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THE RELATIONSHIP BETWEEN ROOSTING ECOLOGY AND DEGREE OF POLYGYNY IN HAREM-FORMING BATS: PERSPECTIVES FROM *CYNOPTERUS*

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Within the broad continuum of polygyny, the mating systems of harem-forming bats exhibit a high degree of interspecific diversity and intraspecific variation. Here, I review the social structure and mating systems of 4 nominal species in the Old World fruit bat genus *Cynopterus*, and explore the relationship between roosting ecology, the size and stability of female groups, and variation in degree of polygyny. Intraspecific comparisons for *C. brachyotis* Sunda and *C. sphinx* suggest that the distribution and availability of suitable roost sites has a strong influence on the dispersion of females among males. Examination of paternity data for *C. sphinx* demonstrates a direct relationship between the environmental potential for polygyny and variance in male reproductive success: a 2-fold increase in mean harem size due to reduction in roost availability produces a 2-fold increase in reproductive skew among males. However, in *C. brachyotis* Sunda, *C. sphinx*, and *C. horsfieldii*, low fidelity of females to roosts or males is consistent, regardless of roost dispersion or permanence. In contrast, female *C. brachyotis* Forest exhibit high short-term fidelity to males, despite low roost fidelity. It is proposed that female lability is influenced by the distribution of potential mates and the benefits of multiple mating and, in *C. brachyotis* Sunda and *C. sphinx*, is likely to promote both behavioral and cryptic female choice, and male sperm competition.

Key words: *Artibeus*, colony, lability, promiscuity, resource defense, *Saccopteryx bilineata*, tent

Despite the tremendous ecological and social diversity of bats, determinants of the evolution and plasticity of chiropteran mating systems have received surprisingly little attention (McCracken and Wilkinson 2000; but see Pitnick et al. 2006; Wilkinson and McCracken 2003). However, some general patterns are evident. The typically gregarious nature of females promotes polygyny and, in species with year-round male–female associations, the dispersion of females among males is intimately linked to roosting ecology (Kunz and Lumsden 2003; McCracken and Wilkinson 2000). Harem-based polygyny (sensu McCracken and Wilkinson 2000) is particularly common in the tropics and is recorded in 21 genera representing 6 families (Emballonuridae, Molossidae, Noctilionidae, Phyllostomidae, Pteropodidae, and Vespertilionidae—Dechmann et al. 2005; McCracken and Wilkinson 2000). Across taxa, harem social structure is strongly associated with the use of cavities in caves and tree trunks, or modified foliage and other plant-associated structures, all of which provide

semienclosed, nonephemeral roosts that are, in theory, defensible by males and attractive to females (Chaverri and Kunz 2006; Dechmann et al. 2005; Hodgkison et al. 2003; Kunz and Lumsden 2003; Kunz and McCracken 1996).

A relationship between interpopulation variation in female group size and stability, and roost characteristics is reported for several species (*Artibeus jamaicensis* [Kunz and McCracken 1996; Morrison 1979; Ortega and Arita 1999], *A. watsoni* [Chaverri et al. 2007], and *Neoromicia nanus* [formerly *Pipistrellus nanus*—Happold and Happold 1996; O’Shea 1980]). However, even when female group composition is relatively stable, within-harem paternity may be high (*Phyllostomus hastatus*—McCracken and Bradbury 1977), moderate (*A. jamaicensis*—Ortega et al. 2003), or low (*Saccopteryx bilineata*—Heckel et al. 1999). Together, these observations suggest that, although the tendency of females to aggregate, minimally discontinuous breeding cycles, and use of defensible, nonephemeral roosts have favored convergence on harem-based social structure in geographically and phylogenetically disparate taxa, considerable variation in degree of polygyny exists both within and among species.

According to the long-standing paradigm for the evolution of mating systems, the spatial and temporal distribution of key resources determines the distribution of receptive females,

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whereas the distribution of females constrains potential variance in male reproductive success, or the environmental potential for polygyny (Clutton-Brock 1989; Emlen and Oring 1977; Shuster and Wade 2003). However, as demonstrated by paternity data in a wide range of mammals, assumptions of stable distributions of females among males may underestimate the environmental potential for female choice and promiscuity (Martin et al. 2007; Ophir et al. 2008; Pemberton et al. 1992; Twiss et al. 2006). Given the high vagility of bats and lack of evidence for male control over the movements of females, is the resource-based model of Emlen and Oring (1977; see also Bradbury and Vehrencamp 1977) sufficient to explain variation in the mating systems of harem-forming species? From the perspective of males, does the spatial clumping of resources necessary to females raise the environmental potential for polygyny? Are patterns of female fidelity to individual males sensitive to differences in the distribution and abundance of key resources? These questions are discussed in relation to the roosting ecology and social structure of species in the Old World fruit bat genus *Cynopterus*.

