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Jay F. Storz
University of Nebraska - Lincoln, jstorz2@unl.edu

J. Balasingh
St. John's College, Palayamkottai, 627 002, India

P. Thiruchenthil Nathan
St. John's College, Palayamkottai, 627 002, India

K. Emmanuel
St. John's College, Palayamkottai, 627 002, India

Thomas H. Kunz
Boston University, 5 Cummington Street, Boston, MA

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Dispersion and site fidelity in a tent-roosting population of the short-nosed fruit bat (*Cynopterus sphinx*) in southern India

JAY F. STORZ*[1], J. BALASINGH†, P. THIRUCHENTHIL NATHAN†, K. EMMANUEL† *and* THOMAS H. KUNZ*

Department of Biology, Boston University, 5 Cummington Street, Boston, MA 02215, USA
†*Department of Zoology, St. John's College, Palayamkottai, 627 002, India*

ABSTRACT. Patterns of dispersion and site fidelity were investigated in a tent-roosting population of the short-nosed fruit bat, *Cynopterus sphinx* (Megachiroptera), in southern India. A local population of *C. sphinx* occupied diurnal roosts in a variable subset of 45 stem tents constructed within the dense foliage of mast trees (*Polyalthia longifolia*). Individually marked tent-roosting bats were visually censused over the course of a 38-d interval spanning the postpartum oestrus period. On any given day, 33.3–85.7% (mean = 60.8%, SD = 14.2) of adult males roosted singly, with the remainder holding harems of 1–10 breeding females (mean = 3.01, SD = 0.79). Average harem sex ratio was 2.8-fold higher than the adult sex ratio of the total tent-roosting population within the study area, indicating the potential for a high variance in male mating success within a single breeding season. Bats of both sexes typically occupied one primary tent, interspersed with shorter periods of residency in alternate tents. Males exhibited a significantly higher degree of roost fidelity than females. Some females roosted sequentially with different males and with different combinations of females, whereas others remained continuously associated with a single male and/or particular female roostmates over the duration of the census period. There were no statistically significant relationships between physical characteristics of tents and rates of occupancy by males or females. Intermittent transfers by females between groups suggest that the defence of diurnal roosts by males represents a more profitable mating strategy than the direct defence of compositionally labile female groups.

KEY WORDS: behaviour, Chiroptera, *Cynopterus sphinx*, dispersion, India, mating system, polygyny, sex ratio, site-fidelity, tent-making bats

[1] To whom correspondence should be addressed. Email: storz@bio.bu.edu

INTRODUCTION

The degree of polygyny within a given population, and the concomitant opportunity for sexual selection, is largely attributable to the mode of mate competition among members of the sex with the higher potential rate of reproduction (Clutton-Brock & Parker 1992, Clutton-Brock & Vincent 1991). In the majority of mammalian species, males provide little or no parental care and reproductive success often may be limited chiefly by opportunities for mating. As a consequence, intrasexual competition for mates is typically more intense among males than females. The outcome of this competition is determined by the relative abilities of males to control mating access to receptive females (Bradbury & Vehrencamp 1977, Clutton-Brock 1989, Davies 1991, Emlen & Oring 1977). Depending on the species, and prevailing ecological and social conditions, this reproductive control may be based on the direct defence of females, defence of resources that attract females, or some combination of direct and indirect defence of access to mating opportunities (Emlen & Oring 1977, Ostfeld 1987). In general, the potential for polygyny is maximized when females form socially or spatially defined breeding groups distributed among burrows, dens, roosts or other discrete sites that males can economically defend as territories.

