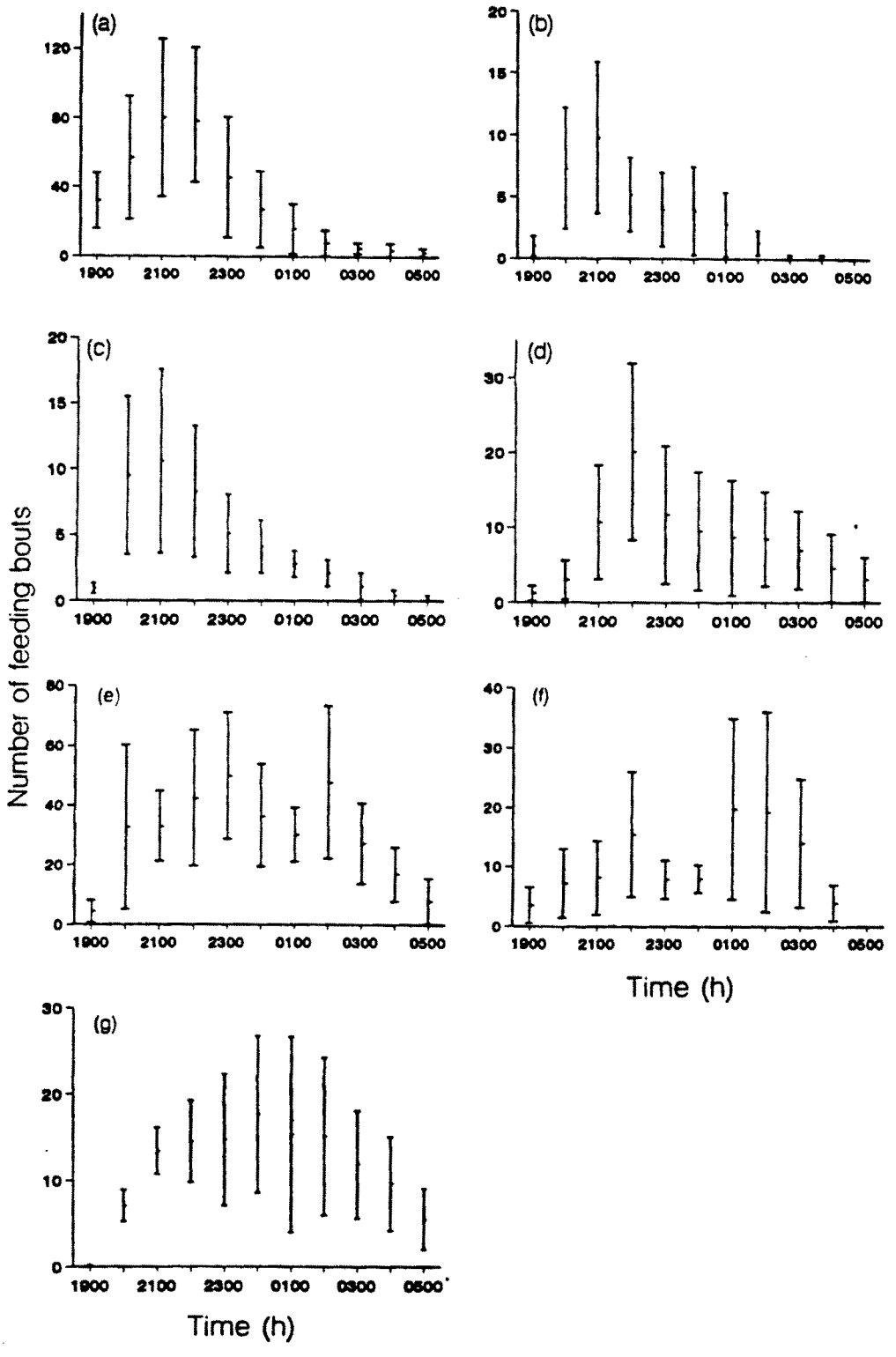
We observed bats foraging on ten species of fruit trees near the Madurai Kamaraj University campus (9°58′N, 78°10′E) for 121 nights between May 1996 and January 1998. The fruit-bearing species that we observed included *Annona squamosa* (nine nights), *Polyalthia longifolia* (18 nights), *Polyalthia pendula* (16 nights), *Achras sapota* (six nights), *Calophyllum inophyllum* (24 nights), *Coccinia indica* (14 nights), *Terminalia catappa* (11 nights), *Ficus religiosa* (five nights), *Ficus benjamina* (11 nights) and *Ficus bengalensis* (seven nights). The three species of *Ficus* have a big-bang fruiting pattern, whereas the other seven plant species exhibit a steady state fruiting pattern (Gentry 1974). The number of feeding bouts of *Cynopterus sphinx* was recorded every hour continuously between 18h00 and 05h00, resulting in *c.* 1331 h of observation. A typical feeding bout resulted in a bat collecting a part or a whole fruit in its mouth. Food abundance was estimated following the method described by August (1981). We captured a total of 16 bats using mist nets, set near fruit trees and attached an aluminium collar, totally covered with reflective tape. The blunt edged collar had a weight of 0.9 g and a width of 4 mm. In addition, a chemiluminescent tag (Cormoran Mini Knicklicht, 3.0 mm × 2.5 mm) was attached to the collar. The collar together with a chemiluminescent tag weighed less than 5% of the body mass of the bat. The reflective tape allowed us to locate bats in the fruit trees with a dim light source in the event that the brightness (which lasted for 8 h) of the chemiluminescent tag deteriorated. One-way analysis of variance and the Student Newman–Keul's test were used to evaluate differences in peak hours of activity. The value of activity which had the highest amplitude was taken as the peak. Data are given as means ± SD.

