

Comparative Roosting Ecology of *Cynopterus* (Chiroptera: Pteropodidae) Fruit Bats in Peninsular Malaysia¹

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ABSTRACT

Although the use of modified roosts has been reported in more than 20 species of bats in the tropics, comparative studies of the roosting ecology of congeneric tent-roosting species are notably lacking. In the Paleotropics, this unique behavior has been described in two species belonging to the genus, *Cynopterus*: *C. sphinx* and *C. brachyotis*. However, it is not known whether tent roosting is an essential component of their roosting ecology, or whether the behavior is found in other members of the genus. In this study we characterize the roosting ecology of four sympatric species of *Cynopterus* in peninsular Malaysia and use these data to address two main questions. (1) Do all four species use modified roosts and, in those that do, is tent-roosting obligate or opportunistic? (2) Do species pairs overlap in roost preferences and roosting habitat and, if so, is there evidence for interspecific interactions in relation to these resources? We radio-tracked bats at two floristically distinct sites and located a total of 249 roosts. Interspecific roost niche overlap was minimal at both sites and we found no evidence for interspecific competition for roost resources at the local level. Species differences in roosting ecology were defined primarily by spatial separation of roosting habitats and secondarily by within-habitat differences in roost selection. Importantly, we found that although periodic use of modified roosts was a characteristic shared by all four species, most roosts were unmodified, indicating that tent roosting is a facultative behavior in Malaysian *Cynopterus*.

Key words: *Cynopterus*; harems; Malaysia; palms; radiotelemetry; roost-selection; tent roosting.

IN MAMMALS, THE TYPES OF STRUCTURES USED FOR SHELTER typically reflect both functional and social attributes of species. For social species in which mating and rearing of young take place in a den, burrow, roost, or nest, selection of optimal shelter may have profound fitness consequences for both males and females. Despite the global distribution and tremendous ecological and taxonomic diversity of bats, reliance on roosts for both shelter and reproductive purposes is a unifying characteristic of all species for which roosting ecology has been described (Kunz 1982).

Of the 1116 currently recognized species of bats (Simmons 2005), more than 50 percent use plants for roosts (Kunz & Lumsden 2003). Among these, 21 species are known to roost in foliage or other plant-associated structures that have been modified into bowl or tent-shaped formations (Kunz & McCracken 1996, Kunz & Lumsden 2003, Dechmann *et al.* 2005). While the construction of roosts has been observed directly in only two species (Balasingh *et al.* 1995, Dechmann *et al.* 2005), all available data indicate that the roosts are modified by bats and not by any other biotic or abiotic agent (Brooke 1990, Kunz *et al.* 1994, Tan *et al.* 1997). Roost-making behavior has evolved independently in the two major radiations of phytophagous bats (Kunz *et al.* 1994), and also in several insectivorous species: the use of modified roosts has been recorded for 17 species in the Neotropical family, Phyllostomidae, three Paleotropical species in the family Pteropodidae, and one species in the family Vespertilionidae (Kunz & Lumsden 2003, Tello & Velazco 2003, Dechmann *et al.* 2005). All species known

to occupy modified roosts are small to intermediate in size (8–65 g; Kunz & Lumsden 2003) and a polygynous, typically harem-based, mating system has been ascribed to all species for which behavioral data are available (Morrison 1979, Brooke 1990, Tan *et al.* 1997, Storz *et al.* 2000a, Hodgkison *et al.* 2003, Dechmann *et al.* 2005).

Whereas roost construction is not an essentially complex behavior, involving partially or completely biting through leaf veins, stems, or fruit strings (Timm 1987, Balasingh *et al.* 1995, Bhat & Kunz 1995), or excavating arboreal termite or ant nests (Kalko *et al.* 1999, Hodgkison *et al.* 2003, Dechmann *et al.* 2005), it is none-the-less remarkable, as any type of modification of existing structures into shelters is comparatively rare in mammals (Hansell 2005). Possibly for this reason, the majority of studies of the roosting ecology of roost-making bats have focused mainly on the physical properties and functional value of modified roosts (Foster 1992, Choe 1993, Kunz *et al.* 1994, Bhat & Kunz 1995, Tan *et al.* 1997, Stoner 2000), while relatively little attention has been paid to the relationship between roost-making and the availability of structures suitable for modification, or to the extent to which species are obligate or opportunistic in their use of modified roosts (Timm 1987). Likewise, comparative data for sympatric roost-modifying species are notably lacking.

In the Old World tropics, *Cynopterus* is the only multispecies genus in which roost modification has been described, and as such provides a unique opportunity for comparative analysis of the relative flexibility and specialization in roost choice, and the prevalence of roost modification among closely related species. Occupation of modified foliage or fruit and flower clusters, termed “tent roosting,” has been described in two of the seven species of *Cynopterus* recognized by Simmons (2005): *C. sphinx* in India and *C. brachyotis* in peninsular Malaysia (Bhat & Kunz 1995, Tan *et al.* 1997). Kunz

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et al. (1994) suggested that tent-making behavior is likely to be a trait shared by other members of the genus, a hypothesis that has yet to be tested.

Studies of the roosting ecology of *C. sphinx* and *C. brachyotis* suggest that both species roost predominantly in modified plant structures and that occupation and defense of modified roosts may play an important role in mediating male reproductive success (Balasingh *et al.* 1995, Bhat & Kunz 1995, Tan *et al.* 1997, Storz *et al.* 2000a). However, because both species have been studied mainly in landscaped and suburban areas where potential roosts include nonnative ornamentals, the extent to which these findings correspond to the behavior of the bats in natural habitats is uncertain. Moreover, roosts have been located using visual searches, a method likely to be biased toward finding modified roosts.

The main objective of the present study was to compare the roosting ecology of the four nominal species of *Cynopterus* that co-occur in peninsular Malaysia: *C. horsfieldi* (50–70 g, $N = 87$), *C. sphinx* (40–57 g, $N = 84$), and *C. brachyotis*, with the latter split into two genetically divergent lineages (Campbell *et al.* 2004). Concordance between molecular, morphological, and ecological data supports the proposition that the two *C. brachyotis* lineages are evolutionarily and ecologically distinct species (Campbell *et al.* in press; Campbell *et al.* 2006). Pending taxonomic revision we refer to the smaller lineage as *C. brachyotis* Forest (24–37 g, $N = 128$), and to the slightly larger lineage as *C. brachyotis* Sunda (32–42 g, $N = 99$; Campbell *et al.* 2004; P. Campbell, pers. comm.). Molecular and morphometric analyses of bats sampled from the *C. brachyotis* colonies studied by Tan *et al.* (1997) in central peninsular Malaysia indicate that this tent-roosting population belongs to the Sunda lineage (Campbell *et al.* 2004; Campbell *et al.* in press).

While broadly sympatric, the four putative species differ in habitat associations (Campbell *et al.* in press). *Cynopterus brachyotis* Sunda and Forest are almost completely allotopic and restricted to anthropogenic and forest habitats, respectively. *Cynopterus sphinx* and *C. horsfieldi* occur in both anthropogenic areas and undisturbed forest, but while *C. horsfieldi* is most abundant in agricultural habitat adjacent to forest edge, *C. sphinx* is strongly associated with anthropogenic habitats and is relatively uncommon in forest.

We used radiotelemetry to characterize the roosting ecology of the four putative species at two floristically distinct sites in peninsular Malaysia. Given the close evolutionary relationships within *Cynopterus* and the ecological and morphological similarities among the Malaysian species, we were interested in the following. First, do all four putative species use modified roosts and, in those that do, is tent-roosting obligate or opportunistic? Second, do species pairs overlap in roosting habitat and in selection of plant species or other structures used as roosts and, if so, is there evidence for ongoing interspecific competition for preferred roost types?