Bats exhibit a wide variety of different mating systems, most of which are variations on a polygynous theme (Bradbury 1977). Female gregariousness at diurnal roosting sites apparently has facilitated a harem-polygynous mating sytem in many species of bats, especially in the tropics (Bradbury & Vehrencamp 1977, Fleming 1988, Wilkinson 1987). Another commonly observed pattern in the social systems of polygynous bats is that juveniles of both sexes disperse from their natal breeding units, and movements of breeding females are apparently unconstrained by territorial males (e.g. *Carollia perspicillata*, Fleming 1988, Porter 1979, Williams 1986; *Desmodus rotundus*, Wilkinson 1985; *Phyllostomus hastatus*, McCracken & Bradbury 1981; *Saccopteryx bilineata*, Bradbury & Emmons 1974, Bradbury & Vehrencamp 1976). Thus, males attach themselves to female groups but have no direct role in maintaining their compositional stability. This provides greater scope for the role of female choice relative to the mating systems of many mammals where males impose themselves on pre-existing female distributions (Armitage 1986, Clutton-Brock 1989, Wrangham & Rubenstein 1986). When breeding females are distributed among defendable mating territories, the potential for polygyny (Emlen & Oring 1977) will largely depend on the site fidelity (or group cohesion) of females. When roost-site fidelity is high for both females and males, multiple females roost consistently with a single male (e.g. *Coleura afra*, McWilliam 1987; *Noctilio leporinus*, Brooke 1997; *P. hastatus*, McCracken & Bradbury 1981; *Tadarida pumila*, McWilliam 1988). When roost-site fidelity is low for females and high for males, females roost in sequential association with multiple males (e.g. *C. perspicillata*, Fleming 1988, Williams 1986; *S. bilineata*, Bradbury &

Emmons 1974, Bradbury & Vehrencamp 1976; *Pipistrellus pipistrellus*, Gerell & Lundberg 1985). In the latter scenario, territorial males may have simultaneous and sequential contact with a large pool of potential mates, but male–female associations are highly transient. The operational sex ratio may be similar in each case, but the latter scenario results in a much-diminished degree of exclusivity in mating access among territorial males and a reduced scope for the maintenance of social bonds within and between the sexes.

In this study we investigated the pattern of dispersion and site fidelity in a day-roosting population of the short-nosed fruit bat, *Cynopterus sphinx* Vahl 1797 (Megachiroptera), at a site in southern India. The purpose was to evaluate how the interplay of male and female reproductive strategies influences the degree and form of polygynous mating in this harem-forming species. Specifically, we used visual census data to evaluate the degree to which the spatial and temporal dispersion of the sexes determines the potential for polygyny.

<div align="center">STUDY SPECIES</div>

Cynopterus sphinx is a medium-sized (40–70 g) frugivorous bat that is distributed throughout much of the Indomalayan region (Storz & Kunz 1999). *C. sphinx* has a polyoestrous reproductive cycle, with two well-defined and highly synchronous parturition periods per year (Krishna & Dominic 1983, Sandhu 1984, Sreenivasan *et al*. 1974). Females give birth to single pups, and can produce a maximum of two young per year (Krishna & Dominic 1983, Sandhu 1984). In peninsular India, parturition typically occurs in March/April (dry season) and July/August (wet season). Once pups are born in March/April, females undergo a postpartum oestrus (Krishna & Dominic 1983, Sandhu 1984, Ramakrishna 1947). Females are simultaneously pregnant and lactating until pups from the March/April cohort are weaned. Following the birth of the July/August cohort, females are anoestrous until October (Krishna & Dominic 1983, Sandhu 1984, Sandhu & Gopalakrishna 1984). Seasonally bimodal peaks in spermatogenic activity in males (Krishna & Dominic 1984, Sandhu 1988) and the timing of conceptions in females (Krishna & Dominic 1983, Sandhu 1984) indicate well-defined periods of mating for *C. sphinx* in peninsular India. Embryo implantation alternates between the two horns of the bicornuate uterus from one pregnancy to the next (Krishna & Dominic 1983, Sandhu 1984, Sandhu & Gopalakrishna 1984). Conception appears to occur shortly after parturition, as lactating females sampled during the postpartum oestrus period had implanted embryos while the contralateral uterine horn was still distended (Krishna & Dominic 1983, Sandhu & Gopalakrishna 1984). Similar evidence from congeneric species and other cynopterine fruit bats indicates that conception can occur within several days or weeks of parturition (Heideman 1988, 1989; Heideman & Powell 1998, Kofron 1997). In peninsular India, postpartum conceptions apparently occur within a particularly compressed window of time, as the interval between the onset of parturition in the dry season (March/April) and wet

season (July/August; Krishna & Dominic 1983, Sandhu 1984, Storz *et al*. 1999) closely approximates the estimated duration of gestation in *C. sphinx* (115–125 days; Gopalakrishna 1969, Moghe 1956, Sandhu 1984). This indicates that the days or weeks spanning the dry-season parturition period constitute a critical window of time for investigating the roosting behaviour of *C. sphinx* in connection with mating activity.