RESULTS

Cynopterus sphinx began visiting fruit trees about 30 min after sunset. Apart from the untagged bats, we had opportunities to observe the bats which had reflective tape for 65 times and the chemiluminescent tagged bats for 178 times. Individuals circled the trees, then briefly hovered or landed on the fruit or on nearby branches and with their mouth removed whole (*Polyalthia longifolia*, *Polyalthia pendula*, *Terminalia catappa*, *Coccinia indica*, *Calophyllum inophyllum*, *Ficus religiosa*, *Ficus benjamina* and *Ficus bengalensis*) or parts of fruits (*Annona squamosa*, *T. catappa*, *C. indica*, *C. inophyllum* and *Achras sapota*). These bats seldom remained in the fruit-bearing trees to feed, but instead carried fruits to feeding roosts, repeating this behaviour several times throughout the night. While transporting whole fruit of *T. catappa*, which weighed 84.8% of the bat's body mass, individual bats sometimes dropped fruits at an average distance of 21.9 ± 11.8 m ($n = 77$) from fruit trees, before reaching a feeding roost. Similarly, bats often dropped whole fruits of *C. inophyllum*, which weighed 23.1% of the bat's body mass, at an average distance of 33.0 ± 13.8 m ($n = 168$) from fruit trees. In only a few instances, bats briefly (3–5 min) fed on fruits in the fruit-bearing trees, especially in *A. squamosa*, *T. catappa* and *A. sapota*. *C. sphinx* fed only on ripe fruits and routinely ignored unripe fruits.