Although the dispersion of feeding resources is a major determinant of social structure in some species of bats (e.g., Bradbury and Vehrencamp 1976, 1977), I focus on roosts as a resource with primary relevance to patterns of female dispersion and male–female associations in *Cynopterus*. Bats in this genus are not known to defend feeding resources and typically remove fruit from the parent tree to solitary feeding roosts (Boon and Corlett 1989; Bumrungsri 2002; Fletcher 2001; Funakoshi and Zubaid 1997; Tan et al. 1998), strongly suggesting that the day roost is the main venue for social interactions, including mating. I review briefly the natural history of the genus, summarize aspects of sociality and roosting ecology that are consistent across species, and identify relevant differences among species. I then explore the relationship between roost distribution and availability, and inter- and intraspecific variation in the social mating systems of 4 nominal species: *C. sphinx*, *C. horsfieldii*, *C. brachyotis* Sunda, and *C. brachyotis* Forest (sensu Campbell et al. 2004). Drawing on paternity data for *C. sphinx*, I ask whether observed distributions of females among males are predictive of variance in male reproductive success. In closing, I identify unresolved questions and suggest approaches that might contribute to a better understanding of the evolution of harem mating systems in bats, and of the factors responsible for their considerable variability.

NATURAL HISTORY AND ROOSTING ECOLOGY

The distribution of the genus *Cynopterus* spans more than 40° of latitude and 60° of longitude in the Old World tropics, extending throughout the Indian subcontinent, across mainland Southeast Asia and Indonesia, reaching its easternmost limit in the Philippine archipelago (Campbell et al. 2004; Corbet and Hill 1992). Throughout this range, species of *Cynopterus* typically account for the majority of fruit bat captures, in habitats ranging from virgin forest to suburban gardens (Bates and Harrison 1997; Heideman and Heaney 1989; Hodgkison

et al. 2004; Lane et al. 2006). Seven species are currently recognized (Simmons 2005) and several more remain to be described (Campbell et al. 2004). In peninsular Thailand and Malaysia, and parts of Indonesia, 2 phenotypically similar but evolutionarily distinct ecotypes in the *C. brachyotis* species complex are broadly sympatric (Campbell et al. 2004, 2007). Genetic, ecological, and morphometric data support the recognition of the 2 ecotypes as distinct species (Campbell et al. 2006b; 2007; K. Helgen, Smithsonian Institution, pers. comm.). Pending taxonomic revision, the slightly smaller, forest-associated ecotype is referred to as *C. brachyotis* Forest, and the disturbed habitat ecotype as *C. brachyotis* Sunda (Campbell et al. 2004).

Based on this proposed taxonomic distinction, social and ecological data are available for 4 species: *C. horsfieldii*, *C. sphinx*, *C. brachyotis* Sunda, and *C. brachyotis* Forest. All exhibit year-round, harem-based group structure, are predominantly plant-roosting, and utilize modified roosts (“tents”) in a nonobligate manner (Balasingh et al. 1995; Campbell et al. 2006a; Tan et al. 1997). Roost modification has been observed in male *C. sphinx* and is presumed to be an activity of males in other congeners (Balasingh et al. 1995; Kunz et al. 1994; Tan et al. 1997). Group sizes vary considerably among species but roosts never contain >1 adult male (Campbell et al. 2006a; Storz et al. 2000a, 2000b). Both males and females periodically roost alone and there is no evidence for the formation of bachelor groups by subadult males (Campbell et al. 2006a; Gopukumar et al. 2005; Storz et al. 2000a, 2000b). Reproduction of females is characterized by seasonal bimodal polyestry, with postpartum estrus and delayed embryonic development following the 1st parturition period (Kofron 1997; Storz and Kunz 1999). However, seasonal birth peaks are less pronounced at lower latitudes, and in peninsular Malaysia (06–01°N) pregnant and lactating females are captured year-round (Campbell et al. 2006c).

Cynopterus horsfieldii, the largest of the 4 species (50–70 g), roosts in foliage, beneath epiphytic ferns, and in limestone solution cavities on open cliff faces or near the mouths of caves (Campbell and Kunz 2006). In peninsular Malaysia, the mature leaves of banana plants (*Musa*) in abandoned agricultural areas near forest edges are preferred roost sites, and are often modified into a tent-shaped structure by partial severing of the midrib midway between base and tip. Banana-leaf roosts remain serviceable for up to 1 month (P. Campbell, pers. obs.).

Cynopterus sphinx (40–70 g) is a habitat generalist that is tolerant of high levels of human disturbance (Campbell et al. 2007; Storz et al. 2000a, 2000b). This species uses a wide variety of roost plants in habitats ranging from mature secondary forest to suburban gardens, and also exploits the eaves of buildings, rock shelters, and limestone solution cavities (Campbell et al. 2006a; Storz and Kunz 1999). In India, modified plant structures include the palmate leaves of fan palms, the strings of fruit and flower clusters of the kitul palm (*Caryota urens*), the stems of the curtain creeper (*Vernonia scandens*), and the stems and leaves of the mast tree (*Polyalthia longifolia*—Storz and Kunz 1999). Roosts used by *C. sphinx* are typically bowl- or bell-shaped, well

TABLE 1.—Variation in the roosting ecology and social mating systems of 4 harem-forming species in the genus *Cynopterus*.