C. sphinx occupies a wide diversity of diurnal roosts and is known to alter different types of foliage to create 'tents' (Balasingh *et al*. 1993, 1995; Bhat 1994, Bhat & Kunz 1995, Goodwin 1979, Kunz *et al*. 1994, Storz *et al*. 1999). In southern India, for example, adult males construct tents within the dense foliage of the mast tree (*Polyalthia longifolia*) by chewing and severing leaf petioles and radial arrays of small, lateral branches. Over a period of about 50 d, a single adult male constructs an entry/exit portal and a partially enclosed, dome-shaped roosting space surrounded by uncut stems and leaves. These tents attract groups of breeding females that are defended as harems by single males (Balasingh *et al*. 1995).

<center>METHODS</center>

This study was conducted in Palayamkottai, Tirunelveli District, Tamil Nadu, India (18°44′N, 77°42′E) over a 38-d period (21 February–29 March 1996). Palayamkottai is situated on the southeastern coastal plain of peninsular India in the rainshadow of the Western Ghats. The surrounding region is characterized by semi-arid tropical scrubland and thorn forest (Mani 1974). In this region, *C. sphinx* is known to construct tents in the dense foliage of mast trees (*Polyalthia longifolia*) and curtain creeper (*Vernonia scandens*; Balasingh *et al*. 1993, 1995). At the outset of the study, we mapped the location of 330 *P. longifolia* trees and searched for day-roosting *C. sphinx* within a delimited area measuring *c*. 1.0 km in diameter. Within the study area, *P. longifolia* trees provided the only potential foliage-roosting sites for *C. sphinx*. We identified a total of 45 *P. longifolia* trees in which tents had been constructed. We searched these tents for bats every day for 38 consecutive days and recorded the total number and sex of bats in each occupied tent. Diurnal roosting groups of bats were typically tightly clustered in the apex of the dome-shaped tent cavities (Balasingh *et al*. 1995) and adult males were easily distinguished from females on the basis of pelage colour (Bates & Harrison 1997, Storz *et al*. 1999).

To determine whether certain architectural features of tents influenced rates of occupancy by bats, we recorded the following linear dimensions of tents constructed in *P. longifolia*: (1) height of the interior crown (distance from base of tree to apex of tent cavity), (2) vertical height of tent cavity (distance from base of entry/exit portal to apex of tent cavity), (3) width of tent cavity (length of cross-sectional major axis), and (4) depth of tent cavity (length of cross-sectional minor axis). Finally, we used compass bearings to measure the horizontal angle of orientation (azimuth) of the entry/exit portal for each tent.

The relationship between physical characteristics of tents and rates of occupancy by bats was assessed using linear regression analysis. Only tents that were occupied on one or more censuses were included in the analyses and the cumulative numbers of male and female bats per tent were square-root transformed to more closely approximate a normal distribution.

Over the course of 18 nights concurrent with the onset of the census period, we captured bats with mistnets at seven different locations surrounding the periphery of the tent-roosting grounds. The mistnets were deployed in flyways that were located 0.1–1.0 km from the nearest set of tents within the study area. These flyways were used by bats as major commuting routes between the tent-roosting area and outlying feeding grounds (Marimuthu *et al*. 1998). Mistnets were monitored from shortly after sundown until sunrise. For each bat captured, we recorded sex, reproductive condition, length of forearm, and body mass. Parity of adult females was assessed by examination of the nipples (Racey 1988, Sandhu & Gopalakrishna 1984). Adult bats were individually marked with a coloured bead necklace and a plastic split-ring forearm band (size 2X, A. C. Hughes, Ltd.) covered with coloured reflecting tape. Females were banded on the left forearm, males on the right. To place the band around the forearm, a small incision was made in the antebrachial membrane (Kunz 1996).

The proportion of day-roosting bats in the study area that were individually marked showed an incremental increase from one day to the next during the period of mistnetting. With the aid of 10×50 binoculars, we recorded the individual identities of marked tent-roosting bats in each of the daily censuses following the onset of mistnetting. Because capturing bats in their tents might disrupt group composition and the general pattern of roosting behaviour, trapping and banding bats at sites away from their tents permitted the subsequent monitoring of individually recognizable day-roosting bats without risking the consequences of direct disturbance. In the 2-d period following the termination of our mistnetting efforts (10–11 March), 67.7–70.8% of adult bats roosting in the monitored tents were individually marked. The remaining unmarked tent-roosting bats in the study area were solitary adult males. On the mornings of 12 and 13 March, all of the remaining unmarked male bats in the study area (n = 10) were trapped in their tents. Bats were captured in their tents using a hoop net attached to an extensible aluminum pole after first surrounding and enveloping the entire tree with a 6-m × 6-m nylon mesh net strung onto six vertical 8-m bamboo poles. After processing, the bats were housed indoors in a mesh cage and were released on the same evening of capture. The censuses of the following morning revealed that all bats had returned to their original tents.