METHODS

STUDY SITES.—Fieldwork was carried out at two main sites in northern peninsular Malaysia: Perlis State Park (Perlis State, 06°42'–39'N,

100°11'E) and Taiping (Perak State, 04°50'–51'N, 100°45'–46'E). Bats were radio tracked at Perlis in June–August 2002, April–May 2003, and November 2003–January 2004. At Taiping, radio tracking periods were September–November 2002 and June–August 2003. Both sites feature tracts of selectively logged primary forest, bordered by secondary growth, small fruit orchards, and human settlements. Bats were radio tracked in forest, ecotonal and anthropogenic habitats at both study sites.

Perlis State Park (50 km²) features steep limestone hills with numerous exposed rock faces and caves. The vegetation is characterized as limestone hill forest; dominant tree species include members of the genera *Shorea*, *Hopea*, and *Parashorea* (Latiff *et al.* 2001, Wong 2002). Tall pinnate-leaved palms such as *Orania sylvicola* and *Arenga westerhoutii* are common throughout most of the forest study area. Pioneer species such as members of the genus, *Macaranga*, are abundant in forest gaps and partially logged areas, while dense thickets of rattan occur in more heavily logged areas. Villages and small agricultural holdings featuring banana plantations, durian orchards, and rice paddies lie along the park's boundaries. Because *C. brachyotis* Sunda was absent from agricultural habitat directly adjacent to the park, we incorporated an additional anthropogenic habitat site at the small village of Bukit Jernih (06°33'N, 100°15'E), 15 km southeast of the forest site. The settlement is built around the bases of a series of limestone tower karsts that rise out of flat fields dominated by rice cultivation, mango orchards, and banana plantations. Coconut palms grow abundantly in the yards of village houses.

At the Taiping site, Larut Hills Forest Reserve comprises 72 km² of mixed lowland dipterocarp forest (Putz 1978). We worked near the edge of the reserve in forest that had been heavily logged and, in some cases, clearcut within the last two decades. *Macaranga* species are abundant in this forest and the palm *Arenga obtusifolia* dominates in clearcut areas. The forest is bordered by small durian orchards and banana plantations, which give way to a series of landscaped parks surrounding the medium-sized town of Taiping. The epiphytic bird's nest fern, *Asplenium nidus*, grows in large numbers on trees in the city parks and occurs at lower abundances in the durian orchards and adjacent secondary forest.

BAT CAPTURE AND SPECIES IDENTIFICATION.—Bats were captured in mist nets set at ground level. Body mass and length of forearm, tibia, and ear were measured for all *Cynopterus* captures. *Cynopterus sphinx* and *C. horsfieldi* were identified based on a suite of morphological characters described in Payne *et al.* (1985) and Bates and Harrison (1997). The two *C. brachyotis* lineages were discriminated based on length of forearm (Forest, mean = 59.5 ± 1.7 mm, $N = 52$; Sunda, mean = 63.8 ± 1.6 mm, $N = 57$), coloration of nuchal collar (Forest = dark orange-red; Sunda = pale orange-yellow), and habitat associations (Campbell *et al.* in press). Approximately 640 base pairs of the mitochondrial control region were sequenced for all radio-tracked individuals to confirm field identifications (methods in Campbell *et al.* 2004). Adults were distinguished from juveniles by relative closure of the phalangeal epiphyses (Anthony 1988) and parity of adult females was assessed by examination of the nipples (Racey 1988) and by palpating the lower abdomen for a detectable fetus. All adults and large juveniles were marked with

uniquely numbered 2.9-mm monel forearm bands (Lambournes Ltd., Birmingham, UK), males on the right, females on the left.

ROOST IDENTIFICATION AND CHARACTERIZATION.—Radiotransmitters (model MD-2C, Holohil, Ontario, Canada) were attached to adult males and nonpregnant adult females with neck collars: cotton thread was passed through holes in the transmitter, threaded through flexible plastic tubing cut to fit comfortably and securely around the bat's neck, and fastened with an aluminum crimp. The transmitters were labeled with reflective tape to increase their visibility in roosts. Transmitters weighing 1.1 g were used for *C. brachyotis* Forest and Sunda, and both 1.1 and 1.9 g transmitters were used for the two larger species, *C. sphinx* and *C. horsfieldi*. All transmitters weighed less than 5 percent of the bat's body mass. Because we were interested in intraspecific differences in roost selection across habitat types, we attached transmitters to *C. horsfieldi* and *C. sphinx* captured in both forest and anthropogenic habitats.

All radio-tagged bats were held for no more than 1 h and released before midnight. Roost searches were initiated the following day using portable receivers (model TRX 1000S, Wildlife Materials, Carbondale, IL, U.S.A.) and five-element Yagi antennae (Wildlife Materials). The location of a roost was determined as closely as possible using telemetry, after which a thorough visual search was made of all surrounding foliage until the bat was seen. Confirmed roosts were marked with flagging, numbered and mapped using a hand-held GPS unit (Magellan 315, Thales Navigation, San Dimas, CA, U.S.A.). Radio-tagged individuals were tracked to their roosts daily for the life of the transmitter (17–46 d), or longer if the bat remained in the same roost (maximum, 77 tracking days). In the majority of cases it was possible to observe the bats in their roosts on a daily basis; roosts were excluded from the present analysis if the transmitter-carrying bat was not seen. Each roost was counted only once, regardless of whether it was later occupied by different individuals; multiple foliage roosts in a single plant or tree were not counted separately. Roost plant species were identified according to Whitmore (1972, 1973, 1998), Uhl and Dransfield (1987), and with assistance from the forestry staff at Perlis State Park. Roost height was measured directly when feasible, or with a clinometer. Additional roosts that were found opportunistically were monitored and characterized in the same manner.

DATA ANALYSIS.—A one-way ANOVA was used to test for the effect of species on roost height, and a posthoc test (Tukey's test, $\alpha = 0.05$) was used to investigate pairwise differences among species. We quantified proportional use of each roost type within species and used these values to estimate interspecific overlap in roost niche, based on Pianka's measure of niche overlap (Pianka 1973). We compared roost type diversity among species, using a rarefaction curve to remove the effect of unequal sample sizes (Sanders 1968). Statistical analyses were carried out in SYSTAT (v. 11; Cranes Software International Ltd., Bangalore, India). Rarefaction curves and measures of niche overlap were obtained using the program, EcoSim (v. 7.0; Gotelli & Entsminger 2001).

RESULTS

During the course of this study (June 2002–January 2004), we found 94 roosts occupied by *C. brachyotis* Forest, 66 occupied by *C. brachyotis* Sunda, 41 occupied by *C. sphinx*, and 48 occupied by *C. horsfieldi*. The majority of roosts were identified using radiotelemetry ($N = 234$). We were able to locate the roosts of 16 of 17 radio-tagged *C. brachyotis* Sunda (94%), 16 of 18 *C. brachyotis* Forest (89%), 10 of 13 *C. horsfieldi* (77%), and 6 of 12 *C. sphinx* (50%). Fifteen additional roosts were found opportunistically while searching for radio-tagged bats. The species identity of non-radio-tagged bats was confirmed by capturing one or more individuals at the roost, using a hoop net and extensible aluminum poles. Complete sample sizes by species, sex, and locality are provided in Table 1. Results for each species are summarized below.