Species and population ^a	Roosts				Roost fidelity		Harem size		♀ social behavior		
	Main type ^b	Spatial dispersion	Permanence/abundance ^c	Alternative roosts? ^d	♂♂	♀♀	\bar{X} (SD)	Maximum	<i>n</i> ^e	♀→♂ fidelity	Maximum no. ♂♂ (census days)
					High	Low				High	Low
<i>C. brachyotis</i> Sunda											
Perlis, Taiping (1, 2)	Palm frond	Clumped	High/high	Y	High	Low	2.4 (1.2)	17	11	Low	5 (30)
Bangi (3)	Palm tent	Clumped	High/low	Y	High	Low	2.5 (2.2)	17	12	Low	—
<i>C. sphinx</i>											
Palayamkottai (4)	Stem tent (<i>Pl</i>)	Clumped	High/high	Y	High	Low	3.0 (0.8)	10	6	Low	≥2 (16)
Palayamkottai (5)	Stem tent (<i>Vs</i>)	Clumped	High/low	Y	High	Low	2.9 (3.4)	19	6	Low	—
Pune, wet season (6)	Stem tent (<i>Cu</i>)	Clumped	High/low	Y	High	Low	6.1 (3.5)	16	19	Low	—
Pune, dry season (6)	Stem tent (<i>Cu</i>)	Clumped	High/low	N	High	Low	13.6 (8.5)	37	14	Low	—
Taiping (1, 3)	Epiphytic fern	Clumped	High/high	Y	High	Low	3.8 (6.3)	28	8	Low	11 (40)
<i>C. brachyotis</i> Forest											
Perlis, Taiping (1, 2)	Foliage, various (1)	Dispersed	Low/high	Y	Low	Low	1.6 (0.8)	4	11	High	2 (30)
<i>C. horsfieldii</i>											
Perlis, Taiping (1, 3)	Banana leaf	Clumped	Low/high	Y	Low	Low	0.9 (0.2)	5	2	Low	5 (36)

^a References: 1, Campbell et al. 2006a; 2, Campbell et al. 2006c; 3, P. Campbell, in litt.; 4, Storz et al. 2000a; 5, Balasingh et al. 1995; 6, Storz et al. 2000b.

^b Main type of roost used in referenced studies: *Pl*, *Polyalthia longifolia*; *Vs*, *Vernonia scandens*; *Cu*, *Caryota urens*.

^c Permanence: high, >1 breeding cycle; low, <1 breeding cycle. Abundance: high, multiple adjacent roosts of same type; low, few or no adjacent roosts of same type.

^d Local availability of alternatives to preferred roost type. Y, yes; N, no.

^e *n*, number of harems censused.

protected from the elements, and long-lasting. For example, titul palm roosts last up to 4 years (Storz et al. 2000b).

Cynopterus brachyotis Sunda (32–42 g) is abundant in disturbed habitats and absent from forest (Campbell et al. 2006c, 2007). Where ornamental fan palms are available most roosts are modified (Tan et al. 1997). Other commonly used roost plants include agricultural, pinnate-leaved palm species such as the oil palm (*Elaeis guineensis*) and coconut palm (*Cocos nucifera*), which are not modified (Campbell et al. 2006a; P. Campbell, pers. obs.). Palm tents of *C. brachyotis* Sunda can remain serviceable for about 1 year (Tan et al. 1997).

The smallest species, *C. brachyotis* Forest (24–37 g), is restricted to forest habitats (Campbell et al. 2006c, 2007). Fan palms are relatively rare in Malaysian forests (Whitmore 1998), but when present most mature plants have several modified leaves, which are occupied sequentially by harem groups and singletons of *C. brachyotis* Forest (Campbell et al. 2006a, 2006c). More commonly used roost plants include a variety of native pinnate-leaved palms and large-leaved trees such as *Macaranga gigantea* (Campbell et al. 2006a). Palm frond roosts may last up to 6 weeks, whereas leaves of *M. gigantea* deteriorate in <4 weeks (P. Campbell, pers. obs.).

THE RELATIONSHIP BETWEEN ROOSTING ECOLOGY AND SOCIAL MATING SYSTEM

Polygynous mating systems are traditionally defined by what males can defend (Clutton-Brock 1989; Emlen and Oring 1977; Ostfeld 1987). In *Cynopterus*, there is no evidence for direct defense of females, food resources, or any territory other than the roost (Balasingh et al. 1995; Campbell et al. 2006c; Storz et al. 2000a, 2000b). Given that roosts are an important resource for reproductive females (Kunz 1982; Kunz and Lumsden 2003), is

variation in roost type, distribution, and abundance predictive of variation in degree of social polygyny in *Cynopterus*?

Cynopterus sphinx and *C. brachyotis* Sunda.—Both species are abundant in agricultural and suburban areas and exhibit notable similarities in roosting ecology and social structure. The roosts of both species typically remain serviceable across multiple breeding seasons and are highly clumped in open, anthropogenic habitats (Campbell et al. 2006a, 2000c; Storz et al. 2000a, 2000b). Male roost fidelity is high and maximum harem sizes are larger than those reported for any other species of harem-forming bat (Table 1; McCracken and Wilkinson 2000; Storz et al. 2000b), suggesting an extremely high reproductive payoff for resource-defending males who successfully recruit females and exclude other males from their roosts. However, 2 main factors mitigate the potential for few males to monopolize most within-season breeding opportunities. First, unlike most harem-forming ungulates (e.g., Carranza et al. 1996; Sánchez-Prieto et al. 2004), and at least 1 species of bat (*S. bilineata*—Bradbury and Vehrencamp 1976; but see Hoffmann et al. 2007), female harem members forage solitarily. Thus, although social interactions outside of the roost cannot be ruled out, cohesion of harem groups depends largely on the independent return of group members to the same roost. Second, because males defend only the roost they occupy, a clumped distribution of desirable roosts promotes a clumped distribution of males. Under these conditions, socially labile females have the opportunity to sample, and potentially mate with, multiple males (Campbell et al. 2006c; Gopukumar et al. 2005; Storz et al. 2000a, 2000b). Intraspecific comparisons for *C. brachyotis* Sunda and *C. sphinx* suggest that variation in quality and quantity of roosts plays an important role in determining the environmental potential for male polygyny, but has less effect on patterns of female fidelity to roosts or males.