The census data for the following 16-d period (14–29 March 1996) were used to calculate the degree of roost fidelity for each individual bat in the study population. The degree of roost fidelity was expressed as the proportion of

censuses that a given individual was resident in a particular tent. Among parous females that were monitored in the subsequent census period, 9/15 had given birth by 10 March, and 15/15 had given birth by 14 March. Thus, the census interval spanned the period of postpartum oestrus when mating activity was expected to be at its peak (Krishna & Dominic 1983, 1984; Sandhu 1984, 1988; Sandhu & Gopalakrishna 1984).

RESULTS

Over the course of seven nights of mistnetting at different sites surrounding the periphery of the tent-roosting grounds, we trapped and marked a total of 154 adult *C. sphinx*. The sex ratio of this population sample (1:1.11, males:females) was not significantly different from unity ($\chi^2 = 0.416$, df = 1, P > 0.05). Both sexes were captured in nearly equal numbers at each site. Including the 10 males that were captured in their tents, a total of 164 adult bats were trapped and marked during the first 22 d of the census period. During the subsequent 16-d census period, 15 marked males and 17 marked females were observed roosting in the study area on one or more censuses. During this period, 86.2–100.0% (mean = 94.2%, SD = 4.4) of bats roosting within the study area were individually marked.

Lengths of forearms of all adult bats conformed to a normal distribution (Kolmogorov–Smirnov one-sample test; z = 1.017, n = 164, P = 0.252) and no inequality of variances was evident between the sexes (Bartlett's test; $\chi^2 = 2.014$, df = 1, P = 0.150). No statistically significant sexual dimorphism was evident; lengths of forearm (mean ± 1 SD) were 67.7 ± 1.8 for males and 67.8 ± 2.2 for females (t = 0.109, df = 162, P = 0.914).

Social dispersion

The total number of tent-roosting adults within the study area ranged from 21 to 38 d^{-1} (mean = 28.42, SD = 3.55; Figure 1) over the course of the total census period. The daily census numbers of adult males (mean = 13.76, SD = 1.40) and females (mean = 14.66, SD = 3.41) were similar. The adult sex-ratio of tent-roosting bats averaged 1:1.08 (males:females) and was not significantly different from unity ($\chi^2 = 0.170$, df = 1, P > 0.05) or the ratio expected from the mistnet sample of bats taken from the vicinity of the tent-roosting area ($\chi^2 = 0.05$, df = 1, P > 0.05).

Within the study area, 28 of the 45 *P. longifolia* tents were occupied on one or more days. On any one census, the minimum number of occupied tents was 11 and the maximum number was 16. Distributions of adult bats among tents revealed pronounced sex differences in the spatial pattern of dispersion. On any given day, 33.3–85.7% (mean = 60.8%, SD = 14.2) of males roosted singly and the remainder roosted in association with 1–10 adult females (mean = 3.01, SD = 0.79; Figure 2). The median size of tent-roosting female groups was two (n = 199). Male-female pairs represented the most common social
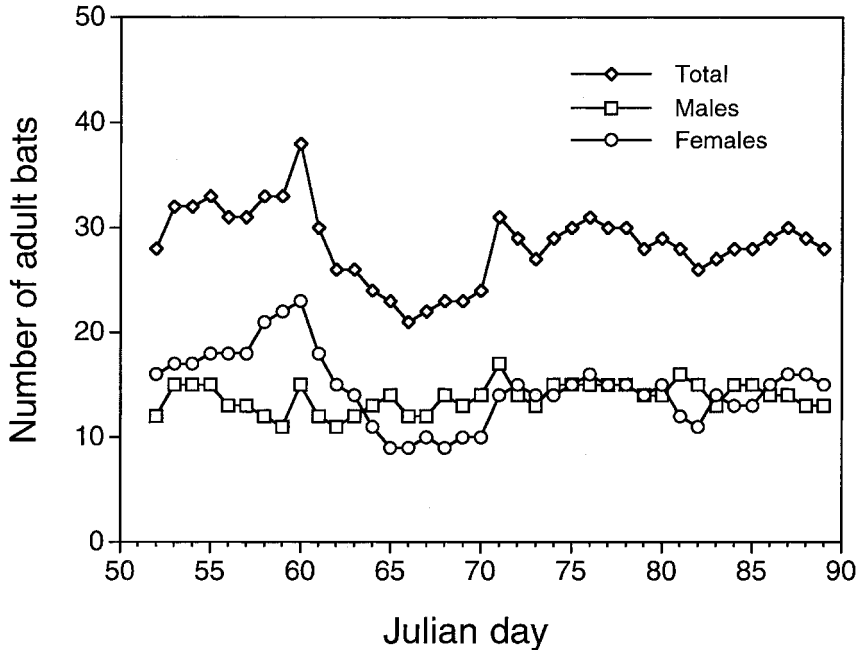
Figure 1.   Census numbers of tent-roosting bats (*Cynopterus sphinx*) within the study area in Palayamkottai, India (21 February–29 March 1996).