Cynopterus brachyotis Sunda was found exclusively in unmodified roosts at both study sites (Table 2). Likewise, only two modified roosts occupied by *C. sphinx* were found during the course of the study. Use of modified roosts was relatively low in *C. brachyotis* Forest (13.8%, $N = 13$) and intermediate in *C. horsfieldi* (39.6%, $N = 19$). This behavior is reported here for the first time for the latter species. There were no clear differences in individual preferences for modified versus unmodified roosts: all radio-tagged *C. brachyotis* Forest and *C. horsfieldi* that were observed in modified roosts also used unmodified roosts at some point during the telemetry period.

TABLE 1. Radiotelemetry sample sizes and number of roosts located for four nominal species of *Cynopterus* at two sites in peninsular Malaysia.

Species	Males		Females		Species total radio tracked ^a	N roosts (telemetry)	Total roosts ^b
	Perlis	Taipung	Perlis	Taipung			
<i>C. brachyotis</i> Forest	4	4	4	4	16	91	94
<i>C. brachyotis</i> Sunda	4	3	4	5	16	63	66
<i>C. sphinx</i>	1	2	1	2	6	35	41
<i>C. horsfieldi</i>	4	2	3	1	10	45	48

^aSample sizes for radioed bats successfully tracked to one or more roosts. N = number of roosts found using radio telemetry.

^bTotal includes roosts found opportunistically.

TABLE 2. Plant species (native or introduced) and other structures used as day roosts by four nominal species of *Cynopterus* at two sites in peninsular Malaysia.

Family	Roost plant species	Native	<i>C. brachyotis</i> Forest		<i>C. brachyotis</i> Sunda		<i>C. sphinx</i>		<i>C. horsfieldi</i>	
			<i>N</i> roosts (site)	<i>N</i> roosts modified	<i>N</i> roosts (site)	<i>N</i> roosts modified	<i>N</i> roosts (site)	<i>N</i> roosts modified	<i>N</i> roosts (site)	<i>N</i> roosts modified
Palmae	<i>Arenga obtusifolia</i>	N	17 ^T	0						
	<i>A. westerhoutii</i>	N	5 ^P	0			1 ^P	0	2 ^P , 1 ^T	0
	<i>Calamus</i> sp.1	N	5 ^P	0						
	<i>Calamus</i> sp.2	N							1 ^P	0
	<i>Caryota mitis</i>	N			1 ^T	0				
	<i>Cocos nucifera</i>	I			41 ^P , 5 ^T	0	1 ^T	0		
	<i>Corypha utan</i>	N					2 ^P	2 ^P		
	<i>Licuala peltata</i>	N	1 ^P	0						
	<i>Maxburretia</i> sp.	N	5 ^P	5 ^P						
	<i>Oncosperma horridum</i>	N	2 ^T	0						
	<i>Orania sylvicola</i>	N	18 ^P	0						
	<i>Plectocomia griffithii</i>	N	1 ^P	0						
	Euphorbiaceae	<i>Endospermum malaccense</i>	N	1 ^P	0					
<i>Macaranga gigantea</i>		N	5 ^P , 14 ^T	0 ^P , 8 ^T						
<i>Macaranga</i> sp.		N	8 ^P	0						
<i>Mallotus</i> sp.		N	2 ^P , 1 ^T	0						
?	Unidentified tree	N	5 ^P	0						
Liliaceae	<i>Dracaena fragrans</i>	I			2 ^T	0				
Dilleniaceae	<i>D. suffruticosa</i>	N	2 ^T	0	15 ^T	0			1 ^T	0
	<i>Dillenia</i> sp.	N	2 ^P	0					1 ^P	0
Musaceae	<i>Musa</i> spp.	N							20 ^P , 15 ^T	10 ^P , 9 ^T
Aspleniaceae	<i>Asplenium nidus</i>	N					28 ^T	0		
Verbenaceae	<i>Tectona grandis</i>	I			2 ^P	0				
Gramineae	<i>Bambusa</i> sp.	N							2 ^T	0
Anacardiaceae	<i>Mangifera</i> sp.	N							2 ^T	0
	Other roost structure									
	Limestone solution cavity						2 ^P	0	3 ^P	0
	Rock crevice						5 ^P	0		
	Abandoned house						2 ^T	0		

N = native; I = introduced; *n* = number of roosts found per species, per site; ^P = Perlis; ^T = Taiping.

Likewise, modified roosts of both species were occupied by both singletons and harem groups.

Interspecific overlap in use of plant species and other roost structures was minimal (Fig. 1), resulting in low estimated niche overlap among species pairs (0–8.46 %; Table 3). *Cynopterus brachyotis* Forest, *C. horsfieldi*, and *C. sphinx* all roosted infrequently in *A. westerhoutii* palms at Perlis and a single *C. sphinx* roost at Taiping was found in a coconut palm (*Cocos nucifera*), a species used extensively by *C. brachyotis* Sunda. Although both *C. brachyotis* Forest and Sunda roosted in the shrub *Dillenia suffruticosa* at the Taiping site, resulting in the highest pairwise measure of niche overlap, the two putative species were spatially segregated across habitat types with nonoverlapping roosting areas. Similarly, *C. horsfieldi* roosts in limestone solution cavities at Perlis were found in agricultural habitat, whereas solution cavities used by *C. sphinx* were in mature forest. Interspecific roost-sharing was never observed.

Across sites, roost diversity was highest in *C. brachyotis* Forest followed by *C. horsfieldi*, *C. sphinx*, and *C. brachyotis* Sunda (Fig. 2). Species had a significant effect on roost height ($F_{3,150} = 7.80$, $P < 0.0001$). However, mean roost heights were similar for *C. brachyotis* Forest (6.99 ± 4.43 m, $N = 77$), *C. brachyotis* Sunda (6.47 ± 4.08 m, $N = 34$), and *C. sphinx* (7.70 ± 4.13 m, $N = 17$), and intraspecific variance was extremely high. Only *C. horsfieldi* occupied roosts were significantly different in height from those of the other species (2.94 ± 0.98 m, $N = 26$, $P < 0.01$ for all comparisons).

CYNOPTERUS BRACHYOTIS FOREST.—While all *C. brachyotis* Forest roosts were located in foliage in forest habitat, the majority were found in areas dominated by secondary growth. This bat roosted in both emergent trees (mature *Macaranga* spp.) and palms (*O. sylvicola*, *Oncosperma horridum*), and in the understory

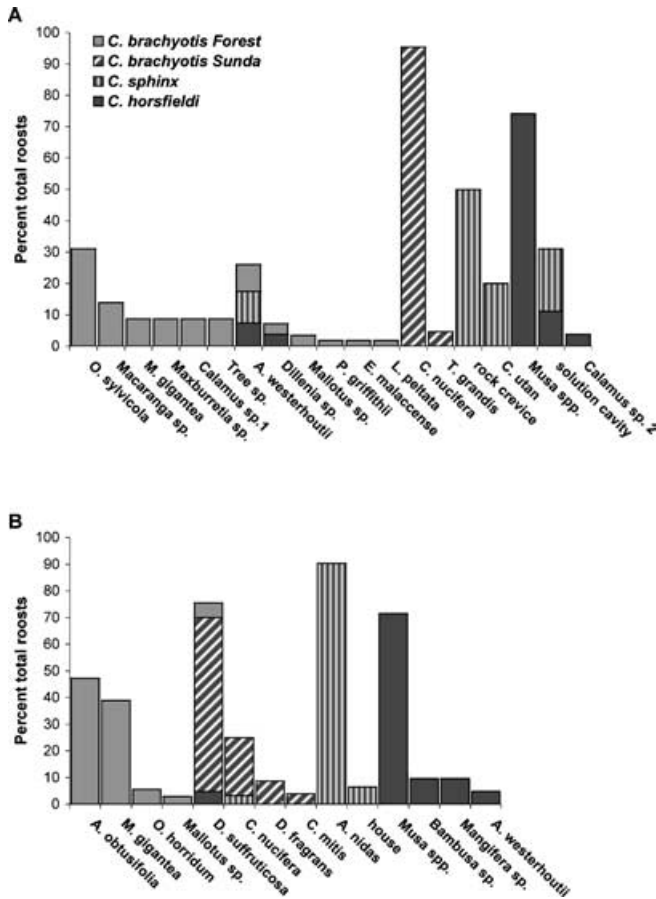


FIGURE 1. Interspecific overlap in roost use among four nominal species of *Cynopterus* at two sites in peninsular Malaysia: (a) Perlis, (b) Taiping. Roost use is quantified as the within-species percent of roosts found in each plant species or other structure. Complete names for identified plant species are provided in Table 2.

in shrubs (*Dillenia* spp.), small palms (*Licuala peltata* and *Maxburretia* sp.), rattan palms (*Plectocomia griffithii* and *Calamus* spp.), and *Macaranga* saplings. Roost plant diversity was considerably lower at Taiping than Perlis (5 vs. 12 species; Table 2), reflecting the lower floristic diversity and higher level of disturbance in the Taiping forest.