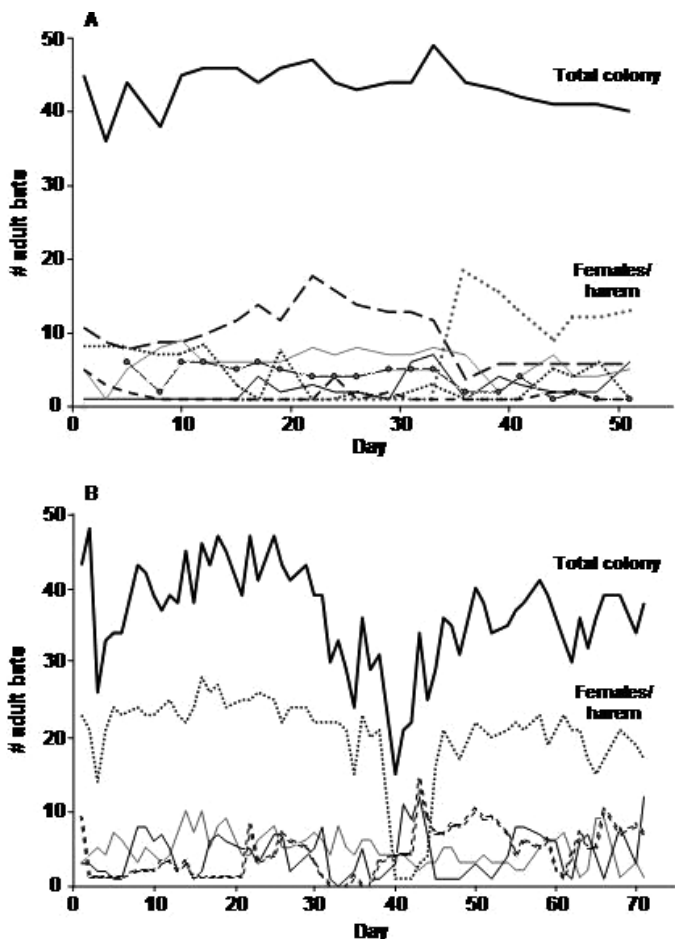


FIG. 1.—Total colony size (thick line, above) and the dispersion of females among harem-holding males (thin lines, below) for 2 species of *Cynopterus* in peninsular Malaysia. A) Colony of *C. brachyotis* Sunda at Bangi, monitored for 51 days, June–July 2000 ($n = 22$ censuses). Changes in the numbers of females/harem are shown for the 6 largest harems. B) Colony of *C. sphinx* at Taiping, monitored for 71 days, June–August 2003 ($n = 63$ censuses). Numbers of females/harem are shown for the 4 largest harems.

In peninsular Malaysia, 2 study populations of *C. brachyotis* Sunda (Perlis, 06°N, 100°E; Taiping, 04°N, 100°E) roosted almost exclusively in coconut palm stands that, although highly clumped, were abundant in the landscape with multiple qualitatively invariant roost sites available within each clump (Table 1; Campbell et al. 2006c). Males exhibited significantly higher roost fidelity than females and female groups were highly unstable both in size and individual composition. Average female group size for individual harem-holding males ranged from 0.8 to 4.5. Males with large maximal harem sizes (≥ 10 females, $n = 3$ males) also experienced high harem instability and spent 48–76% of the time (19–30 of 40 consecutive census days) roosting with 1 or no females. Notably, during daily census periods of 30 days, focal males ($n = 11$) and females ($n = 15$) had approximately the same mean number of opposite-sex roost-mates (2.4 females/male; 2.3 males/female), suggesting that the sequential movements of

females among males may reduce variance in male reproductive success (Campbell et al. 2006c).

A study population of *C. brachyotis* Sunda at a 3rd Malaysian site (Bangi, 02°N, 101°E) occupied modified roosts in a discrete stand of fan palms (*Corypha utan*) in an open, landscaped area (Table 1). All potential roosts in the 17 palms were surveyed with binoculars every 2–3 days for a period of 51 days ($n = 22$ census days). Thirteen to 18 of 41 tents were occupied on any given day, indicating that roost-sites were not limiting within the stand. However, in contrast to the homogenous roosting habitat occupied by the other 2 study populations, in which multiple clumps of coconut palms were distributed across the landscape, no qualitatively similar roosts were available nearby. Other species of roost plants used by *C. brachyotis* Sunda in the vicinity (see Tan et al. 1997) were searched regularly for bats but were not occupied during the study period, suggesting that the roosts in *C. utan* were used preferentially. Although the number of females in all harems fluctuated on a daily basis, the number of adults in the colony was relatively stable with an approximately 2:1 female-biased sex ratio (females: $\bar{X} = 27.9$, range, 23–32; males: $\bar{X} = 15.5$, range, 12–17), indicating that most females moved among males within the colony (Fig. 1A). Mean harem size was only slightly greater than in the coconut palm-roosting populations (2.5 females), but of 12 males that consistently occupied the same roosts, 3 maintained harems for 75–100% of the survey period. The largest harems averaged 7.0 (± 3.79 SD, range, 1–15), 5.3 (± 6.47 SD, range, 0–17), and 4.9 (± 2.02 SD, range, 0–7) females, respectively (Fig. 1A). If variance in the distribution of females among males can be taken as a 1st approximation of reproductive skew (Wade and Shuster 2004; discussed below) these observations suggest that, despite female lability, a small number of harem-holding males in the tent-roosting population succeeded in monopolizing reproductive access to a larger proportion of available females than did males occupying coconut palm roosts.