The temporal distributions of feeding bouts of *Cynopterus sphinx* which fed on steady state and big-bang fruits are shown in Figures 1 and 2, respectively. The number of feeding bouts reached a peak during the pre-midnight hours when bats fed mostly on steady state fruits. The peak of activity occurred during the post-midnight hours when they fed upon the big-bang fruits. However, we found differences in the times at which the peak occurred, depending on which species the bats were feeding. For example, the peak of nightly visits occurred at 21h00 when bats fed on *Annona squamosa* (Figure 1a; $F = 9.1$, $df = 10, 88$; $P < 0.001$), *Polyalthia pendula* (Figure 1b; $F = 15.2$, $df = 10, 165$, $P < 0.001$) and *Polyalthia longifolia* (Figure 1c; $F = 7.5$, $df = 10, 187$; $P < 0.001$). When bats fed on *Coccinia indica* the peak visits occurred at 22h00 (Figure 1d; $F = 7.6$, $df = 10, 143$; $P < 0.001$) and in *Achras sapota* they occurred at 23h00 (Figure 1e; $F = 4.5$, $df = 10, 55$; $P < 0.001$). Although the peak of feeding visits occurred at 22h00 in *Terminalia catappa*, another extended period of feeding was observed from 01h00 to 03h00 (Figure 1f; $F = 4.8$, $df = 10, 110$; $P < 0.001$). As bats visited *Calophyllum inophyllum* trees, the number of feeding bouts steadily increased from 19h00, reached a peak at 24h00, and declined thereafter (Figure 1g; $F = 2.6$, $df = 10, 253$; $P < 0.05$). When bats fed at trees of *Ficus religiosa* (Figure 2a; $F = 34.5$, $df = 10, 44$; $P < 0.001$), *Ficus benjamina* (Figure 2b; $F = 8.5$, $df = 10, 110$; $P < 0.001$) and *Ficus bengalensis* (Figure 2c; $F = 9.1$, $df = 10, 66$; $P < 0.001$), the peak feeding bouts occurred at 02h00, 03h00 and 04h00, respectively.

Only solitary bats visited and fed at trees which have steady state fruiting phenologies. On 15 occasions, we observed one *Cynopterus sphinx* chasing another bat away while the latter was feeding upon *Annona squamosa*. By contrast, group


(a)
(b)
(c)
(d)
(e)
(f)
(g)
Number of feeding bouts
Time (h)
Time (h)
1900
2100
2300
0100
0300
0500

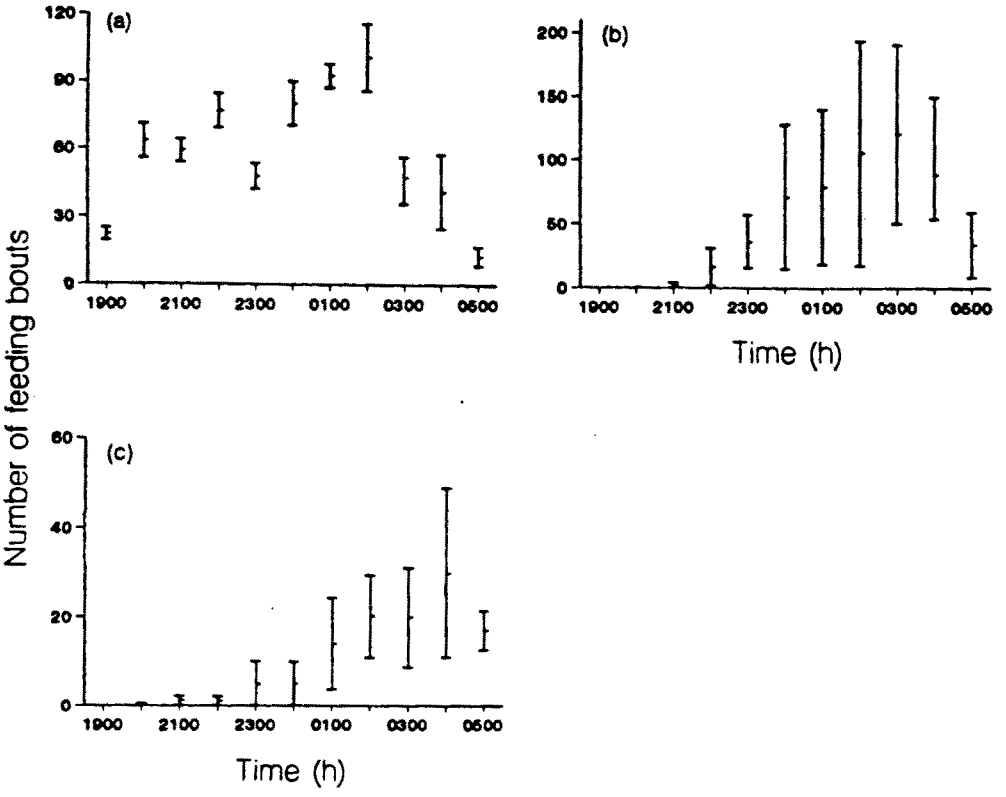


Figure 2. Temporal patterns of nightly foraging in *Cynopterus sphinx* when feeding on tree species which have big-bang fruiting phenologies:(a) *F. religiosa*, (b) *F. benjamina* and (c) *Ficus bengalensis*. Data are given as means ± SD.

