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Tent Construction by the Short-nosed Fruit Bat *Cynopterus sphinx* (Chiroptera: Pteropodidae) in Southern India

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Abstract

The short-nosed fruit bat *Cynopterus sphinx* (Chiroptera: Pteropodidae) constructs shelters by severing stems of the curtain creeper, *Vernonia scandens*, and stems and leaves of the mast tree, *Polyalthia longifolia*, creating partially enclosed cavities (stem tents) in which to roost. Our observations indicate that the construction and maintenance of stem tents are primarily, if not exclusively, the behaviour of single males. A stem tent is formed in *V. scandens* when a single male *C. sphinx* severs up to 300 small- to medium-sized stems creating a partially flattened, bell-shaped cavity, and in *P. longifolia* when a male severs a few medium- to small-sized branches and many leaf petioles, creating an entry/exit portal and space in which to roost. A tent constructed in *V. scandens* is completed in approximately 30 d, whereas one in *P. longifolia* is completed in about 50 d. Stem-tent construction takes place mostly at night, but some stem chewing occurs in late afternoon. At night a stem tent is occupied by a single male, whereas females are usually absent. During the day the number of bats occupying completed tents is highly variable, ranging from two to 19 females (and their pups) and a single adult male. Tent construction is annually bimodal, which corresponds to a biannual breeding season. A dominant male sometimes deposits saliva on branches inside his tent cavity and actively defends this space from intrusions by other males. Both behaviours suggest forms of scent marking and territorial display. Our observations indicate that dominant males construct tents, recruit females and then defend the tents (and their female occupants) for the purpose of gaining reproductive access. The variance in harem group size indicates that some tent-making males are more successful than others in recruiting females.

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Introduction

Fifteen species of neotropical bats and three species of palaeotropical bats are known to either roost in or construct tents in leaves and other plant parts from

over 80 species of vascular plants (KUNZ et al. 1994). PHILLIPS (1924) first reported that *Cynopterus brachyotis* (Pteropodidae) modified the 'seed strings' of the kitul palm, *Caryota urens*, which bats used as roost sites. Altered palm leaves as first described by BARBOUR (1932) and CHAPMAN (1932), and attributed to bats, were termed 'tents' (CHAPMAN 1932). Although different types of altered plant structures (leaves, flower and fruit clusters, and stems) are now referred to as bat tents (KUNZ 1982; TIMM 1987; KUNZ et al. 1994), there are no published reports of bats engaged in the act of tent-making. Evidence for tent-making behaviour to date has been largely circumstantial, based primarily on observations that bats roost in these structures. In their review of tent architecture and roosting-group composition in two species of neotropical bats, KUNZ & MCCrackEN (1995) postulated that bat tents are constructed by males. Recent observations of tent-roosting in *Cynopterus sphinx* (BALASINGH et al. 1993; BHAT & KUNZ 1995) support this hypothesis.

Eight different architectural styles of bat tents have been described, including four styles (pinnate, bifid, paradox and boat) unique to the Neotropics, one style (stem tent) unique to the Palaetropics, and three styles (conical, palmate umbrella, and apical) common to both biogeographic regions (KUNZ et al. 1994). Tent-roosting and/or tent-making behaviour has been attributed to 15 species from the highly diverse microchiropteran family Phyllostomidae (subfamily Stenoderminae), two species of the family Pteropodidae, and one species of Vespertilionidae. What is striking about tents and their use by bats is that most are used (and likely constructed) by species that form polygynous mating systems (*Uroderma bilobatum*: TIMM & CLAUSON 1990; TIMM & LEWIS 1991; *Vampyressa nymphaea*: BROOKE 1987; *Ectophylla alba*: BROOKE 1990; *Artibeus jamaicensis*: KUNZ & MCCrackEN 1995). Both males and females have been observed roosting alone in tents, although each species commonly forms groups of varying size, consisting of a single male and several females (BROOKE 1990; LEWIS 1992; KUNZ & MCCrackEN 1995). The limited information on mating systems of tent-roosting species, however, has made it difficult to determine whether these polygynous mating systems are based on resource-defence or female-defence strategies.

According to EMLEN & ORING (1977), the evolution of a resource-defence mating system requires that critical resources be in limited supply and that they be economically defensible. In such a system, a male would gain access to critical resources that are important to females and then defend these resources to gain reproductive access. By contrast, conditions considered necessary for the evolution of a female-defence system require that females form groups independent of males. In the latter system, females would form groups because doing so would confer some benefit, and males would be expected to join these groups and defend them against other males (BRADBURY & VEHCAMP 1977; MCCrackEN & BRADBURY 1981). If females construct and occupy tents independent of males, and males later attach themselves to these groups and defend them to gain reproductive access, then one could argue for a female-defence mating system.

In his review of mammalian mating systems, CLUTTON-BROCK (1989) proposed that mating systems represent different forms of mate guarding adapted to

the spatial and temporal distribution of receptive females, which in turn depends on variation in resource distribution, predation pressure, the costs of social living, and activities of other males. We suggest that the construction and defence of tents by male bats, and the subsequent recruitment of females, provides one type of resource and represents one form of mate guarding that would lead to the evolution of resource-defence polygyny. The argument that bat-altered leaves, vines, or stems (tents) are critical and potentially defensible resources (KUNZ & MCCrackEN 1995) is based on the hypothesis that tents are structurally similar to tree cavities (MORRISON 1978, 1979; MORRISON & MORRISON 1981) and solution cavities in caves (MCCrackEN & BRADBURY 1981; KUNZ et al. 1983), each of which are potentially defensible by males (KUNZ & MCCrackEN 1995). These tents may be important to females if they provide protection from inclement weather (TIMM 1987; CHOE 1994) and reduce risks of predation (BOINSKI & TIMM 1985). Tents may also confer thermoregulatory advantages (BROOKE 1990) or provide opportunities for females to share information about the location of food resources (BRADBURY 1977; MCCrackEN & BRADBURY 1981; WILKINSON 1987). Alternatively, a tent may serve as an indicator of male quality. If females are able to assess the quality of a tent constructed by a male, and these qualities are associated with male fitness, then females would benefit by choosing to roost (and mate) with such a male. The tent would not have to benefit the female directly if the quality of the resource provides the female with a means of assessing the quality of the male (BRADBURY & VEHRENCAMP 1977).

The purpose of this study is to describe the stem tents constructed by *Cynopterus sphinx*, to quantify group size and composition, to describe tent-making behaviour, and to evaluate this behaviour in the context of mammalian mating systems (CLUTTON-BROCK 1989).