Studies of *C. sphinx* suggest a similar pattern, in which the distribution of females among males is influenced by the distribution and availability of preferred roosts, whereas female lability is consistently high regardless of ecological context. For example, short-term census data for study populations in southern India (Palayamkottai, 08°N, 77°E) implicate roost type as a determinant of female group size (Storz et al. 2000a). Males defending stem tents in *P. longifolia* roosted with 1–10 females (harem size: $\bar{X} = 3.0$ females), and although there was some evidence for short-term female group cohesion, most females moved among males in an uncoordinated manner and used 2 or more tents during a 16-day observation period (Table 1). Approximately 66% of available tents were unoccupied on any given day and most males roosted singly for at least part of the census period. Among-male variation in number of female roost-mates suggested that 4 (27%) of 15 males succeeded in monopolizing reproductive access to 12 (69%) of 17 colony females (Storz et al. 2000a). An earlier study at the same locality found larger maximum harem sizes (range, 1–19 females) but not higher harem stability in *C. sphinx* roosting in tents in *V. scandens*, suggesting that this

type of roost supports larger aggregations of females but does not affect the lability of individuals (Balasingh et al. 1995).

At a more northern latitude in India (Pune, 18°N, 73°E), colonies of *C. sphinx* roosting in kitul palm stem tents were characterized by larger harem sizes relative to southern study populations (annual \bar{X} = 9.9, maximum = 37 females), a higher degree of reproductive synchrony among females across biannual birth peaks, and significant seasonal differences in harem sizes (Table 1; Storz et al. 2000b). Although the highly clumped kitul palm roosts were used year-round, alternative foliage roosts were not available during the dry-season reproductive period when deciduous trees lost their leaves (Storz et al. 2000b; J. Storz, University of Nebraska, Lincoln, pers. comm.). Average harem size was 2.2 times larger in the dry season (\bar{X} = 13.6 females) versus the wet season (\bar{X} = 6.1 females), indicating a strong seasonal shift in the environmental potential for polygyny experienced by males. However, across-breeding season turnover in colony males was high: of 16 tent-defending males banded during the wet season reproductive period, only 4 were recaptured in their original colonies during the subsequent dry season. Likewise, although within-breeding season fluctuations in harem sizes mainly reflected the movements of females among adjacent roosts, female fidelity to males or to their colony was low across breeding seasons. Of 234 adult females captured in study colonies over the course of 2 breeding seasons, only 26 (11.1%) were recaptured in the same colonies during the 3rd season, of which 14 (6.0%) remained associated with the same male (Storz et al. 2000b).

Examination of within-breeding season data for a study population of *C. sphinx* in peninsular Malaysia (Taiping) suggests a comparable degree of polygyny but a less insular colony structure. At this site the bats roosted in the unmodified root masses of bird's nest ferns growing on the trunks and branches of large trees in an open suburban area (Campbell et al. 2006a). Although these clumped, well-protected roosts supported large harems, colony size fluctuated considerably because of movements of females (Fig. 1B). Eleven of 20 available fern roosts were occupied at least once during the 71-day census period and on any given day 5–10 roosts were in use. Colony size ranged from 21 to 48 adults (\bar{X} = 36.1 \pm 6.97 *SD*); the largest harem comprised an average of 18.9 females (\pm 6.13 *SD*, range, 1–28), and 3 smaller harems averaged 4.7 (\pm 2.80 *SD*, range, 0–13), 4.4 (\pm 2.79 *SD*, range, 0–11), and 3.3 (\pm 2.0 *SD*, range, 0–8) females, respectively (Fig. 1B; Table 1; Campbell et al. 2006b). One radiotracked female used 13 different roosts and roosted with 11 different males during a 40-day tracking period. Five of her male roost-mates defended roosts within the colony; 6 occupied similar fern roosts a maximum of 0.24 km distant. In contrast, 4 individually marked males used single roosts within the colony for the duration of the census period.