configuration and accounted for 6.7–33.3% (mean = 12.4%, SD = 7.5) of occupied tents. Females were never found roosting in the absence of a male and no more than one male ever occupied the same tent. Males occupied 11–15 (mean = 13.8, SD = 1.4) of the 45 available tents on any given day. Females exhibited a highly clumped distribution, occupying only 2–8 (mean = 5.2, SD = 1.8) of the available tents. The variance/mean ratio of the number of adult females per tent was 2.51. Over the course of the entire census period, 11.6% of monitored tents contained one or more females, and 30.6% contained males (n = 1710 tents × censuses).

Site fidelity

Census data based on individually marked bats revealed pronounced sex differences in roost-site fidelity. The majority of males remained faithful to a single tent, whereas most females used one primary tent and one or more alternate tents (Table 1). Overall, 73.3% (11/15) of marked males and 35.3% (6/17) of marked females remained continuously faithful to a single tent within the study area. Although 4/15 of marked males made use of one or more alternate roosts during the census period, males were never observed roosting in more than one tent within the study area. By contrast, 11/17 of marked females made use of one or more alternate roosts during the census period, and seven of them used two different tents within the study area on separate days. Tents
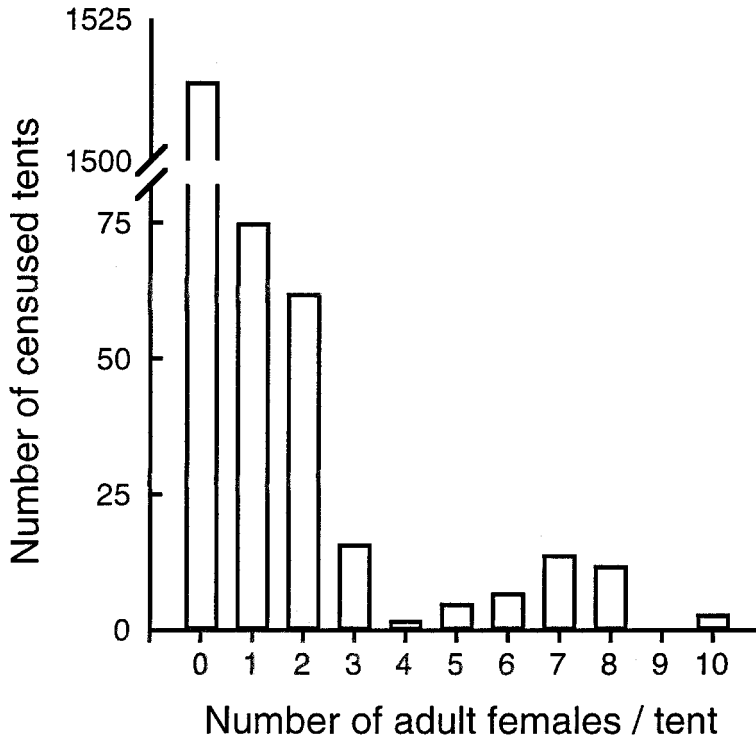
Figure 2.   Distribution of day-roosting female *Cynopterus sphinx* among tents.