Methods

Study Species

Cynopterus sphinx (Pteropodidae) is one of the most common plant-visiting bats in the Old-World tropics. It is a widely distributed species, occurring eastward from India to Burma and Indo-China, and is known from the islands of Sumatra, Java, Bali and Timor (COBBET & HILL 1992). Throughout its range this bat occupies a variety of habitats including forests, cultivated regions and urban areas (BROSSET 1962; BHAT 1995). Individuals and small groups of *C. sphinx* have been observed roosting in altered spaces of the mast tree, *Polyalthia longifolia*, in tents formed from the leaves of palms such as *Borassus flabellifer*, *Corypha umbraculifera*, *Corypha* sp., *Livistona chinensis* and *Roystonea regia* (GOODWIN 1979; BHAT 1995), and in altered flower and fruit clusters of *Caryota urens* (BHAT & KUNZ 1995). *C. sphinx* has also been observed roosting under banana leaves (*Musa* sp.), beneath leaf clusters of avocado, *Persea gratissima*, inside clumped leaves of *Philodendron giganteum* (BHAT 1995), in cavities of *Ficus* trees, in recesses beneath the bark and aerial roots of banyan (*Ficus*) trees, and in spaces of human-made structures such as eaves of houses and partially enclosed porches (BROSSET 1962; KHAJURIA 1979; ADVANI 1982; SANDU 1984, 1988; KUNZ et al. 1994; BHAT 1995; BHAT & KUNZ 1995). Tents constructed in palm leaves and in flower and fruit clusters may be occupied for a year or more (BHAT 1995; BHAT & KUNZ 1995), whereas spaces in human-made structures are often occupied for considerably longer periods (BHAT 1995).

Cynopterus sphinx is a seasonally polyestrous species with two annual breeding seasons (KRISHNA & DOMINIC 1984; SANDU 1984; J. BALASINGH pers. obs.), yet there is considerable geographic variation

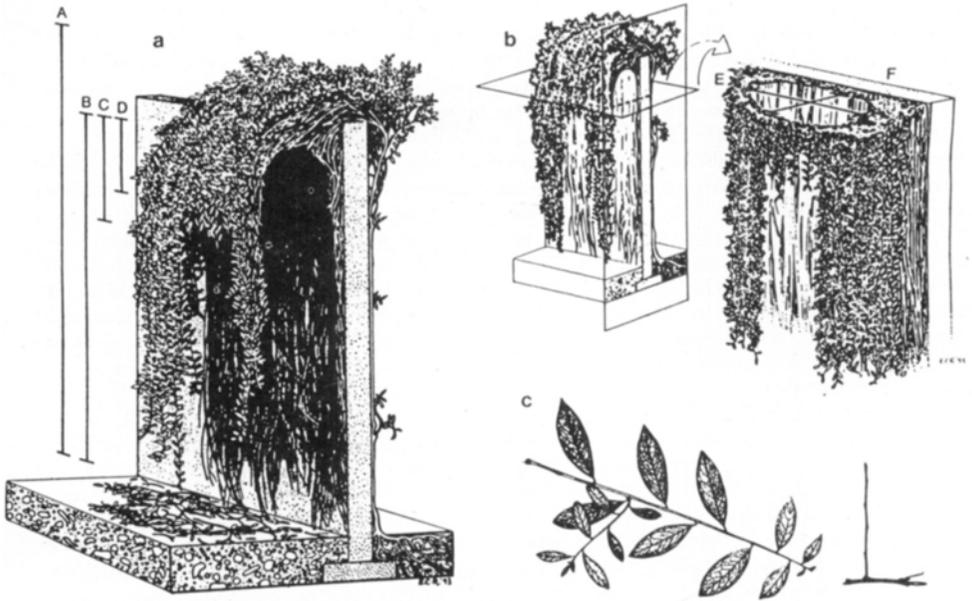


Fig. 1: (a) Schematic view of a *Vernonia scandens* stem tent constructed by *Cynoptyerus sphinx* illustrating dimensions A–D as summarized in Table 1; (b) schematic view of a *V. scandens* stem tent illustrating dimensions E and F as summarized in Table 1; (c) examples of *V. scandens* stems severed by *C. sphinx* during the construction of a stem tent

in reproductive phenology (SREENIVASAN et al. 1974; MOTE & NALVADE 1982). In southern India, pregnancies that commence in Oct. and Nov. are followed by parturition in Mar. and early Apr. The latter period of parturition is followed by a post-partum oestrus at which time females are simultaneously pregnant and lactating. Births from the latter pregnancy occur mostly in July. Females are reproductively quiescent in Aug. and Sep. (J. BALASINGH, pers. obs.).

Study Site and Duration of Study

Our study was conducted in Tirunelveli, southern India (8° 44' N, 77° 42' E) on the campus of St John's College. Preliminary observations were begun in Jan. 1992 and most observations of bats in tents were made from mid-Aug. 1992 through late Jul. 1993. The climate in the vicinity of Tirunelveli is typical for southern India. The period from Mar. through May is hot and dry, with daytime temperatures often averaging 39°C. At our study site, precipitation varied seasonally and several months passed with only trace amounts recorded. The rainy season normally occurs from Oct. to Dec.

Measurements and Observations

We recorded the dimensions of stem tents that bats constructed in the curtain creeper, *Vernonia scandens* (Fig. 1a, b). These dimensions include the height of the exterior crown (A), height of the interior crown (B), vertical length of tent cavity, including overhanging vines (C), vertical length of the tent cavity (D), width of tent cavity (E) and depth of tent cavity (F). The tent volume, which approximates a partially flattened, domed cylinder, was estimated using the formula:

$$V = [\pi (a \cdot b) \cdot h] + [2/3 \pi \cdot b^2 \cdot a]$$

where a and b represent one-half the depth (F) and width (E) of a stem tent, respectively, and h represents the vertical height of the tent cavity (C). We also recorded the number, type, and size of stems that were severed during tent construction (Fig. 1c). When we began our observations in Jan. 1992, four tents had already been completed and we arbitrarily assigned a number to each ranging from I to IV. These assignments were based on the linear arrangement of tents along a garden wall, and do not necessarily reflect the order in which the tents were constructed. Observations at these tents were made over a complete year, during which time two additional tents (V and VI) were constructed in the same cluster of vines. We also made observations of *C. sphinx* and recorded evidence of tent construction in a mast tree, *Polyalthia longifolia*, located in the town of Tirunelveli.