In sum, examination of comparative social data for *C. brachyotis* Sunda and *C. sphinx* indicates that both within- and among-population variation in roost type and distribution can produce considerable differences in the environmental potential for polygyny experienced by males, whereas female lability is

a consistent feature of the social structure of both species. The tendency of both species to form aggregations, in which associations among roost-mates are embedded within the larger social context of a colony, is more pronounced in *C. sphinx* and may contribute to the higher degree of polygyny in this species. This additional level of social structure is found in several harem-forming species in the Neotropics (e.g., *A. jamaicensis* [Ortega and Arita 1999], *P. hastatus* [McCracken and Bradbury 1981], and *S. bilineata* [Bradbury and Vehrencamp 1976]) and, in the Palearctic, at least 3 species of *Pteropus* are characterized by colonial roosting aggregations, subdivided into harems (McCracken and Wilkinson 2000 and references therein; Welbergen 2006). In *C. brachyotis* Sunda and *C. sphinx*, however, colony formation seems enhanced by the artificially clumped distributions of roost plants in anthropogenic environments. *C. brachyotis* Sunda is restricted to disturbed habitats, whereas *C. sphinx* also occurs in forest (Campbell et al. 2007). Whether polygyny in *C. sphinx* is reduced in habitats that more closely approximate the environment in which this species evolved is a question that deserves further investigation.

Cynopterus brachyotis Forest and *C. horsfieldii*.—Although *C. brachyotis* Forest and *C. horsfieldii* differ considerably in social structure and habitat choice, both species are distinguished from *C. brachyotis* Sunda and *C. sphinx* by small harem sizes, low roost fidelity in both sexes, and avoidance of highly disturbed areas (Campbell et al. 2006a, 2006c). Moreover, recent common ancestry makes this interspecific comparison particularly interesting. The mitochondrial lineage of *C. horsfieldii* is paraphyletic with respect to *C. brachyotis* Forest and mean divergence between the 2 species is only slightly greater than divergence within *C. brachyotis* Forest (Campbell et al. 2004).

The social structure of *C. brachyotis* Forest is unusual among harem-forming bats in that males do not defend a single roost or preexisting groups of females, nor do they exclude other males from their roosting home ranges (Campbell et al. 2006c). In peninsular Malaysia, study populations at Perlis and Taiping occupied foliage roosts that were abundant and randomly distributed in primary and secondary forest habitats (Table 1; Campbell et al. 2006a, 2006c). Harem sizes were small (\bar{X} = 1.6 females), reflecting an overdispersion of females and consequently low environmental potential for polygyny relative to *C. brachyotis* Sunda and *C. sphinx*. Males and females exhibited equally low fidelity to particular roosts within small, nonexclusive roosting home ranges (Campbell et al. 2006c). On average, however, males switched roosts almost twice as often as females (n = 8 males, 1 roost switch/2.2 days \pm 1.31 *SD*; n = 10 females, 1 roost switch/4.3 days \pm 3.03 *SD*).

Small group sizes in *C. brachyotis* Forest are potentially explained by this species' reliance on steady-state, low-density feeding resources (Hodgkison and Balding 2004) and relatively ephemeral roosts (Campbell et al. 2006c), both of which may place an upper limit on harem size. However, neither feeding nor roosting ecology readily account for the lack of interchange between harem groups of *C. brachyotis* Forest and the maintenance of male–female associations, despite frequent

roost changes. For example, 13 (87%) of 15 individually marked females roosted with a single male during a 30-day census period, and some harem groups remained associated for at least 6 weeks (Campbell et al. 2006c). Although it was not possible to assess directly which sex initiated roost switches, the higher frequency of roost switching in males, together with the lack of coordinated female-only movements, suggests that females may follow males to new roosts.

Why maintain high social fidelity to 1 male? Male–female pairs are common in *C. brachyotis* Forest and some females roost singly for periods of several weeks, observations that indicate that female–male associations are not a secondary consequence of female–female social attraction. Likewise, the combination of low roost fidelity and high social fidelity suggests that individual roosts are not primary attractants for females. One reasonable hypothesis is that social fidelity in female *C. brachyotis* Forest is mediated by the spatial dispersion of potential mates and the probability of finding a mate during the relatively brief postpartum period of receptivity. This species' reliance on abundant but unpredictably distributed roosts may result in a low encounter rate between unfamiliar individuals, favoring short-term fidelity to a single male (Campbell et al. 2006c).

Examination of radiotracking data for *C. horsfieldii* from the same Malaysian sites suggests that, although roosting behavior of males and degree of polygyny is similar to that of *C. brachyotis* Forest, social lability of females is comparable to that of *C. brachyotis* Sunda and *C. sphinx*. Like *C. brachyotis* Forest, male *C. horsfieldii* do not invest in the defense of particular roost sites; both sexes exhibited low roost fidelity and males averaged more frequent roost switches than females ($n = 4$ males, 1 roost switch/3.3 days \pm 2.07 SD; $n = 4$ females, 1 roost switch/5.2 days \pm 4.39 SD). Likewise, harem sizes were small (Table 1). However, harem groups were compositionally labile, male–female associations were rarely maintained as individuals moved between roosts, and some female *C. horsfieldii* roosted with multiple males over short periods of time. For example, 2 unassociated radiotracked females roosted sequentially with 5 different males during 36-day tracking periods.

Although both roosting and feeding ecology may minimize the environmental potential for polygyny in *C. brachyotis* Forest, the ecological correlates of female dispersion and group stability in *C. horsfieldii* are unclear. As one of the heaviest foliage-roosting species for which harem-based social structure is described (Kunz et al. 1994; Muñoz-Romo and Herrera 2003), it is possible that small harem sizes and low roost fidelity in this species are due to the relatively low load capacity of banana leaves. However, *C. horsfieldii* exhibits equally low fidelity to limestone solution cavities (Campbell et al. 2006a) and comparably small harem sizes are found in bird's nest ferns (range, 2 or 3 females—Tan et al. 1999), a roost type that supports large harems in *C. sphinx* (see above). Likewise, in old-growth forest, *C. horsfieldii* exploits transient, high-density feeding resources (Hodgkison and Balding 2004), a foraging ecology predictive of larger, more stable groups in emballonurid bats (Bradbury and Vehrencamp 1976, 1977).