Table 1. Roost fidelity of 32 individually marked bats (*Cynopterus sphinx*) observed on one or more occasions during the course of a 16-d census period (14–29 March 1996). The degree of roost fidelity is expressed as the proportion of censuses in which an individual was observed roosting in a particular tent.

Male I.D.	Roost fidelity index	Tent number	Female I.D.	Roost fidelity index (1st tent)	First tent number	Roost fidelity index (2nd tent)	Second tent number
904M	1.00	3	366F	1.00	3		
957M	0.75	6	337F	1.00	3		
687M	1.00	7	776F	0.06	6		
614M	1.00	11	724F	0.31	32	0.13	14
696M	1.00	14	769F	1.00	32		
966M	0.25	18	396F	1.00	32		
971M	1.00	32	300F	1.00	32		
191M	1.00	34	344F	1.00	32		
959M	1.00	36	760F	0.38	32		
634M	0.17	37	316F	0.94	32		
940M	1.00	38	347F	0.94	32		
948M	0.81	39	341F	0.31	32	0.19	34
991M	1.00	40	788F	0.19	36	0.13	6
992M	1.00	44	343F	0.44	38	0.19	39
996M	1.00	45	777F	0.75	44	0.25	38
			787F	0.75	44	0.25	38
			745F	0.50	44	0.25	38
Mean	0.865			0.684		0.199	
SD	0.277			0.342		0.054	

used on different days by the same female were separated by distances of 12–110 m (median = 25 m, n = 5 pairs of tents). To assess differences in the degree of roost fidelity between the sexes, 26 individuals (13 males and 13 females) that were present within the study area on $\geq$ 8 censuses were compared. Within this subset of marked bats, males exhibited a significantly higher degree of roost fidelity than females (mean = 0.97 vs. 0.68; Mann–Whitney test, U = 50.0, P = 0.037). While some females roosted sequentially with different males and with different combinations of females, others remained continuously associated with a single male and/or particular female roostmates over the duration of the census period.

Three distinct groups of females could be distinguished in the study area. A total of nine marked females roosted in tent 32 (in association with male 971M), but no more than six to eight females occupied the tent simultaneously. Within this set of females, eight maintained roost fidelity indices of 0.94–1.0 (Table 1). A slightly less cohesive group of three marked females (745F, 777F, and 787F) maintained roost fidelity indices of 0.5–0.75 in tent 44. The same three bats jointly relocated to tent 38 for a period of 4 d and then jointly returned to tent 44. Meanwhile, the males resident in tents 38 and 44 (940M and 992M, respectively) remained continuously site-faithful. One pair of nulliparous females, 366F and 337F, consistently roosted in tent 3 and remained associated with the same male (904M) continuously over the duration of the census period. Although unmarked bats of both sexes occasionally made transient appearances within the study area, unmarked females were never observed to join established harems and unmarked males were never observed to occupy tents that had been previously occupied by other males earlier in the census period.

Assuming that matings occur exclusively in diurnal roosts and that conceptions were equally likely over the duration of the 16-d census of individually marked bats, 69.0% of all mating opportunities within the study area were monopolized by only four males, and 35.8% were monopolized by 971M alone. The proportion of days a male held a harem ($\geq$ female roostmate) was strongly correlated with average harem size (Spearman's r_s = 0.986, n = 15, P < 0.001). Among those males present on $\geq$ 75% of censuses (n = 13), there were no statistically significant correlations between male forearm length and harem size (r_s = 0.439, P > 0.05) or male body mass and harem size (r_s = 0.279, P > 0.05).

Tent selection by bats

Tents in *P. longifolia* were typically constructed at a height just below the top-most quarter of the tree (4.70–9.59 m from base of tree to apex of tent cavity). Although the cumulative numbers of males and females per tent were strongly correlated (r_s = 0.805, n = 45, P < 0.001), there was no evidence to suggest that rates of tent occupancy by either sex were influenced by architectural features of tents.

Table 2. Characteristics of stem tents constructed in mast trees (*Polyalthia longifolia*) by short-nosed fruit bats (*Cynopterus sphinx*) in Palayamkottai, India. The mean ± 1 SD (range) is reported for measurements of tents occupied by bats on one or more censuses and tents that remained unoccupied over the duration of the census period. Equality of means for linear dimensions of tents was tested using an approximate t-test for samples with unequal variances (Sokal & Rohlf 1995). Equality of means for the azimuths of entry/exit portals was tested using the two-sample Watson–Williams test (Zar 1999). No differences in means between occupied and unoccupied tents exceeded two-tailed critical values of the t-distribution ($\alpha = 0.05$).