When tents were measured or bats were observed, we tried to avoid disturbing or flushing bats from their roosts. To facilitate recognition of individual bats in tents, we captured some individuals with a hoop net and attached a uniquely coloured, plastic-beaded necklace to each captured bat (BALASINGH et al. 1992). In late Aug. 1992, one male was captured in tent V and marked in this manner. On 24 Apr. 1993, approximately 2 wk after all young were born, we also captured and marked an adult male, four lactating females, and four pups that roosted in tent III. After being marked and measured, these bats were returned to their original tents. In this preliminary study we did not capture or mark other bats to avoid disrupting group composition.

We observed bats in tents during the day and at night by illuminating them with a beam of dim, red light. During the day, observations and roost censuses were made in the early morning and again in late afternoon. Some of our observations were aided with binoculars. At each census we recorded the number and sex of adults and the number of pups present in each tent. Because harem males usually had distinct marks on their shoulders and were slightly larger than females, these characteristics made it possible to visually distinguish them from adult females. Young bats were distinguished from brownish adults by their smaller size and grayish pelage. During the day, a harem male often roosted adjacent to but separate from the more tightly clustered group of females (Figs 2b, 6b). At approximately 2-wk intervals, over a period of nearly 8 mo (eight complete lunar cycles), we recorded the behaviour of a single adult male that roosted in tent II. These observations were begun at the onset of nightly emergence and continued until the last females returned from foraging. We recorded the amount of time (in min) that this male allocated to different activities (e.g. foraging, rest, tent construction, food consumption and grooming). However, in many instances we were unable to distinguish feeding (chewing and food consumption) from stem chewing, or resting from tent maintenance. Thus, the only unambiguous behaviours that we recorded were foraging (time absent from the roost) and grooming.

We also recorded the daily and seasonal patterns of tent-making activity by collecting and recording the numbers and types of stems and leaves severed during the construction of one *V. scandens* tent (V), and at the one *P. longifolia* tent beginning at the onset of construction and continuing until the tents were completed. Voucher specimens of plant parts that were severed by bats during tent construction in *V. scandens* and *P. longifolia* have been deposited in the Stuart Harris Herbarium at Boston University.

Results

Plants Used as Roosts

Cynopterus sphinx used at least six different species of plants as roost sites. These include the mast tree, *Polyalthia longifolia*, curtain creeper, *Vernonia scandens*, palmyrah palm, *Borassus flabellifer*, areca palm, *Areca catechu*, banyan tree, *Ficus bengalensis*, and banana, *Musa paradisiaca*. Because *C. sphinx* most commonly roosted in *P. longifolia* and *V. scandens*, we concentrated our observations on tents that were constructed in these two plant species.

Characteristics of Stem Tents in *Vernonia scandens*

The six stem tents that we observed in the vines of *V. scandens* cascaded over a west-facing stone and stucco wall on the St John's College campus (Fig. 2a).

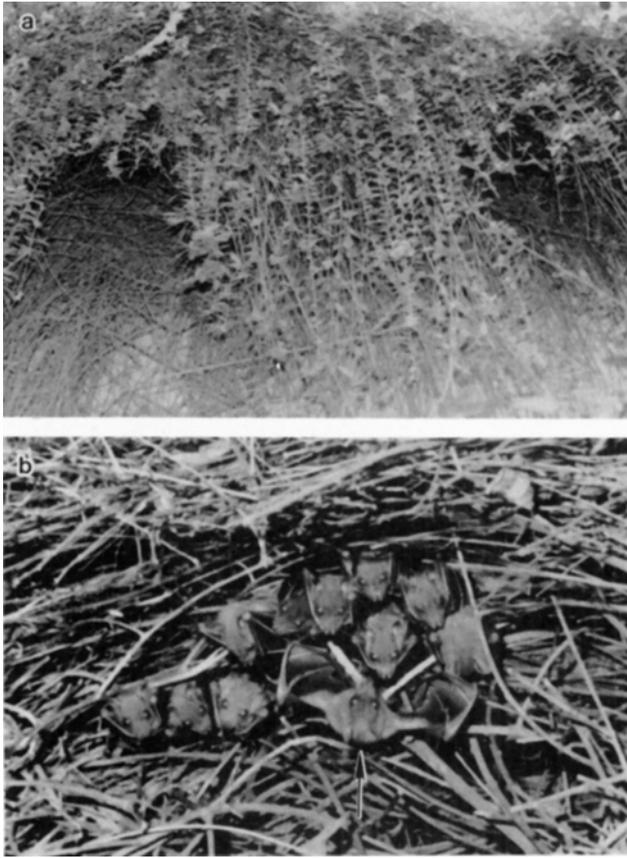


Fig. 2: (a) Two stem tents constructed in *Vernonia scandens* showing the openings used by bats. (b) A small harem group of *Cynopterus sphinx* roosting in the crown of a *V. scandens* stem tent. Note the position of the harem male (arrow) relative to the females. (Photos by J. BALASINGH)

When we began our study, four tents had already been constructed and each was intermittently occupied by a single male and several adult females (Fig. 2b). In late Mar. 1992 a new tent (v) was constructed in the same mass of vines adjacent to tent I, and this was followed by the construction of another tent (vi) in the period from late Aug. to late Oct. 1992.

Selected measurements of the six *V. scandens* tents are summarized in Table 1 and depicted in Fig. 1 (a, b). Each completed tent assumed the shape of a partially flattened, cylindrical cavity that was open from below (Fig. 1a), and was distinguished by an archway of partially cut vines. The exterior crowns (A) of these six tents were uniformly about 6 m above the ground and were characterized by numerous, slender, alternate-leaved stems that extended downward from the woody crown. The heights of the interior crowns (B) ranged from 5.3 to 5.8 m. The vertical length of the tent cavities, as measured from the interior crown to the

Table 1: Characteristics and dimensions of tents constructed by the bat *Cynopterus sphinx* in *Vernonia scandens*, and mean (\pm SD) group size of *C. sphinx*. Tent dimensions are expressed in m. See Fig. 1 for illustrations of dimensions. Mean group size for adults, pups, and total for each tent is based on census data summarized in Fig. 4. Mean values including all tents ($n = 6$) represent grand means