Across sites, a high proportion of roosts were in pinnate palm leaves (51.1%, $N = 48$; Table 2). Bats typically hung from or near the midrib at the apex of the inverted v-shaped structure formed by the downward drooping fronds. The relatively stiff leaflets of *O. sylvicola*, *O. horridum*, and *A. westerhoutii* afforded the bats natural protection from rain and wind. *Arenga obtusifolia* leaflets are more flexible and more widely spaced along the rachis; roosts in this species were all under leaves that were overlain by one or more other leaves, creating a thatched effect. Twenty-nine percent ($N = 27$) of all roosts were in the large leaves of *Macaranga* species (Table 2). Most unmodified *Macaranga* roosts were naturally slightly domed, with the bats hanging from the highest point of the dome.

TABLE 3. Estimated interspecific overlap in roost niche calculated using Pianka's measure of niche overlap (Pianka 1973) and expressed as percent overlap among species pairs; Taiping above diagonal, Perlis below.

Pairwise percent overlap	<i>CbF</i>	<i>CbS</i>	<i>Ch</i>	<i>Cs</i>
<i>CbF</i>		8.46	0.59	0
<i>CbS</i>	0		6.13	1.11
<i>Ch</i>	2.57	0		0
<i>Cs</i>	3.74	0	6.73	

CbF = *C. brachyotis* Forest; *CbS* = *C. brachyotis* Sunda; *Ch*, = *C. horsfieldi*; *Cs* = *C. sphinx*.

Modified *Macaranga* roosts were all in *Macaranga gigantea* and were distinguished by having two to three sharp angles where the veins of the leaf had been partially severed. At Taiping, 57 percent ($N = 8$) of identified *Macaranga* roosts were modified; none were modified at Perlis.

All modified roosts found at the Perlis site were in the palmate leaves of an unidentified species of *Maxburretia* (Fig. 3a), a Malaysian endemic that is restricted to limestone habitat (Whitmore 1998). This palm was rare within the study site: only five individuals were located during the course of the study, all of which had modified leaves that were periodically occupied by *C. brachyotis* Forest. Although multiple leaves were modified on each plant, only one was occupied by bats at a given time. Maximum observed harem size for *C. brachyotis* Forest at both study sites ($N = 4$ adult females) was recorded in a modified *Maxburretia* roost.

At Perlis, two solitary radio-tagged bats (1 male, 1 female) roosted periodically in an unidentified tree species whose leaves were smaller than the length of the bats' bodies (ca 10 cm). Both bats hung from small branches in dense foliage.

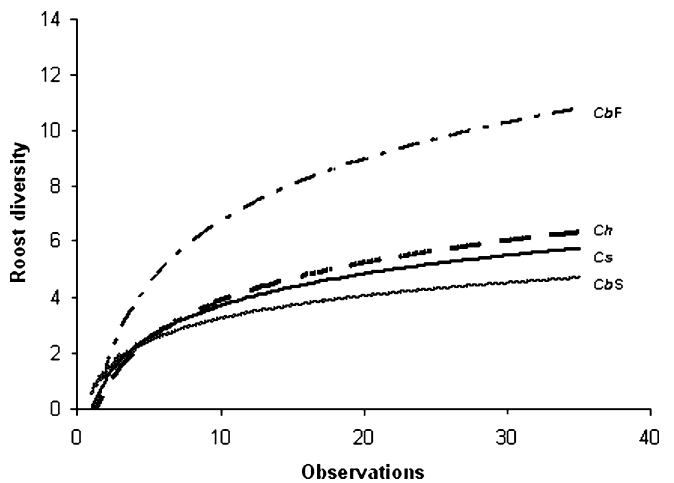


FIGURE 2. Rarefaction curve for roost type diversity in four nominal species of *Cynopterus* at two sites in peninsular Malaysia. *CbF* = *C. brachyotis* Forest; *Ch* = *C. horsfieldi*; *Cs* = *C. sphinx*. *CbS* = *C. brachyotis* Sunda.

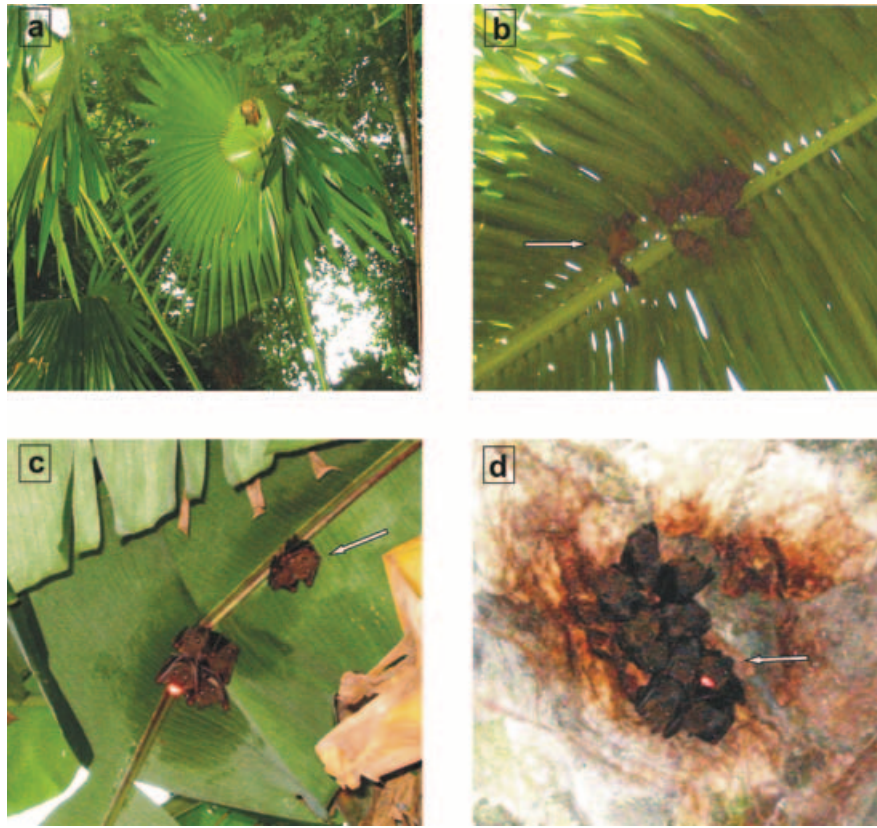


FIGURE 3. Diversity of roost types used by four nominal species of *Cynopterus* in peninsular Malaysia. (a) *Cynopterus brachyotis* Forest modified roosts in a forest-restricted palm (*Maxburretia* sp.) with a male–female pair occupying the central tent. (b) *Cynopterus brachyotis* Sunda harem group in an unmodified coconut palm (*Cocos nucifera*) roost. (c) *Cynopterus horsfieldi* harem group in a modified banana leaf (*Musa* sp.). (d) *Cynopterus sphinx* harem group in a limestone solution cavity on an open cliff face. Arrows indicate harem males; reflective tape-covered transmitters are visible in (c) and (d).