Finally, similarities between *C. horsfieldii* and *C. brachyotis* Forest are noteworthy because they raise the question as to whether a trait such as low roost fidelity in males is shared due to recent common ancestry, or similar response to local ecological conditions. Conversely, is short-term fidelity of females to males a derived characteristic of *C. brachyotis* Forest? As for *C. sphinx*, additional comparative data are needed for *C. brachyotis* Forest and *C. horsfieldii* to better separate species-level social structure from population-level response to ecological variables such as the distribution and relative permanence of roosts or feeding resources.

DOES FEMALE DISPERSION PREDICT MALE REPRODUCTIVE SKEW?

Although social structure and genetic mating system are intimately linked, they are rarely equivalent (Heckel et al. 1999; Munshi-South 2007; Pemberton et al. 1992). Based on within–breeding season variance in the distribution of females among males, *C. sphinx* has the highest projected variance in number of mates per male of any harem-forming species (Storz et al. 2000b; Wade and Shuster 2004). Is variance in female group size predictive of male reproductive skew? Multiseason paternity estimates for the study population of *C. sphinx* in Pune, India, suggest that it is (Storz et al. 2001b). However, these data also illustrate some of the challenges inherent to studying the reproductive behavior of mobile, socially labile species with overlapping generations, attributes that are common to many species of harem-forming bats.

As described in the previous section, the size and number of harems present in Pune study colonies varied dramatically across seasons: fewer, significantly larger harems were found in the dry season when the loss of deciduous foliage roosts constrained reproductive females to tent roosts in kitul palms (Storz et al. 2000b; J. Storz, University of Nebraska, Lincoln, pers. comm.). Across-season differences in the distribution of paternities among males demonstrate that increased clumping of females promoted higher within-season variance in male reproductive success (Storz et al. 2001b). Paternities for 118 pups conceived during the wet season when females were more dispersed were divided among 54 males, and only 21% of this cohort ($n = 25$ pups) was sired by colony males ($n = 20$ males). A maximum of 11 pups were sired by a single male. In contrast, 67 pups conceived in the dry season were sired by a total of 15 males; 78% of these paternities ($n = 52$ pups) belonged to 9 territory-holding males in the pups' natal colonies and a maximum of 20 pups were sired by a single male (Storz et al. 2001b).

Although the across-season shift in the distribution of paternities among successful males is striking (wet season conceptions: $\bar{X} = 2.2/\text{male}$; dry season conceptions: $\bar{X} = 4.5/\text{male}$), maximum paternity estimates for both reproductive periods indicate that a significant number of males fail to reproduce each season. However, low recapture rates for tent-defending males (Storz et al. 2000b; see above) suggest that high within–breeding season variance in male reproductive success should be minimized across breeding seasons by high

turnover of males. Examination of paternity data for pups born in the study colonies supports this expectation. Across 2 consecutive breeding seasons a total of 63 males sired 185 pups, but only 6 (9.5%) of these males sired offspring in both cohorts (Storz et al. 2001b).

A caveat to these results is that the low reproductive tenure of males within a given colony does not necessarily indicate that absent males failed to reproduce elsewhere. In *C. sphinx*, as in other congeners, the combination of high female lability and postpartum estrus means that harem males are unlikely to be the fathers of pups born to current female roost-mates. Thus, for the Pune colonies, pups born in the wet season were sired during the dry season and vice versa (Storz et al. 2001b). Because fewer females were present in the colonies during the wet season, it is likely that some pups sired by colony males during the dry season went unsampled. Likewise, the dry season influx of females into the colonies increased the probability of sampling pups sired by males whose contribution to the previous offspring cohort was unknown.

Life expectancy has not been documented in *C. sphinx*, but is probably comparable to that of *C. brachyotis* Sunda, which is estimated as 4.5–7 years (Heideman and Heaney 1989; J. Seyjagat, Lubee Bat Conservancy, Gainesville, pers. comm.). Male *C. sphinx* have their 1st opportunity to mate during their 2nd year (Storz and Kunz 1999); thus, at a conservative estimate, males may have the opportunity to contribute to 6 offspring cohorts (1 in year 2, 2 in years 3–4, and 1 in year 5). Longitudinal paternity analyses of other long-lived polygynous mammals, including 1 species of temperate bat, indicate that the lifetime reproductive success of males may be strongly skewed, with few males contributing disproportionately to total paternities (Coltman et al. 2002; Rose et al. 1998; Rossiter et al. 2006). It remains to be determined whether lifetime reproductive success in male *C. sphinx* conforms to this pattern or, as suggested by short-term paternity data, is cumulatively randomized across breeding seasons.