Tent characteristics and group size	Tent number						n	$\bar{X} \pm$ SD	CV
	I	II	III	IV	V	VI			
Height of exterior crown (A)	5.96	5.96	5.96	5.96	5.96	5.96	6	5.96	—
Height of interior crown (B)	5.66	5.30	5.50	5.70	5.50	5.80	6	5.58 \pm 0.18	3.2
Vertical length of tent cavity, including pendulous stems (C)	1.65	—	1.63	—	1.75	1.27	4	1.57 \pm 0.21	13.3
Vertical length of tent cavity (D)	1.01	0.68	1.0	0.58	1.22	—	5	0.89 \pm 0.26	29.2
Width of tent cavity (E)	0.46	0.58	0.48	0.51	0.63	0.99	6	0.60 \pm 0.20	33.3
Depth of tent cavity (F)	0.25	0.28	0.30	0.41	0.46	0.51	6	0.38 \pm 0.09	23.6
Tent volume (V)	0.14	0.11	0.13	0.12	0.33	—	5	0.17 \pm 0.09	52.9
Mean adult group size	2.9	10.4	2.6	1.3	4.0	2.3	6	3.9 \pm 3.4	86.7
Mean pup group size	0.9	5.0	0.6	0.1	1.3	0.5	6	1.3 \pm 1.7	126.5
Mean total group size	4.0	15.4	3.2	1.4	5.1	2.8	6	5.3 \pm 5.1	96.5

top of the arch (C) ranged from 0.85 to 1.01 m, but when the pendulous stems were included the tent cavities (D) ranged from 1.27 to 1.75 m in length. The horizontal width and depth of the tents ranged from 0.46 to 0.99 m and 0.25 to 0.51 m, respectively. The tent volume ranged from 0.11 to 0.32 m³. A completed tent provides access from below, and makes it possible for flying bats to freely enter and depart without being impeded by surrounding vegetation. Severed stems were of variable length and ranged from 1 to 2 mm in diameter (Fig. 1c).

Group Size, Composition and Stability

Regular censuses of bats roosting in the six *Vernonia scandens* tents, made from late Jan. to late May 1993, indicate that (with one exception) the overall population was relatively stable, ranging from 20 to 26 adults over this 4-mo period (Fig. 3a). A slight decrease in numbers was observed in the adult female population beginning in mid-Apr. Roosting group size was highly variable, both within and among tents. The total population of bats began to increase with the birth of pups in early Mar., reaching a peak in early Apr. (Fig. 3b). At this time each tent was occupied by one male and groups of 1 to 19 females and their single pups (Fig. 3c). The greatest number of bats roosted in tent II ($\bar{X} = 15.4 \pm 2.5$ SD). Except for this tent, there were seldom more than four adults roosting in each of the other tents during this period (Table 1). Although the total population occupying the six tents remained relatively stable, variations in the number of bats present suggest some daily movement of individuals from one tent to another. Tent IV consistently housed the fewest adult bats, ranging from one to four individuals ($\bar{X} = 1.3 \pm 0.7$ SD). The most recently constructed tent (VI) had few occupants in the period from mid-Oct. to early Dec. 1992, but the number of occupants peaked at 10 individuals by mid-Dec. From mid-Dec. until mid-Jan.,

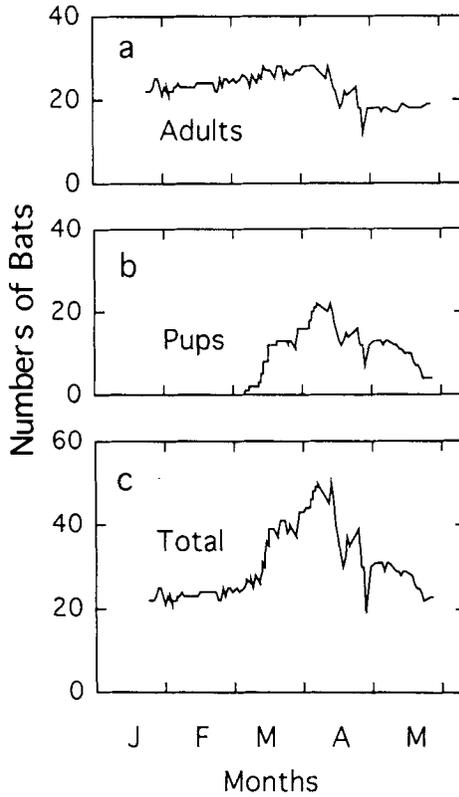


Fig. 3: Population census of adults (females and one dominant male) and pups of *Cynopterus sphinx* occupying six adjacent tents constructed in *Vernonia scandens* in 1993

a single male was the only resident of this tent. From mid-Jan. to late Apr. 1993, the number of occupants ranged from 1 to 10 adults ($\bar{X} = 2.3 \pm 1.7$ SD), although there were seldom more than four individuals present at any time. These data indicate that female and pup recruitment to a given tent was highly variable (Fig. 4).

We tested the hypothesis that differences in group size reflect differences in tent quality, as judged by the linear dimensions and volume of each tent (Table 1). Although tent occupancy by adult females and tent dimensions were highly variable, we found few significant correlations between tent dimensions and average group size of adults (Table 2). Group size was most highly correlated with the height of the interior crown ($r = -0.84$) and the vertical length of the tent, when pendulous stems were included ($r = 0.80$). From these results we tentatively conclude that tent volume and most other tent dimensions confer no advantage to females or to males in the recruitment of females. Our data suggest that the height of the interior tent crown and the vertical length of the tent cavity (including pendulous stems) may be important criteria used by females to choose

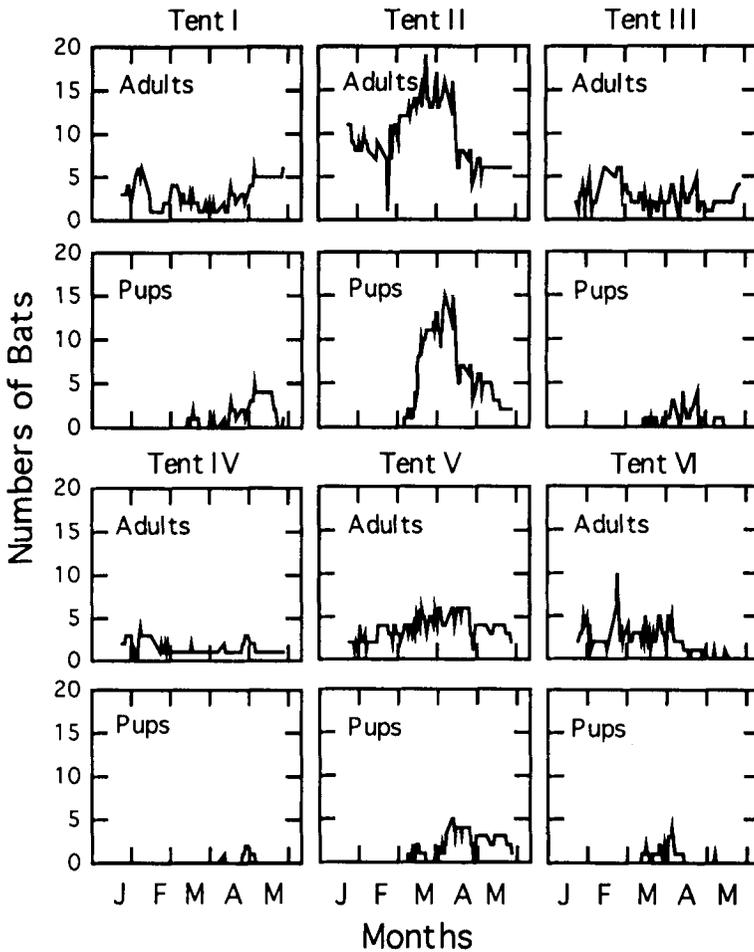


Fig. 4: Comparison of group size in six occupied tents constructed by *Cynopterus sphinx* roosting in *Vernonia scandens*. Each adult group consists of females and one dominant (harem) male