CYNOPTERUS BRACHYOTIS SUNDA.—All *C. brachyotis* Sunda roosts were discovered in anthropogenic habitat, often in areas that experienced relatively high levels of human traffic. A significant proportion of roosts were found in nonnative plant species (76%, $\chi^2 = 17.52$, $P < 0.001$; Table 2). In Perlis at the Bukit Jernih site, one solitary male roosted between the large leaves of teak trees (*Tectona grandis*) planted along a roadside. The remaining 41 of 43 identified roosts were in coconut palms (*C. nucifera*) in the gardens and yards of rural houses (Fig. 3b). The bats either hung from the rachis of horizontally positioned leaves, or against the leaflets of partially broken, vertically positioned leaves. As with the native pinnate palms used by *C. brachyotis* Forest, the downward angled and relatively rigid fronds of *C. nucifera* created a natural roof-shaped shelter, providing protection from direct sunlight, rain, and wind. Observed harem size ranged from 1 to 17 adult females. The bats showed no apparent preference for leaf height: the height of coconut palm roosts ranged from 1.2 to 11.4 m.

At the Taiping site, roosts were concentrated in coconut palms growing in suburban gardens and in the shrub, *D. suffruticosa*, which grew densely around the edges of an artificial lake in a city park. Like *C. brachyotis* Forest, *C. brachyotis* Sunda roosted spo-

radically under *D. suffruticosa* leaves. However, more stable harems (1–7 adult females) were found in natural bowl-shaped cavities formed by intertwined *D. suffruticosa* branches, overlain with an unidentified creeper. Additional roosts were located beneath the leaves of the fishtail palm, *Caryota mitis*. One radio-tracked female roosted in the unmodified foliage of a common ornamental plant, *Dracaena fragrans*, 4 m above a busy walkway in the Taiping zoo.

CYNOPTERUS HORSFIELDI.—Regardless of whether transmitters were placed on bats captured in forest or anthropogenic habitats, all *C. horsfieldi* roosts were found either in transitional habitat between cultivated land and secondary forest, or less than 0.25 km inside the forest. All identified *C. horsfieldi* roosts were less than 5 m above the ground.

Across sites, 73 percent ($N = 35$; Table 2) of all identified roosts were in the leaves of wild and cultivated bananas (*Musa* spp.). Fifty-four percent of occupied banana leaf roosts were modified into an inverted v-shaped structure by the partial severing of the midrib of the leaf approximately half-way between the stem of the plant and the tip of the leaf (Fig. 3c). Bats roosting beneath collapsed leaves

were often only visible from directly below the roost. A maximum harem size of five adult females was observed in modified banana roosts.

In Perlis at the Bukit Jernih site, two radio-tagged individuals roosted in abandoned agricultural habitat around the base of the limestone tower karsts. Both bats moved between banana leaf roosts and limestone solution cavities. Two solution cavity roosts were located on open rock faces and two were in a horizontal cave, located 2 and 24.5 m from the cave mouth. At the Taiping site, a solitary male occupied a naturally domed enclosure in a stand of bamboo, overgrown with an unidentified creeper.

CYNOPTERUS SPHINX.—*Cynopterus sphinx* was the only species whose roosts were found in both relatively undisturbed forest and in anthropogenic areas. At the Taiping site, all identified roosts were in suburban habitat and 90 percent of these ($N=28$) were in the epiphytic fern, *Asplenium nidus* (Table 2). The dead leaves of *A. nidus* droop downwards in a rosette around the root mass, which is embedded in a dense humus of decomposing leaf litter (Whitmore 1984). Solitary *C. sphinx* and groups comprising up to 28 adult individuals roosted beneath the root masses of ferns growing on trees planted along and, in the case of one roost, directly overhanging busy roadways. During an observation period of 73 d, a loosely defined colony of *C. sphinx* (mean colony size = 36 ± 7.0 adults) occupied ferns growing on a 30-m long row of large trees in an open grassy area between houses.

We found no evidence for modification of *A. nidus* roosts by *C. sphinx*: the surfaces of root mass cavities occupied by this species were rough and uneven rather than smooth, and fallen plant debris was never observed beneath newly occupied roosts. *Asplenium nidus* growing in secondary forest and in durian orchards near the forest edge at Taiping were inspected regularly for bats but *Cynopterus* species were never observed in ferns in this habitat.

At the Perlis forest site, two radio-tracked *C. sphinx* roosted primarily in solution cavities and crevices in exposed limestone cliff faces (Fig. 3d). The only apparent difference between these roosts and the cliff solution cavities occupied by *C. horsfieldi* at the 15 km distant Bukit Jernih site was their location in mature forest. The only modified roosts occupied by *C. sphinx* were found in palmate umbrella tents in two solitary *Corypha utan* palms growing in rice paddies on the edge of secondary forest.

DISCUSSION

USE OF MODIFIED ROOSTS.—While the modification of roosts in foliage or other plant structures is a shared, derived trait of the *Cynopterus* species treated in this study, it is not an essential component of the roosting ecology of any of the four putative species, nor is it a requirement for the formation of social groups. Broad comparisons have been drawn between the roosting ecology of *Cynopterus* species and that of roost-modifying phyllostomids in the New World tropics (Kunz *et al.* 1994, Kunz & McCracken 1996, Kunz & Lumsden 2003). However, the results of this study indicate that, while the relatively unspecialized roosting ecology of

Cynopterus species in Malaysia may be comparable to that of larger habitat generalists in the Neotropics such as *Artibeus jamaicensis* and *A. literatus* (Morrison 1979, Ortega & Arita 1999, Muñoz-Romo & Herrera 2003), it is quite distinct from that of smaller, more forest-dependent species such as *A. watsoni*, *A. phaeotis*, *A. gnomus*, *Ectophylla alba*, *Rhinophylla pumilio*, and *Vampyressa pusilla*, in which tent roosting is apparently obligate (Timm 1987, Chaverri & Kunz 2006).

Improved predator avoidance and reduction of thermoregulatory costs in modified roosts, and more effective roost defensibility by males have all been proposed as factors that might promote the evolution of roost-modifying behavior (Timm 1987, Brooke 1990, Kunz *et al.* 1994). Why should this apparently adaptive behavior be obligate in some species and opportunistic in others? One potential explanation is that the thermoregulatory advantage conferred by modified roosts relative to roosts in open foliage is important to small-bodied bats but may be nonessential to species whose body masses exceed a certain value. In the Old World tropics, that value may fall between *Balionycteris maculata* (12–14 g), another harem-forming species that consistently roosts in cavities excavated in the root masses of epiphytic plants or arboreal termite nests (Hodgkison 2001, Hodgkison *et al.* 2003), and *C. brachyotis* Forest (24–37 g), which roosts in both modified and unmodified foliage.

Interspecific differences in the prevalence of tent roosting were consistent between the two study sites: use of modified roosts was observed most frequently in *C. horsfieldi*, intermittently in *C. brachyotis* Forest, rarely in *C. sphinx*, and not at all in *C. brachyotis* Sunda. However, we suggest that this result likely reflects both natural and human-mediated variation in the availability of plant species suitable for modification, and may be a poor indicator of fixed interspecific differences in roosting behavior.