Tent characteristics	Occupied tents (n = 28)	Unoccupied tents (n = 17)	t (df = 43)	P
Height of interior crown (m)	6.37 ± 1.19 (4.70–9.59)	6.93 ± 0.95 (4.93–8.36)	1.644	0.107
Vertical height of tent cavity (m)	1.40 ± 0.37 (0.41–1.83)	1.41 ± 0.22 (1.04–1.73)	0.097	0.924
Width of tent cavity (m)	0.64 ± 0.18 (0.33–1.02)	0.65 ± 0.09 (0.48–0.76)	0.116	0.908
Depth of tent cavity (m)	0.49 ± 0.12 (0.28–0.76)	0.50 ± 0.08 (0.38–0.64)	0.070	0.944
Azimuth of entry/exit portal	135.9 ± 56.9°[1] (225°)[2]	131.9 ± 58.2°[1] (237°)[2]	0.680	0.500

[1]Mean azimuth and mean angular deviation were calculated from Cartesian coordinates of the mean angle and length of the mean vector.
[2]Smallest arc spanning all values of the circular distribution.

The distribution of compass directions of entry/exit portals was highly concentrated around the mean azimuth (Rayleigh's test for circular uniformity, z = 9.681, n = 45, P < 0.002), but there was no statistically significant difference between occupied and unoccupied tents in this regard (Table 2). Linear-circular regression (Zar 1999: 651–653) revealed no statistically significant relationship between azimuth of the entry/exit portal and the cumulative number of resident males ($r^2 = 0.054$, SE = 1.724, F = 0.711, df = 2, 25; P = 0.501) or females ($r^2 = 0.048$, SE = 3.757, F = 0.431, df = 2, 17; P = 0.657). Likewise, occupied and unoccupied tents were not significantly different with respect to linear measurements (Table 2), and multiple linear regression revealed no statistically significant associations between any combination of tent dimensions and the cumulative number of resident bats of either sex. Variability of tent dimensions explained < 12% of the variation in the cumulative number of resident males ($r^2 = 0.119$, SE = 1.735, F = 0.779, df = 4,23; P = 0.550) and < 8% of the variation in the cumulative number of resident females ($r^2 = 0.079$, SE = 3.934, F = 0.324, df = 4,15; P = 0.858). Partial regression coefficients for tent dimensions did not exceed critical values of the t-distribution ($\alpha = 0.05$). Cumulative numbers of bats per tent conformed to a normal distribution following square-root transformation (Kolmogorov–Smirnov one-sample test; z = 0.955, 0.947; n = 28, 20; P = 0.321 and 0.332 for males and females, respectively) and plots of the residuals revealed no heterogeneity of variances.

<div align="center">DISCUSSION</div>

Social dispersion

The average harem sex ratio, 1:3.01 (males:females), was 2.8-fold higher than the adult sex ratio of tent-roosting bats within the study area and indicates the potential for a high variance in male mating success within a single

breeding season. The extent to which this potential is realized will depend on the ability of harem males to maintain exclusive mating access to female roostmates during the postpartum oestrus period. Polygynous mating appears to be greatly facilitated by the clustering of females within the confines of partially enclosed roosting spaces that can be economically defended by males. Whatever the underlying causes of female aggregation, it appears that the spatial clustering of females is not a forced option imposed by a limited number of diurnal roosting sites.

Studies of day-roosting populations of *C. sphinx* at other sites in peninsular India have revealed highly skewed, female-biased sex-ratios (Sandhu 1984, Sandhu & Gopalakrishna 1984, Storz *et al*. 1999). Sandhu (1984) sampled a day-roosting population of *C. sphinx* in central India and attributed the female-biased adult sex ratio to a higher mortality rate for males, since young of both sexes were present in equal numbers prior to weaning. An alternative explanation is that a given sample of diurnal roosting groups will include only those males that have successfully defended territories and recruited females. Such males obviously represent a small, non-random fraction of the total adult male population in the local area. Thus, the skewed sex ratio in a sample of roosting groups would simply reflect the fact that a large fraction of the adult male population is excluded from diurnal roosting sites used by females. The present study is the first to document sex ratios of a day-roosting population and a larger (and presumably random) sample of foraging bats in the same local area. The skewed sex ratio of day-roosting groups reflects the mode of social organization but does not necessarily provide an accurate demographic profile of the total adult population.