tents (or males), but we can probably rule out height of the interior tent crown as an important variable because this dimension is determined by the height of the plant, not by the tent-making activity of the bat. In the present study, height of the tent crown was essentially the same for all tents. Because we chose not to mark most of the bats in this study, we were unable to establish which females moved from one tent to another and which females were loyal to a given tent or particular male. Thus, we cannot rule out the possibilities that female group size reflects the age of the male (KUNZ et al. 1983), age of the tent, or the tenure or quality of the male (FLEMING 1988).

Behaviour of Males in *Vernonia scandens* Tents

We observed a single male *C. sphinx* in the act of constructing a new tent (VI)

Table 2: Correlation matrix comparing characteristics of stem tents in *Vernonia scandens* and adult female, pup and total group size in *Cynopterus sphinx*. Correlations are based on tent dimensions and group sizes summarized in Table 1

Tent dimensions ¹	Group size		
	Adult	Pup	Total
Height of interior crown (B)	-0.84*	-0.83*	-0.83*
Vertical length of tent cavity, including pendulous stems (C)	0.80*	0.74	0.80*
Vertical length of tent cavity (D)	-0.21	-0.24	-0.24
Width of tent cavity (E)	-0.08	-0.07	-0.08
Depth of tent cavity (F)	-0.04	-0.03	-0.04
Tent volume (V)	-0.13	-0.14	-0.16

* Statistically significant at $p < 0.05$

¹ Height of the exterior crown is excluded from this analysis because this dimension did not vary and is not affected by the tent-making behaviour of bats

in *Vernonia scandens*. Over a period of about 30 d, beginning in Aug. 1992, this male chewed and severed more than 300 separate stems. Most of the chewing and stem severing took place at night, but a few stems were chewed and severed in late afternoon. In the early days of tent construction this male severed up to 30 small stems and stem segments in a single night. As the tent neared completion, the number of severed stems decreased to one or two per night. Even after the tent was apparently 'completed', and occupied by a few females, the male continued to chew and sever stems, especially the long outer ones that may have interfered with flight access to the tent cavity. During the period of tent construction, this male spent more time in his tent each night than males that occupied older, already completed tents. At night this male often chased other bats (males?) away from the vicinity of the tent and at times deposited saliva on the stems on the interior crown of the roost cavity. After tent VI was completed, a few females began to occupy the tent during the day, although group membership as noted above was highly variable in the subsequent months.

On 18 d and nights, spanning eight lunar cycles, from 12 Oct. to 21 May 1993, we recorded the amount of time that this same male engaged in different roost activities (Fig. 5). During the day, this male roosted with his eyes open and was unusually alert, whereas females were generally inactive. This male often assumed a posture with partially spread wings (Fig. 2b) and an occasionally protruding tongue. At night, this male intermittently engaged in short foraging bouts to nearby fruit trees, subsequently returning to its tent where it consumed fruit and leaves, rested, chewed and licked stems, and engaged in grooming.

The relative amount of time that this male allocated to foraging generally increased from mid-Oct. to late May (Fig. 5a). From Dec. to Mar., approximately 20 % of the nightly time budget was allocated to foraging, but from late Apr. to late May, foraging time almost doubled from previous levels. In the period from mid-Oct. to late Jan., this male allocated about 40–80 % of its nightly time budget to rest (Fig. 5b). The amount of time allocated to tent maintenance was negligible

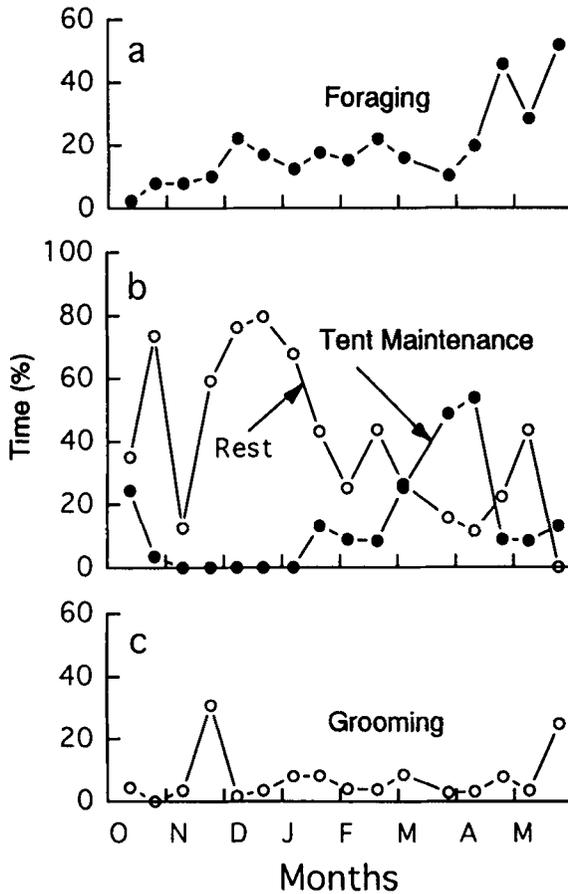


Fig. 5: Time activity budget of a harem male *Cynopterus sphinx*, indicating the frequencies of occurrence for each selected activity during the period of stem tent construction in *Vernonia scandens*. Data are based on observations made at tent II in 1993 (see Table 3)

from late Oct. to late Feb. Tent maintenance appeared to increase in early Mar. and reached a peak in early Apr., but this activity decreased precipitously in late Apr. (Fig. 5b). Because we were unable to distinguish stem chewing from feeding behaviour on most nights, our estimates of time allocated to these activities should be considered tentative (Table 3). The relative amount of time that this male allocated to grooming (Fig. 5c) was relatively constant, usually accounting for less than 10 % of its nightly time budget.