Ultimately, the manner in which animals select and utilize resources in their environment depends on the availability of preferred resources to a given population. The findings of this study for *C. brachyotis* Forest, and that of a previous study of *C. brachyotis* Sunda (Tan *et al.* 1997), suggest that both putative species preferentially occupy and, presumably, modify the palmate leaves of fan palms where these are available. While palm diversity in Malaysia is extremely high (>220 species), most of the approximately 54 species of fan palms that are native to the Malay peninsula have highly restricted distributions (Uhl & Dransfield 1987, Saw 1997, Whitmore 1998). Consequently, this resource is not widely available to *C. brachyotis* Forest populations. While this bat occupied modified roosts under the large leaves of *M. gigantea* at the Taiping site, the majority of roosts at both sites were in unmodified pinnate-leaved palms. In the case of *C. brachyotis* Sunda, the distribution of fan palms in the suburban and agricultural areas to which peninsular Malaysian populations of this bat are restricted is artificially determined by civic and individual preferences for these species as ornamentals. Our results indicate that, where palmate-leaved palms have not been planted, *C. brachyotis* Sunda will readily occupy unmodified roosts in a variety of other plant species.

The use of modified roosts was most prevalent in *C. horsfieldi*, a species in which this behavior has not been described previously

(Funakoshi & Zubaid 1997, Tan *et al.* 1999). However, all modified *C. horsfieldi* roosts were in wild and cultivated banana plants (*Musa* spp.), which were abundant along the forest edges at both of our study sites. Whether frequent use of modified roosts is a characteristic of *C. horsfieldi* as a species, or only of *C. horsfieldi* populations occupying banana groves, will require additional studies of the roosting ecology of this bat at sites where banana plants are not abundant.

We observed two modified *C. sphinx* roosts in the fan palm, *C. utan*; all other *C. sphinx* roosts, including those in bird's nest ferns (*A. nidus*), were apparently unmodified. The spotted-winged fruit bat, *B. maculata*, which also roosts in *A. nidus*, excavates the root mass, creating smooth-sided, bell-shaped cavities (Hodgkison 2001, Hodgkison *et al.* 2003). While we cannot rule out the possibility that *C. sphinx* may modify fern roosts in a similar fashion, we found no evidence for this behavior in our study populations.

In contrast, in anthropogenic habitat in India, *C. sphinx* constructs structurally diverse roosts in a range of plant species. These include the leaves of fan palms, the stems of overhanging creepers, and the fruit and flower clusters of the kitul palm, *Caryota urens*, which *C. sphinx* males modify over a period of several weeks by biting off pendant clusters to create a domed, semi-enclosed roost (Goodwin 1979, Bhat & Kunz 1995, Balasingh *et al.* 1995). While our sample size for *C. sphinx* was relatively small, the lack of evidence for any such labor-intensive roost modification by this species in Malaysia was somewhat surprising. However, the extensive literature on tent-roosting bats provides no direct evidence that a modified roost is inherently more attractive to females than an unmodified roost that provides equivalent benefits. In fact, studies of the social structure of the harem-forming phyllostomid, *A. jamaicensis*, implicate higher group stability and larger harem sizes in solution cavity roosts, relative to more ephemeral tent roosts in palms (Kunz *et al.* 1983, Kunz & McCracken 1996, Ortega & Arita 1999). Like the stem tents used by *C. sphinx* in India, the solution cavities, rock crevices, and epiphytic ferns occupied by Malaysian populations of this species are long-lasting, well-protected from the elements and terrestrial predators and, in the case of bird's nest ferns, highly clumped in space, promoting colony formation.

DO INTERSPECIFIC INTERACTIONS INFLUENCE ROOST SELECTION?—Within sites, we found little evidence for present day interspecific interactions in relation to roost choice. The roosts of *C. brachyotis* Sunda and Forest were spatially segregated in highly disturbed and forest habitats, respectively, and *C. horsfieldi* was the only species strongly associated with the transition zone between forest and cultivated land. *Cynopterus sphinx* overlapped spatially with both *C. brachyotis* Forest and Sunda, but differed in roost selection.

Roost plants that were modified were never used by more than one species, strongly suggesting that, in sympatry, each species modifies a unique subset of plants and does not occupy roosts modified by congeners. In general, overlap in roost plant selection was minimal: plants used by two or more species were used sporadically by several species, as was the case for *C. sphinx*, *C. horsfieldi*, and *C. brachyotis* Forest in *A. westerhoutii*, or frequently by one species and rarely by another, as was the case for *C. brachyotis* Sunda and

C. sphinx in coconut palms, or were used by single species within-habitat type, as was the case for *C. brachyotis* Forest and Sunda roosts in *D. suffruticosa*. The same pattern was observed in the similar but habitat-segregated solution cavity roosts occupied by *C. sphinx* and *C. horsfieldi*.

However, at a broader geographic scale, intraspecific variation in occupation of roost plant species, particularly *A. nidus* ferns, suggests that roost choice may be influenced to some extent by the presence or absence of congeners with similar roost preferences and habitat associations. In this study, we found that *A. nidus* roosts in anthropogenic areas were occupied exclusively by *C. sphinx*. In contrast, roost surveys conducted in Selangor State, south of the known peninsular distribution of *C. sphinx*, found that *A. nidus* ferns in landscaped habitat were occupied frequently by *C. brachyotis* Sunda (Tan *et al.* 1997) and occasionally by *C. horsfieldi* (Tan *et al.* 1999). Assuming that these semipermanent, well-protected roost sites are desirable, the absence of *C. brachyotis* Sunda and *C. horsfieldi* from *A. nidus* roosts at our two study sites suggests that *C. sphinx* may out-compete other congeners for this resource.

DETERMINANTS OF ROOST CHOICE.—Unlike larger Old World fruit bats such as members of the genera *Rousettus* and *Pteropus*, *Cynopterus* species do not forage over large distances (Funakoshi & Zubaid 1997, Palmer & Woinarski 1999, Bumrungsri 2002, Hodgkison *et al.* 2004). In this study, each species roosted primarily in the habitat in which they were most frequently captured (Campbell *et al.* in press), suggesting a close relationship between roosting and foraging ecology. Most roosts were located in plants and trees that were common within the preferred habitat type of each species; roost plants common only at one site were often replaced by structurally similar species that were common at the second site. For example, the majority of identified *C. brachyotis* Forest roosts were either in the large-leaved *Macaranga* species that were abundant at both sites, or under the pinnate fronds of the palms, *O. sylvicola* and *A. obtusifolia*, which were abundant in the forest at Perlis and Taiping, respectively. Likewise, *C. sphinx* roosts in both anthropogenic and forest habitats were characteristically bowl-shaped and, at least in the case of *A. nidus* ferns, abundantly available. These observations suggest that, within the local subset of roost structures that meet the ecological requirements of each species, the abundance of structurally equivalent roost sites may be an important criterion for roost selection.

From a functional perspective, the two smaller putative species, *C. brachyotis* Forest and Sunda, exhibited similar preferences for particular roost structures. While restricted to floristically distinct habitat types, both putative species roosted frequently in pinnate-leaved palms, sporadically in open foliage, and typically used roosts that were more exposed than those occupied by *C. horsfieldi* or *C. sphinx*. Although we did not specifically measure the load capacity of roosts, interspecific differences in roost selection suggest that body mass may place constraints on the range of roost types available to each species. For example, the solution cavities and epiphytic ferns used by *C. sphinx* were clearly more robust than the foliage roosts occupied by its two smaller congeners. Likewise, only the lightest bat in this study, *C. brachyotis* Forest, roosted beneath the

relatively fragile leaves of forest trees. This relationship was not strongly apparent in the heaviest species, *C. horsfieldi*, which used solution cavities but favored ephemeral roosts beneath the easily damaged leaves of banana plants.