Site fidelity

Bats of both sexes typically occupied one primary tent, interspersed with shorter periods of residency in alternate tents (Table 1). Males generally showed a higher degree of roost-site fidelity than females, a commonly observed pattern in polygynous bats (Bradbury & Emmons 1974, Bradbury & Vehren-camp 1976, Fleming 1988, Gerell & Lundberg 1985, Happold & Happold 1996, Lewis 1995, Park *et al*. 1998, Williams 1986). However, alternate roosts used by males were apparently distributed over a larger area since they were absent from the study area when they were not resident in their primary tent. By contrast, alternate tents used by females were often in close proximity to their primary tent. Although males may be more site-faithful with respect to particular tents, evidence for sex differences in site-fidelity at a broader spatial scale must await genetic and/or large-scale mark-recapture studies.

The intermittent transfers among tents by females indicate that individual roosting associations are relatively fluid, both within and between the sexes. However, subsets of harems remained remarkably cohesive on a day-to-day basis and compositional turnover was typically limited to a small fraction of the total group membership. A similar pattern was observed in a previous study

of tent-roosting *C. sphinx* in the same site. During the course of observations that spanned the dry-season parturition period, six adjacent harems roosting in *V. scandens* tents exhibited fluctuations in harem size on a day-to-day basis, indicating that females periodically shuttled among tents (Balasingh *et al*. 1995). In the present study, observations of coordinated relocations of female groups suggest that group cohesion may be at least partly attributable to actively maintained affiliative relationships among females as opposed to fidelity to the same tent (or to the male defending the tent). At a site in western India (Pune), females often remained associated as roostmates from one breeding season to the next, and group cohesion was unaffected by harem male turnover. Despite the cohesiveness of subsets of harem females, recapture records indicated a high overall rate of compositional turnover between consecutive breeding seasons (Storz *et al*. 1999). As in other polygynous bats (e.g. *C. perspicillata*, Fleming 1988, Williams 1986; *P. hastatus*, McCracken & Bradbury 1981), the continued association of female *C. sphinx* was not attributable to fidelity to the same male (Storz *et al*. 1999).

Males typically continued to defend a single tent in the absence of females. Likewise, harem-holding males invariably continued to defend a single tent in spite of turnover in female group composition. Intermittent transfers by females among groups suggest that the territorial defence of diurnal roosts by males represents a more profitable mating strategy than the direct defence of compositionally labile female groups. The same basic pattern was observed in Pune, where territorial males defended the same roost (or a new roost adjacent to the original roost) from one breeding season to the next (Storz *et al*. 1999). This form of resource-defence polygyny also conforms to the pattern observed in several other species of polygynous bats in which access to breeding females is tied to the territorial defence of particular roost sites (e.g. *Artibeus jamaicensis*, Kunz *et al*. 1983, Kunz & McCracken 1996, Morrison 1979, Morrison & Handley 1991; *C. perspicillata*, Fleming 1988, Williams 1986; *S. bilineata*, Bradbury & Emmons 1974, Bradbury & Vehrencamp 1976; *T. pumila*, McWilliam 1988).

The average sex ratio of harems during the postpartum oestrus period represents the operational sex ratio (simultaneous number of breeding males to number of potentially fertilizable females; Clutton-Brock & Parker 1992, Emlen & Oring 1977) to the extent that matings occur exclusively in diurnal roosts. Interpreting the sex ratio of harems as an empirical measure of the potential for polygyny, the expected variance in male mating success (and concomitant opportunity for sexual selection) apparently is subject to a considerable degree of temporal variation. Comparison of the present census data with those from a previous study of *C. sphinx* in the same study area (Balasingh *et al*. 1995) revealed marked differences in average harem size during the same phase of the reproductive cycle. Harems roosting in *V. scandens* tents (no longer in existence in 1996) were on average 1.86-fold larger than harems roosting in *P. longifolia* tents in the present study. Thus, changes in the availability of

diurnal roosts that influence the pattern of female dispersion may be expected to produce geographic and temporal variation in the potential for polygyny. This indicates that roosting habitat may be a primary determinant of the opportunity for sexual selection in *C. sphinx* and other harem-forming bats in which males pursue a mating strategy of resource-defence polygyny.

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