Behaviour of Bats in *Polyalthia longifolia* Tents

We also observed a small group of *C. sphinx* roosting in a mast tree *Polyalthia longifolia* (Fig 6). When this group was first observed in Feb. 1991, the tent

Table 3: Nocturnal time budget of a male *Cynopterus sphinx* occupying a *Vernonia scandens* stem tent (no. 11). Time is expressed in min. Values in parentheses represent % of time the male allocated to each activity from onset of nightly emergence until the last bat returned to the roost on a given night

Observation date	Lunar phase	Night roosting activity							Total time
		Foraging	Resting	Tent maintenance	Feeding and tent maintenance	Resting and tent maintenance	Grooming		
12-13 Oct. 1992	Full moon	8 (2.3)	122 (35.0)	83 (24.3)	113 (33.1)	0 (0.0)	15 (4.3)	341	
25-26 Oct. 1992 ¹	New moon	31 (7.9)	287 (73.5)	14 (3.6)	56 (14.3)	0 (0.0)	2 (0.5)	390	
10-11 Nov. 1992	Full moon	28 (7.9)	44 (12.5)	0 (0.0)	74 (21.0)	194 (55.1)	12 (3.4)	352	
25-26 Nov. 1992	New moon	22 (10.1)	129 (59.1)	0 (0.0)	0 (0.0)	0 (0.0)	67 (30.7)	218	
09-10 Dec. 1992	Full moon	102 (22.0)	353 (76.2)	0 (0.0)	0 (0.0)	0 (0.0)	8 (1.7)	463	
22-23 Dec. 1992	New moon	44 (16.8)	209 (79.7)	0 (0.0)	0 (0.0)	0 (0.0)	9 (3.4)	262	
08-09 Jan. 1993	Full moon	45 (12.4)	245 (67.8)	0 (0.0)	0 (0.0)	0 (0.0)	29 (8.0)	362	
22-23 Jan. 1993	New moon	45 (17.5)	111 (43.2)	34 (13.2)	46 (17.9)	0 (0.0)	21 (8.1)	257	
06-07 Feb. 1993	Full moon	69 (15.2)	113 (25.1)	40 (8.9)	62 (13.7)	149 (33.0)	18 (4.0)	451	
21-22 Feb. 1993	New moon	77 (21.8)	142 (43.7)	27 (8.3)	30 (9.2)	38 (11.7)	11 (3.9)	325	
08-09 Mar. 1993	Full moon	50 (15.8)	84 (26.4)	80 (25.2)	46 (14.5)	30 (9.4)	27 (8.5)	317	
23-24 Mar. 1993	New moon	30 (10.4)	45 (15.7)	140 (48.7)	17 (5.9)	47 (16.3)	8 (2.8)	287	
06-07 Apr. 1993	Full moon	77 (19.7)	45 (11.5)	210 (53.7)	47 (12.0)	0 (0.0)	12 (3.1)	391	
21-22 Apr. 1993	New moon	122 (45.7)	60 (22.4)	24 (8.9)	26 (9.7)	14 (5.2)	21 (7.9)	267	
05-06 May 1993	Full moon	88 (28.3)	135 (43.5)	26 (8.4)	30 (9.7)	20 (6.5)	11 (3.5)	310	
21-22 May 1993	New moon	40 (51.9)	0 (0.0)	10 (13.0)	8 (10.4)	0 (0.0)	19 (24.6)	77	

¹ Festival with fireworks

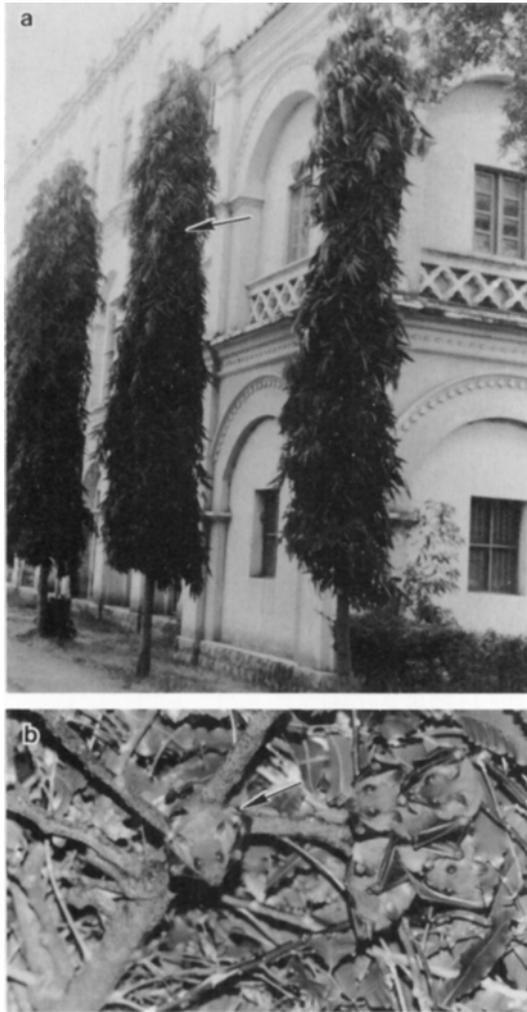


Fig. 6: (a) Photo of *Polyalthia longifolia* tree used by *Cynopterus sphinx* in the construction of stem tents. Arrow near the top of tree denotes an opening used by bats for entry and exit to the tent cavity (photo by J. BALASINGH). (b) Small harem group of *C. sphinx* roosting in a cavity formed when a single male severed stems and leaves (photo by S. MISTRY). Note the position of the harem male (arrow) relative to the females

was located approximately 4 m above the ground. This tent was abandoned approximately 1 yr later. In the following year a new tent was constructed in the same tree at a height of about 7 m. The construction of a third tent was observed in the tree beginning in Feb. 1993. The latter tent was located about 10 m above the ground (Fig. 6a, arrow), and formed an open space in which the bats roosted (Fig. 6b). During the construction of this tent, approximately 80 individual leaves and leaf clusters, about 30 small branches, and three to five larger branches were