Relative to *C. brachyotis* Forest and Sunda, roost selection in *C. horsfieldi* and *C. sphinx* appears to be slightly more specialized. Whereas the height of banana leaf roosts used by *C. horsfieldi* was clearly limited by the height of the plants, roosts in taller plants such as *A. westerhoutii* palms and bamboo were consistently low, suggesting that this bat may actively select lower roosts than do the other *Cynopterus* species treated in this study. *Cynopterus sphinx*, the species with the broadest roosting habitat associations, might be expected to exploit the widest range of structures as roosts. Instead, we found that the diversity of roost types used by *C. sphinx* was low, and that this species consistently favored relatively enclosed roosts that were either permanent or long-lasting and could contain and support a large number of individuals, suggesting that the relationship between roost choice and social structure may be particularly salient in this species (Storz *et al.* 2000a).

CONCLUSIONS.—Our investigation of the roosting ecology of sympatric species of *Cynopterus* in peninsular Malaysia supports the contention that the roost-modifying behavior described in *C. brachyotis* and *C. sphinx* is likely to be found in other members of the genus (Kunz *et al.* 1994). Determining whether this trait is expressed throughout the genus awaits studies of the roosting ecology of the two Indonesian species, *C. titthaechilus* and *C. nusatenggara*, and of the genetically divergent and geographically isolated lineages of *C. brachyotis* in the Philippines, on the island of Sulawesi, and in southwest India and Sri Lanka (Kitchener & Maharadatunkamsi 1991, Campbell *et al.* 2004). Our results clearly indicate, however, that the species treated in this study use modified roosts opportunistically and are, particularly in relation to obligate tent-roosting phyllostomids, flexible in their choice of plant species and other structures used as roosts.

The wide range of roost plants and roost structures identified in this and previous studies of *Cynopterus* fruit bats cautions against defining species-typical aspects of roosting ecology based on single roost characteristics such as plant species, or on data from few samples sites. The local abundances of preferred roost structures may be important in determining interpopulation differences in roost plant selection; interspecific differences in the structural capacity of roosts suggest that body size may play a role in determining the range of roost structures available to each species. It is likely, however, that a reciprocal relationship exists between roost selection and multiple other factors, including the distribution and abundance of feeding resources, degree of polygyny, and population density (Morrison 1978, Storz *et al.* 2000b, Vonhoff & Fenton 2004).

Whereas the protection of appropriate roosting habitat for bats is a major conservation concern in both tropical and temperate areas (Mickleburgh *et al.* 2002, Kunz & Lumsden 2003, Racey & Entwistle 2003), the results of this study suggest that *Cynopterus* species are not highly sensitive to human disturbance and that some human activities, such as the planting of ornamental palms, may actually increase the availability of roosts (Tan *et al.* 1996). We found that both *C. brachyotis* Sunda and *C. sphinx* were remarkably toler-

ant of urban development and the close proximity of humans and that *C. horsfieldi*, while roosting in relatively more secluded areas, was strongly associated with cultivated banana plants. Although *C. brachyotis* Forest is mainly restricted to forest habitats, this bat's use of fast-growing pioneers such as *Macaranga* species, and the location of roosts in areas that had been clear-cut, indicate that this putative species is not dependent on primary forest for roosting habitat and may preferentially select patches of forest that have experienced high levels of disturbance in the past.

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LITERATURE CITED

- ANTHONY, E. L. P. 1988. Age determination in bats. In T. H. Kunz (Ed.), *Ecological and behavioral methods for the study of bats*, pp. 47–58. Smithsonian Institution Press, Washington, DC.
- BALASINGH, J., A. J. KOILRAJ, AND T. H. KUNZ. 1995. Tent construction by the short-nosed fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae) in southern India. *Ethology* 100: 210–229.
- BATES, P. J. J., AND D. L. HARRISON. 1997. *Bats of the Indian subcontinent*. Harrison Zoological Museum, Sevenoaks, U.K.
- BHAT, H. R., AND T. H. KUNZ. 1995. Altered fruit/flower clusters of the kitul palm used as roosts by the short-nosed fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae). *J. Zool. (London)* 235: 597–604.
- BROOKE, A. P. 1990. Tent selection, roosting ecology and social organization of the tent-making bat, *Ectophylla alba*, in Costa Rica. *J. Zool. (London)* 221: 11–19.
- BUMRUNGSRI, S. 2002. The foraging ecology of the short-nosed fruit bat, *Cynopterus brachyotis* (Muller, 1838), in lowland dry evergreen rain forest, southeast Thailand. PhD dissertation, University of Aberdeen.
- CAMPBELL, P., C. J. SCHNEIDER, A. ZUBAID, A. M. ADNAN, AND T. H. KUNZ. 2006. Morphological and ecological correlates of coexistence in Malaysian fruit bats (Chiroptera: Pteropodidae). *J. Mammal.* In press.
- CAMPBELL, P., C. J. SCHNEIDER, A. M. ADNAN, A. ZUBAID, AND T. H. KUNZ. 2004. Phylogeny and phylogeography of Old World fruit bats in the *Cynopterus brachyotis* complex. *Mol. Phylogenet. Evol.* 33: 764–781.
- , ———, ———, ———, AND ———. 2006. Comparative population structure of *Cynopterus* fruit bats in peninsular Malaysia and southern Thailand. *Mol. Ecol.* 15: 29–47.
- CHAVERRI, G., AND T. H. KUNZ. 2006. Roosting ecology of the tent-roosting bat *Artibeus watsoni* (Chiroptera: Phyllostomidae) in Southwestern Costa Rica. *Biotropica* 38: 77–84.
- CHOE, J. C. 1993. Ingenious design of tent roosts by Peter's tent-making bat, *Uroderma bilobatum* (Chiroptera: Phyllostomidae). *J. Nat. Hist.* 28: 731–737.