foraging was common when bats visited the three species of *Ficus*. During the pre-midnight hours, small groups of up to six individuals were observed feeding at *Ficus* trees, and during the post-midnight hours, larger groups of up to 13 bats circled around and fed at these trees. One light-tagged bat fed on *Polyalthia pendula* during the pre-midnight hours and foraged on *Ficus religiosa* during the post-midnight period. The fruit mass and daily availability of fruits recorded during the study period are summarized in Table 1.

DISCUSSION

Patterns of nightly visits by *Cynopterus sphinx* to fruit-bearing trees suggest that the abundance of fruits influences the foraging activity of these bats. Based upon our predictions, the bats fed upon the steady state fruits mainly during

Figure 1. Temporal patterns of nightly foraging in *Cynopterus sphinx* when feeding on tree species which have steady state fruiting phenologies:(a) *Annona squamosa*, (b) *Polyalthia pendula*, (c) *Polyalthia longifolia*, (d) *Coccinia indica*, (e) *Achras sapota*, (f) *Terminalia catappa*, and (g) *Calophyllum inophyllum*. Data are given as means ± SD.

Table 1. Fruit mass and estimated number of fruits available daily to *Cynopterus sphinx*, from ten species of trees in and around M.K. University campus.

Tree species	Fruit mass (g)	Number of fruits available per tree
Steady state species		
Annona squamosa	126.0 ± 5.8	3
Polyalthia pendula	1.5 ± 0.5	62
Polyalthia longifolia	1.8 ± 0.2	*
Coccinia indica	3.7 ± 1.3	5
Achras sapota	83.8 ± 9.8	7
Terminalia catappa	40.8 ± 11.9	18
Calophyllum inophyllum	11.1 ± 2.1	20
Big-bang species		
Ficus religiosa	1.1 ± 0.2	36 480
F. benjamina	1.2 ± 0.3	19 636
F. bengalensis	2.1 ± 0.3	8470

*Data not collected

the early hours of the night and fed on the big-bang fruits mainly during the later hours of the night. Similarly, patterns of nightly activity reported for some neotropical species are influenced by either food quality or quantity (Fleming 1988). The nightly activity patterns of some microchiropteran species also may be influenced by the relative abundance of insects (Erkert 1982). Our results suggest that trees with less abundant fruits promote early foraging by single bats. This behaviour presumably makes it possible for bats to exploit available resources so as to avoid interference competition from conspecifics. Similarly, the neotropical, short-tailed fruit bat, *Carollia perspicillata* (Phyllostomidae) is mostly a solitary forager because its preferred food plants only produce ripe fruits in small quantities (Fleming 1982). However, another neotropical frugivore, *Artibeus jamaicensis*, forages in groups, and feeds mostly on *Ficus* fruits which are usually available in large numbers over a relatively short period (Handley & Morrison 1991).

We suggest that high abundance of fruits promotes group foraging during the later hours of the night because of an apparent lack of competition between conspecifics. Individual bats often visit more than one fruit tree during the same night (Charles-Dominique 1991). Heithaus *et al.* (1974) found that larger phyllostomids foraged in groups and smaller species foraged alone. Temporal differences in foraging were also reported for *Carollia perspicillata* based on the quality of available fruits. In the early evening hours individuals fed on protein-rich but scarce fruits and during later hours they switched to energy-rich fruits (Fleming 1988). Our study indicates that *Cynopterus sphinx* employs both solitary and group foraging behaviours, and that these are largely influenced by the temporal availability of fruits.

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