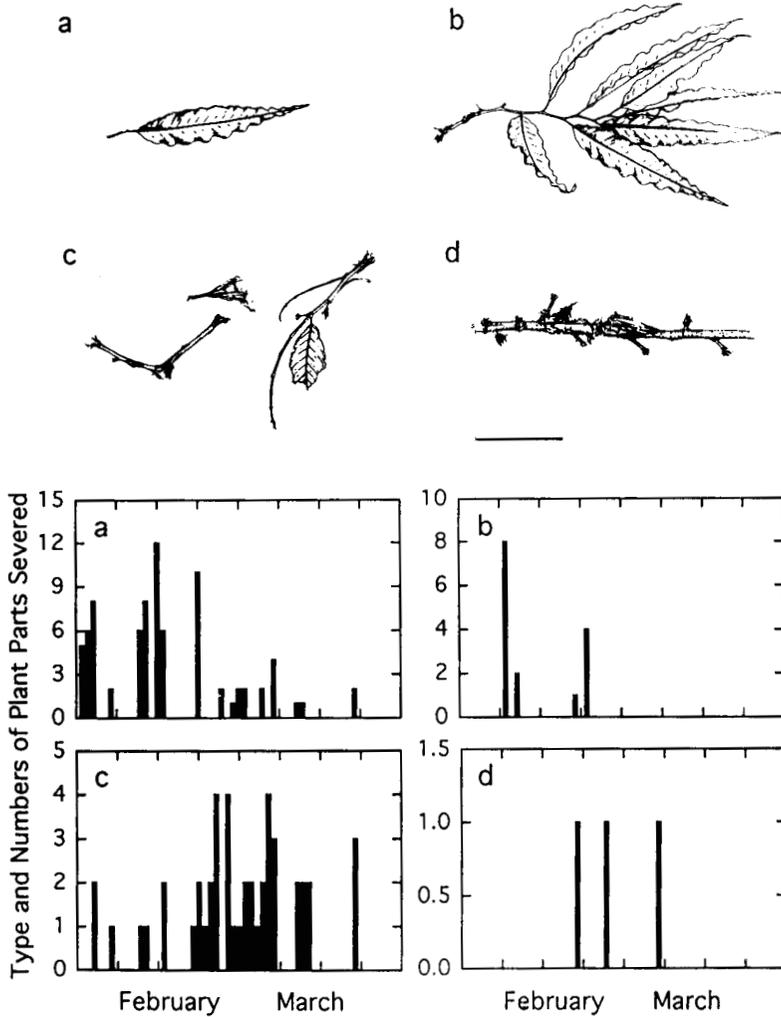


Fig. 7: Types (above) and numbers (below) of (a) individual leaves, (b) leaf clusters, (c) small stems and (d) large stems severed by *Cynopterus sphinx* in the construction of a stem tent in a *Polyalthia longifolia* tree. Scale bar (applies to all four drawings) = 20 cm. Note differing vertical scales in histograms

severed (Fig. 7). Up to 12 leaf petioles, four small stems, and eight leaf clusters were sometimes severed in a single night. Only one large stem was cut every 5 to 10 d. The severed petioles and stems of small leaf clusters ranged from 1 to 2 mm in diameter (Fig. 7a, b), whereas the short and large stems averaged 2.2 to 21.0 mm in diameter, respectively (Fig. 7c, d). From the onset of tent construction, it took nearly 50 d for the leaves, leaf clusters, and small and large branches to be chewed and severed. Judging from the relative numbers of leaves and small branches that were found beneath the tree in the morning and again in the evening, tent

construction appears to occur mostly at night. Because of the dense foliage on this tree, we were unable to consistently observe bats in the act of tent construction.

Discussion

Tent Construction

We describe tent-making behaviour by *Cynopterus sphinx* in which single males sever stems of *Vernonia scandens* and leaf petioles and stems of *Polyalthia longifolia* to create cavities or spaces into which females are recruited. These tents provide refuges for females which give birth to pups and resources that males defend against intrusion by other males. Earlier accounts of 'tent-making' behaviour of bats have been based largely on circumstantial evidence (KUNZ et al. 1994; KUNZ & MCCRACKEN 1995). This is the first report of bats observed in the act of tent-making and of the social organization and mating system in *C. sphinx*. Our observations that single males of *C. sphinx* construct and defend tents in *V. scandens* and *P. longifolia* support the hypothesis of KUNZ & MCCRACKEN (1995) that tent-making is an exclusive male behaviour.

PHILLIPS (1924) was the first to suggest that the centre 'seed strings' of the kitul palm, *Caryota urens* were severed by *Cynopterus sphinx* (= *brachyotis*), creating a bell-shaped cavity in which bats roosted (see PHILLIPS 1980 for a name re-assignment). This type of stem-tent construction in the flower and fruit clusters of *Caryota urens* has been described (BHAT & KUNZ 1995) and referred to as a stem tent (KUNZ et al. 1994). Stem tents constructed in flower and fruit clusters of *C. urens* are similar to those formed in the curtain creeper, *Vernonia scandens*, and in the inner spaces of the mast tree *Polyalthia longifolia* (BALASINGH et al. 1993; BHAT 1995). In each instance, the stems of vines and trees and the pendulous strings of the flower and fruit clusters are completely severed, creating a partially enclosed cavity. Stem tents constructed by *Cynopterus sphinx*, in vines of *Vernonia scandens*, flower and fruit clusters of *Caryota urens*, and in palm leaves, are entered from below (BHAT & KUNZ 1995; KUNZ & MCCRACKEN 1995), whereas tents constructed in *Polyalthia longifolia* are entered through portals that bats fashion by severing leaves and leaf clusters on the outer margin of the tree (Fig. 6a). The fundamental difference between stem tents and leaf tents is that in the former plant, tissues are completely severed. By contrast, a leaf tent is formed when bats partially chew the veins and surrounding tissue, causing the leaves or leaf segments to weaken and collapse downward to form a partially enclosed cavity (KUNZ et al. 1994).

The height of a stem tent above the ground is highly variable, because *C. sphinx* is known to construct tents in several different species of plants, each of which may vary in age and stature. In the present study, the height of stem tents in *Vernonia scandens* was about 5.6 m above the ground, whereas the stem tents constructed in *Polyalthia longifolia* ranged from 4 to 10 m above the ground. BHAT (1995) also noted that stem tents in *P. longifolia* were sometimes located up to 10 m above the ground. Tents formed in palm leaves and attributed to *C. sphinx* (GOODWIN 1979) ranged upwards from 2.4 to 6 m above the ground, whereas

those observed in flower and fruit clusters of the kitul palm, *Caryota urens*, ranged from 4 to 5 m above the ground (BHAT & KUNZ 1995). In contrast to palm leaves (e.g. *Corypha*, *Caryota*, *Livistona*) and mast trees, *Polyalthia longifolia*, the vines of the curtain creeper *Vernonia scandens* require physical support from other structures (e.g. garden walls), and in these situations tent height is usually proportional to the height of the supporting structure. Because the height of a stem tent in *P. longifolia* should depend largely on the maturity and height of the tree, older trees provide *C. sphinx* with opportunities to construct tents at several different heights. The height of stem tents constructed in flower and fruit clusters of the kitul palm *Caryota urens* is determined by the height of mature flower clusters (BHAT & KUNZ 1995).