- DECHMANN, D. K. N., E. K. V. KALKO, B. KÖNIG, AND G. KERTH. 2005. Mating system of a Neotropical roost-making bat: The white-throated, round-eared bat, *Lophostoma silvicolum* (Chiroptera: Phyllostomidae). *Behavioural Ecol. Sociobiol.* 58: 316–325.
- FOSTER, M. S. 1992. Tent roosts of Macconnell's bat (*Vampyressa macconnelli*). *Biotropica* 24: 447–454.
- FUNAKOSHI, K., AND A. ZUBAID. 1997. Behavioral and reproductive ecology of the dog-faced fruit bats, *Cynopterus brachyotis* and *C. horsfieldi*, in a Malaysian rainforest. *Mammal Study* 22: 95–108.
- GOODWIN, R. E. 1979. The bats of Timor: Systematics and ecology. *Bull. Am. Mus. Nat. Hist.* 163: 72–122.
- GOTELLI, N. J., AND G. L. ENTSMINGER. 2001. EcoSim: Null models software for ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. Available at: <http://homepages.together.net/~gentsmin/ecosim.htm>
- HANSELL, M. 2005. *Animal architecture*. Oxford University Press, Oxford, UK.
- HODGKISON, R. 2001. The ecology of fruit bats (Chiroptera: Pteropodidae) in a Malaysian lowland dipterocarp forest, with particular reference to the spotted-winged fruit bat (*Balionycteris maculata*, Thomas). PhD dissertation, University of Aberdeen.
- , S. T. BALDING, A. ZUBAID, AND T. H. KUNZ. 2003. Roosting ecology and social organization of the spotted-winged fruit bat, *Balionycteris maculata* (Chiroptera: Pteropodidae), in a Malaysian lowland dipterocarp forest. *J. Trop. Ecol.* 19: 667–676.
- , ———, ———, AND ———. 2004. Temporal variation in the relative abundance of fruit bats (Megachiroptera: Pteropodidae) in relation to the availability of food in a lowland Malaysian rain forest. *Biotropica* 36: 522–533.
- KITCHENER, D. J., AND MAHARADATUNKAMSI. 1991. Description of a new species of *Cynopterus* (Chiroptera: Pteropodidae) from Nusa Tenggara Indonesia. *Rec. West. Aust. Mus.* 51: 307–363.
- KALKO, E. K. V., D. FRIEMEL, C. O. HANDLEY, AND H. U. SCHNITZLER. 1999. Roosting and foraging behavior of two Neotropical gleaning bats, *Tonatia silvicola* and *Trachops cirrhosus* (Phyllostomidae). *Biotropica* 31: 344–353.
- KUNZ, T. H. 1982. Roosting ecology of bats. In T. H. Kunz (Ed.). *Ecology of bats*, pp. 1–55. Plenum Press, New York, New York.
- , AND L. F. LUMSDEN. 2003. Ecology of cavity and foliage roosting bats. In T. H. Kunz and M. B. Fenton (Eds.). *Bat ecology*, pp. 3–89. University of Chicago Press, Chicago, Illinois.
- , AND G. F. MCCrackEN. 1996. Tents and harems: Apparent defense of foliage roosts by tent-making bats. *J. Trop. Ecol.* 12: 121–137.
- , V. P. AUGUST, AND C. D. BURNETT. 1983. Harem social organization in cave roosting *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Biotropica* 15: 133–138.
- , M. S. FUJITA, A. P. BROOKE, AND G. F. MCCrackEN. 1994. Convergence in tent architecture and tent-making behavior among Neotropical and Paleotropical bats. *J. Mammal. Evol.* 2: 57–78.
- LATIFF, A., K. OSMAN, I. FARIDAH-HANUM, AND R. AMAT. 2001. Perlis State Park at Wang Kelian: An introduction. In I. Faridah-Hanum, K. Osman, and A. Latiff (Eds.). *Kepelbagaian biologi dan pengurusan taman negeri perlis: Persekitaran fizikal dan biologi wang kelian*, pp. 19–27. Jabatan Perhutanan Negeri Perlis, Kangar, Malaysia.
- MICKLEBURGH, S. P., A. M. HUSTON, AND P. A. RACEY. 2002. A review of the global conservation status of bats. *Oryx* 36: 18–34.
- MORRISON, D. W. 1978. Influence of habitat on the foraging distances of the fruit bat, *Artibeus jamaicensis*. *J. Mammal.* 59: 622–624.
- . 1979. Apparent male defense of tree hollows in the fruit bat, *Artibeus jamaicensis*. *J. Mammal.* 60: 11–15.
- MUÑOZ-ROMO, M., AND E. A. HERRERA. 2003. Leaf modifying behavior in *Artibeus literatus*. *Acta Chiropt.* 5: 273–276.
- ORTEGA, J., AND H. T. ARITA. 1999. Structure and social dynamics of harem groups in *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *J. Mammal.* 80: 1173–1185.
- PALMER, C., AND J. C. Z. WOJNARSKI. 1999. Seasonal roosts and foraging movements of the black flying fox (*Pteropus alecto*) in the northern territory: Resource tracking in a landscape mosaic. *Wildl. Res.* 26: 823–838.
- PAYNE, J., C. M. FRANCIS, AND K. PHILLIPPS. 1985. *A field guide to the mammals of Borneo*. The Sabah Society, Kota Kinabalu, Malaysia.
- PIANKA, E. R. 1973. The structure of lizard communities. *Annu. Rev. Ecol. Syst.* 4: 53–74.
- PUTZ, F. E. 1978. A survey of virgin jungle reserves in Peninsular Malaysia. Forest Research Institute, Pamphlet No. 73. Forestry Department Peninsular Malaysia, Kuala Lumpur, Malaysia.
- RACEY, P. A. 1988. Reproductive assessment in bats. In T. H. Kunz (Ed.). *Ecological and behavioral methods for the study of bats*, pp. 31–45. Smithsonian Institution Press, Washington, DC.
- , AND A. C. ENTWISTLE. 2003. Conservation ecology of bats. In T. H. Kunz and M. B. Fenton (Eds.). *Bat ecology*, pp. 690–743. University of Chicago Press, Chicago, Illinois.
- SANDERS, H. L. 1968. Marine benthic diversity: A comparative study. *Am. Nat.* 102: 243–282.
- SAW, L. G. 1997. A revision of *Licuala* (Palmae) in the Malay Peninsula. *Sandakanian* 10: 1–95.
- SIMMONS, N. B. 2005. Order Chiroptera. In D. E. Wilson and D. M. Reeder (Eds.). *Mammal species of the world: A taxonomic and geographic reference* (2nd edition), pp. 312–529. Johns Hopkins University, Baltimore, Maryland.
- STONER, K. E. 2000. Leaf selection by the tent-making bat *Artibeus watsoni* in *Asterogyne martiana* palms in southwestern Costa Rica. *J. Trop. Ecol.* 16: 151–157.
- STORZ, J. F., H. R. BHAT, AND T. H. KUNZ. 2000a. Social structure of a polygynous tent-making bat, *Cynopterus sphinx* (Megachiroptera). *J. Zool. (London)* 251: 151–165.
- , J. BALASINGH, P. T. NATHAN, K. EMMANUEL, AND T. H. KUNZ. 2000b. Dispersion and site fidelity in a tent-roosting population of the short-nosed fruit bat (*Cynopterus sphinx*) in southern India. *J. Trop. Ecol.* 16: 1–15.
- TAN, K. H., A. ZUBAID, AND T. H. KUNZ. 1996. Landscaping and bat conservation. *Malay. Nat.* 1996: 39–39.
- , ———, AND ———. 1997. Tent construction and social organization in *Cynopterus brachyotis* (Muller) (Chiroptera: Pteropodidae) in Peninsular Malaysia. *J. Nat. Hist.* 31: 1605–1621.
- , ———, AND ———. 1999. Roost selection and social organization in *Cynopterus horsfieldi* (Chiroptera: Pteropodidae). *Malay. Nat. J.* 53: 295–298.
- TELLO, J. G., AND P. M. VELAZCO. 2003. First description of a tent used by *Platyrrhinus helleri* (Chiroptera: Phyllostomidae). *Acta Chiropt.* 5: 269–272.
- TIMM, R. M. 1987. Tent construction by bats in the genera *Artibeus* and *Uroderma*. *Fieldiana Zool.* 39: 187–212.
- UHL, N. W., AND J. DRANSFIELD. 1987. *Genera Palmarum: A classification of palms based on the work of Harold E. Moore, Jr.* Allen Press, Lawrence, Kansas.
- VONHOF, M. J., AND M. B. FENTON. 2004. Roost availability and population size of *Thyroptera tricolor*, a leaf-roosting bat, in north-eastern Costa Rica. *J. Trop. Ecol.* 20: 291–305.
- WHITMORE, T. C. (Ed.). 1972. *Tree flora of Malaya, Volume 1*. Longman Group Limited, Kuala Lumpur, Malaysia.
- . (Ed.). 1973. *Tree flora of Malaya, Volume 2*. Longman Group Limited, Kuala Lumpur, Malaysia.
- . 1984. *Tropical rain forests of the far east* (2nd edition). Clarendon Press, New York, New York.
- . 1998. *The palms of Malaya* (3rd edition). Oxford University Press, Oxford, U.K.
- WONG, S. L. 2002. *Pearl of Perlis: Perlis state park guide*. Jabatan Perhutanan Negeri Perlis, Kangar, Malaysia.