CONCLUSIONS AND OPEN QUESTIONS

Does clumping of males promote female promiscuity?—Comparison of the social mating systems of 4 species of *Cynopterus* suggests that the classic ecological model of mating system evolution is not sufficient to explain the diversity and plasticity of social behavior that can arise within the framework of harem-based polygyny in bats. The spatial distribution and abundance of roosts is predictive of female group size in *C. brachyotis* Sunda, *C. sphinx*, and *C. brachyotis* Forest, but not of female fidelity to either roosts or males, suggesting that the relationship between female reproductive behavior and the spatial distribution of males deserves further investigation in *Cynopterus* and other species of harem-forming bats. For example, if the proximity of multiple males promotes female promiscuity, then selection for male sperm competition, or cryptic female choice, or both should be significantly stronger in *C. sphinx* and *C. brachyotis* Sunda than in *C. brachyotis* Forest. Based on the positive relationship between testis size and the opportunity for sperm competition

in bats and other mammals (Hosken 1998; Ramm et al. 2005; Wilkinson and McCracken 2003) comparative analysis of testis size in *Cynopterus* would be informative in this regard.

How does female lability affect male reproductive skew?—Examination of paternity data for *C. sphinx* indicates that, when females are highly clumped, short-term variance in male reproductive success can be high, despite the frequent movements of females among males (Storz et al. 2001b). In theory, where receptivity is sufficiently asynchronous, a male defending a large, compositionally labile harem may have the opportunity to mate with a larger number of females than that estimated from mean harem size. However, where labile females are more dispersed such that harems are maintained for shorter periods of time, male reproductive success is likely to be less than mean harem size because more transient mating opportunities are distributed across a larger number of males. Examination of comparative paternity data for colonial versus dispersed populations of *C. brachyotis* Sunda would provide a strong test of this hypothesis.

What are females choosing?—The correlates of female choice are unknown in most species of bats (McCracken and Wilkinson 2000; but see Voigt et al. 2005). Given the high opportunity for sexual selection in *C. sphinx*, this species is a good candidate for study in this area. It has been suggested that, in tent-roosting bats in general, females may either use properties of the roost to infer male quality, or choose males based on roost quality (Balasingh et al. 1995; Kunz and McCracken 1996; Kunz et al. 1994). In tent-roosting Indian populations of *C. sphinx*, however, there is no relationship between harem size and quantifiable kitul palm roost characteristics (Storz et al. 2000b). Unlike *A. jamaicensis*, in which size of males is positively correlated with reproductive success (Ortega et al. 2003), solitary and harem-holding male *C. sphinx* do not differ in size (Gopukumar et al. 2005; Storz et al. 2000b). Although a latitudinal cline in the magnitude and direction of sexual size dimorphism—with larger males at more polygynous northern localities—suggests geographic variation in the strength of sexual selection on male size (Storz et al. 2001a), the role of size in male–male competition or female choice remains to be established in this species. Intriguingly, anecdotal evidence suggests that male *C. sphinx* incorporate both visual and pheromonal displays in attempts to attract females to their roosts (Vanitharani and Vijaya 2007). Chemical and visual signals are central components of the reproductive behavior of male *S. bilineata* (Voigt et al. 2005; Voigt and von Helversen 1999) and certainly warrant further investigation in *C. sphinx*.

Throughout this review I have attempted to emphasize the dynamic nature of harem-based social structure in tropical bats, using *Cynopterus* as an example. Despite considerable intraspecific variation in degree of polygyny, some aspects of sociality such as female lability and the lack of cohesion in female groups seem consistent at the species level and above. I hope that this review will stimulate future comparative studies of the social and genetic mating systems of closely related species, which take into account the potential for intraspecific variation in the context of population ecology. Well-studied neotropical genera such as *Artibeus*, *Carollia*, and the family Emballonuridae are likely candidates for this approach.

RESUMEN

Dentro de la generalización de la poliginia, entre los Murciélagos, el sistema de formación de harén presenta un alto grado de diversidad inter-específica y variación intra-específica. En este estudio reviso de la estructura social y de los sistemas de cuatro especies nominales de Murciélagos de fruta del genero *Cynopterus* del Viejo Mundo, además exploro la relación entre la ecología de percha, el tamaño, la estabilidad del grupo de hembras, y la variación del grado de poliginia. Comparaciones intraespecíficas de *C. brachyotis* Sunda y *C. sphinx* sugirien que la distribución y la disponibilidad de sitios de percha tienen una fuerte influencia en la dispersión de hembras entre los machos. Datos de paternidad del *C. sphinx* han demostrado una relación directa entre el potencial ambiental de la poliginia y la varianza en el éxito de reproducción de los machos: un aumento doble en el promedio tamaño del harén debido a la reducción en disponibilidad produce incremento doble en el sesgo reproductivo del macho. Sin embargo, en *C. brachyotis* Sunda, *C. sphinx* y *C. horsfieldi*, la baja fidelidad a los sitios de percha de las hembras o de machos es consistente, sin importar la dispersión o permanencia en los sitios de percha. En contraste, las hembras del *C. brachyotis* Forest se encuentra una fidelidad de los machos alta, pero por periodos cortos, sin importar la baja fidelidad a los sitios de percha. Aquí se propone que la hembra dispuesta al cambio es influenciada por la distribución de potenciales parejas y el beneficio de múltiples apareamientos, y en *C. brachyotis* Sunda y *C. sphinx*, es posible que promueva tanto un comportamiento como un selección críptica por parte de la hembra, y la competición de esperma de los machos.

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