Tent construction by *C. sphinx* takes place when a bat crawls on and hangs from the stems, petiole and leaves of plants. KUNZ & MCCrackEN (1995) found tooth marks and claw marks on both surfaces of palm leaves, and suggested that bats modified leaves by chewing veins as they crawled upon the upper surface, and chewed on the leaf plications from below. BARBOUR (1932) suggested that the initial bites in tent construction were made when bats hovered beneath the plant. However, given the thick and fibrous veins and rachis of palms such as *Corypha* and *Livistona*, and the highly fibrous stems of *Vernonia scandens* and *Polyalthia longifolia*, it seems quite unlikely that *C. sphinx*, or any other tent-making bat, could chew and sever leaves and stems while hovering. In fact, we question whether a bat the size of *C. sphinx* (wing span 0.56 m, NORBERG & RAYNER 1987) could hover in a confined space the size of a typical stem-tent cavity (Table 1), and simultaneously chew and sever the leaves and stems.

Our observations of tent-making support the hypothesis that this behaviour is a time-consuming and probably an energetically expensive activity (KUNZ 1982). However, depending on the type of plant material that is chewed, the costs associated with tent construction and maintenance are expected to vary widely. A male *C. sphinx* may engage in tent-making activity upwards to 30 d in *V. scandens* and at least 50 d in *P. longifolia* before a tent is completed. By contrast, a tent constructed in a succulent leaf of *Philodendron* sp. or *Anthurium* sp., where only a few veins are only partially chewed (KOEPCKE 1984; TIMM 1987) may be completed in a single night. The number of veins chewed may range up to 80 in the large palmate leaves of *Prichardia* (BARBOUR 1932), *Sabal* and *Coccothrinax* (KUNZ & MCCrackEN 1995). If veins and plications of these palms are severed at the same rate as the stems in *V. scandens*, tents constructed in palmate-shaped leaves could be completed in two to three nights. Once a leaf tent is constructed no further alteration is required. However, a stem tent will require continued maintenance as long as there is new growth of stems and leaves, especially those which impede flight access or make the tent otherwise unsuitable for roosting.

Tent Construction and Female Recruitment

Our study has shown that *Cynopterus sphinx* engages in two annual periods of tent construction; one during Feb. and Mar. and another in Sep. and Oct. These periods of tent construction generally coincide with a biannual breeding

season reported for this bat (KRISHNA & DOMINIC 1984; SANDU 1984; J. BALASINGH, pers. obs). Once a tent is completed, females begin to roost in the tent, and males engage in tent maintenance and defensive behaviour, prior to and during the parturition period. Female recruitment appears to be a seasonal phenomenon and fidelity of females to a particular tent (or male) appears to be highly variable. Judging from our analysis of tent characteristics, the vertical length of a tent (which includes the pendulous stems) may be an important criterion used by females to assess tent (or male) quality. The periodic pruning of pendulous stems and new leaves by males may be an important maintenance function, because well-formed entry arches in *Vernonia scandens* (Fig. 2a) and portals in *Polyalthia longifolia* (Fig. 6a) are important for bats for gaining unimpeded access to and from a tent cavity. A greater vertical tent length (in *V. scandens*) may also make it easier for males to defend a tent cavity and its female occupants from potential male intruders.

High roost occupancy by harem males, especially when females are receptive, appears to be an important behaviour for the successful defence of a tent. Judging from our observations at one tent over a period of 4 mo, a harem male appears to spend most of a 24-h period occupying the tent it constructed. On 16 nights, spanning eight lunar cycles, this male was absent from its tent for no more than 8–122 min on any given night. This and other harem males spent the least amount of time away from the tent during the parturition period in Mar. and early Apr., when females experienced a post-partum oestrus (SANDU 1984, 1988). The deposits of saliva that males make on the stems on the interior of their tents may also be important for repelling other males, or may make it possible for females to identify a particular male's tent even when he is absent. On several occasions at night we observed harem males chasing other bats in the vicinity of their tent, suggesting that both passive and active defence strategies are employed.

Observations that male *C. sphinx* make several short foraging flights each night (J. BALASINGH, pers. obs.) are consistent with observations that harem males of *Artibeus jamaicensis*, *Phyllostomus hastatus* and *Carollia perspicillata* feed predominantly in the vicinity of their day roost (MORRISON 1979; MORRISON & MORRISON 1981; MCCracken & BRADBURY 1981; FLEMING 1988). The accumulation of rejected fruit and leaf pellets and seeds beneath harem roosts can largely be attributed to males returning to their tent to consume fruit and other plant parts following their short foraging bouts (BHAT 1995; BHAT & KUNZ 1995). Reduced foraging time for males, relative to females, is consistent with the hypothesis that there is a trade-off between successful roost surveillance and maintenance, on the one hand, and time spent foraging on the other. Thus, harem males appear to maximize the time spent in their tent at night by returning with food which is eaten while defending the tent. Although, in the present study, the harem male from tent II departed to forage each night, an examination of the nightly time budget suggests that this bat did not always return to consume food in its tent. It should be noted that this bat did not return to the roost at night with food in the period from late Nov. to early Jan. (Table 3) when females are pregnant (SANDU 1984) and males are reproductively quiescent (KRISHNA &

DOMINIC 1984). This suggests that tent-guarding and harem maintenance is reduced when females are not receptive and there is no threat of paternity loss.

Tent Characteristics and Resource Defence

Tents constructed by *C. sphinx* appear to satisfy the conditions necessary for the formation of a resource-defence mating system (BRADBURY & VEHCAMP 1977; EMLÉN & ORING 1977; CLUTTON-BROCK 1989). Tents not only provide shelter and potential protection from predators, but their unique architectural style also makes it possible for a male to successfully defend a tent and its female occupants. Observations that a single male *C. sphinx* constructs and defends a tent suggest that this individual should gain preferred reproductive access to the females that occupy his tent. If stem tents are relatively time consuming and energetically expensive for males to construct and maintain, such an investment presumably is sufficient to ensure their preferential access to females during the breeding season. Because harem males construct tents and remain with the females they recruit, at least through the parturition period and the post-partum oestrus (SANDU 1984, 1988), males would be in a preferred position to secure exclusive copulations at the time females become receptive. Our observations suggest that high variance in some roost dimensions may explain why females choose certain males with which to roost and subsequently mate. However, whether females select males on the basis of other aspects of tent quality or some characteristics of the male invites further study.

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