Resource Partitioning in Sympatric *Cynopterus* bats in Lowland Tropical Rain Forest, Thailand

Sara Bumrungsri[1], **Watcharee Leelapaibul,** and **Paul A. Racey**

School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 2TZ, UK

ABSTRACT

Diet and habitat use of the closely related and size-overlapping sympatric *Cynopterus brachyotis* and *C. sphinx* were established in lowland dry evergreen forest, Thailand, between March 1998 and March 2000. Feces from netted bats were analyzed, and the recapture rate determined. Although both species share a set of food plants, and fruits from early successional forest contribute about half of their diet, *C. brachyotis*, the smaller of the two species, ate a significantly greater proportion of fruits from early successional forest than *C. sphinx*. The latter ate a significantly greater proportion of fruit species in larger size classes. More *C. brachyotis* were captured in early successional forest in almost every month, while *C. sphinx* is more common in old-growth forest. However, the capture rate of *C. sphinx* increased in early successional forest in the mid-dry season when its preferred fruits become available. The recapture rate of *C. brachyotis* in early successional forest was significantly higher than that of *C. sphinx*, and the reverse situation was observed in old-growth forest. Male *C. sphinx* had a significantly higher recapture rate in early successional forest than females. Fruit size and habitat use are the major determinants of resource partitioning between these size-overlapping congeners.

Key words: brachyotis; Cynopterus sphinx; diet; fruit bats; habitat use; interspecific variation.

UNDERSTANDING THE MECHANISMS OF SPECIES COEXISTENCE remains a major goal of community ecology (Ricklefs 1990, Begon *et al.* 1996). Morphologically similar species often predominate in local bat faunas, and this had led to the prediction that competitive niche arrangements play a minor role in bat community organization (Arlettaz 1999). In addition most bat species appear to be opportunistic foragers, which readily exploit patchily distributed resources, and this is unlikely to lead to competitive niche partitioning. The alternative is that the organization of bat communities is under the control of non-deterministic processes (Willig & Moulton 1989, Findley 1993, Arita 1997).

As there are few comprehensive data about dietary niches, foraging strategy and habitat use simultaneously available from the same guilds (Saunders & Barclay 1992), it is difficult to understand how bat communities are structured (Kalko 1998). Detailed studies of resource use among morphologically similar bats are needed to accompany the molecular resolution of their taxonomic status (*e.g.*, Campbell *et al.* 2004) and to provide new insights into the structuring of communities.

Among Old World Megachiroptera, the lesser short-nosed fruit bat, *Cynopterus brachyotis* Muller, overlaps in size with the greater short-nosed fruit bat, *C. sphinx* Vahl. Furthermore, they are genetically close relatives in a genus that is thought to have undergone speciation approximately 350,000 yr ago (Schmitt *et al.* 1995) and whose phylogenetic structure has recently been revealed (Campbell *et al.* 2004).

Fruit bats of the genus *Cynopterus* are very common, with a distribution covering most of South and SE Asia. *Cynopterus*

brachyotis and *C. sphinx* occur sympatrically over a wide range from southwest India, Sri Lanka, Thailand, Cambodia, Vietnam, and Indonesia (Lekagul & McNeely 1977, Corbet & Hill 1992, Bates & Harrison 1997, Campbell *et al.* 2004). Although both species are found in a variety of habitats, they are both frequently associated with secondary forest, fruit orchards, and urban areas (Heideman & Heaney 1989, Bhat 1994, Storz & Kunz 1999). Although they feed mainly on fruits (Bhat 1994, Tan *et al.* 1998), it is not known how they partition food and other resources where they coexist. The present study is the first to investigate both food and habitat partitioning between these fruit bat species, which occur sympatrically in early successional forest mixed with old-growth forest. A number of physiological and ecological characters scale allometrically with body size (Gaston & Blackburn 1996, Pyron 1999). Fleming (1991) related body size to diet and habitat use among the species of Neotropical frugivorous bat, *Carollia*. He hypothesized that the size of fruits consumed increases with body size, and the bats made less use of secondary forest. When foraging, fruit bats often carry fruit to a nearby tree before eating it (Bonaccorso 1979, Hodgkison 2001). Although the size of exploited food is an important factor in resource partitioning in both Neotropical and Palaeotropical frugivorous bat communities (Heithaus *et al.* 1975, Fleming 1986, Kalko *et al.* 1996, Hodgkison 2001), Giannini (1999) found it did not apply to two species of *Sturnira* in the Andes. Whether Fleming's hypothesis is valid for the genus *Cynopterus* is also examined in the present study. Furthermore, wing morphology has been recognized to influence habitat use, and thus play an important role in food partitioning in Palaeotropical fruit bat communities (McKenzie *et al.* 1995, Hodgkison *et al.* 2004a). Wing morphology of the two species of *Cynopterus* considered in the present study differs only slightly (Norberg & Rayner 1987) and whether this results in differences in preferred habitats is also considered.

METHODS

STUDY SITE.—The study was carried out in Khao Ang Runai Wildlife Sanctuary (102,218 ha), southeast Thailand (13°22′ N, 101°50′ E) between March 1998 and March 2000 (Bumrungsri 2002). The study site is characterized by lowland semi-evergreen forest on relatively flat terrain of less than 200 m asl. The forest canopy is dominated by deciduous trees, *e.g.*, *Lagerstroemia calyculata* Kurz, *Pterocymbium javanicum* R. Br., *Irvingia malayana* Olive ex A. Benn. mixed with evergreen subcanopy trees such as *Aglaia pirifera* Hance, and *Diospyros* sp. The forest was selectively logged during 1970–1990. Patches of former rice fields and orchard remnants from short-term settlements are also interspersed among the old-growth forest. The former rice fields are covered by successional species such as *Peltophorum dasyrachis* Kurz, *Anthocephalus chinensis* Rich. ex Walp, *Macaranga* sp. and *Cratoxylum* spp., exotic herbs such as *Eupatorium odoratum* L. and grasses. The abandoned orchards contain several commercial fruits such as mango (*Mangifera indica* L.), guava (*Psidium guajava* L.), Indian jujube (*Ziziphus mauritiana* Lamk.) and jackfruit (*Artocarpus heterophyllus* Lamk.), and other useful plants such as kapok (*Ceiba pentandra* Gaertn.). Fruit trees such as *Ficus benjamina* L. and *Eugenia cumini* Druce were planted near the wildlife sanctuary's headquarters and the nearby research station for habitat restoration. Several patches of an exotic tree, *Muntingia calabura* L, (with two to eight trees each) are also present close to the offices in abandoned rice fields.

Habitats in the wildlife sanctuary were classified into two general categories: early successional forest which is defined as successional vegetation in former paddy fields and abandoned orchards, and old-growth forest that is defined as relatively intact selectively logged, dry evergreen forest. The climate is largely influenced by seasonal monsoons and average annual rainfall is 1588 mm. Three seasons are recognized: rainy (mid-April to October), cool dry (November–January) and hot dry season (February to mid-April). However, the two latter seasons are often pooled as the dry season. The average monthly rainfall over the 10 yr 1991 to 2000 was highest in September (297 mm), and lowest in December and January (10–12 mm). The 1998 dry season was particularly hot and dry, lasted 2 mo longer than the 10-yr average, due to the El Niño Southern Oscillation (Wright *et al.* 1999, Wich & van Schaik 2000), and the rainy season began 2 mo late.

BAT TRAPPING AND DIET ANALYSES.—Bats were captured using mist nets set at ground level across trails or around fruiting trees in early successional and in old-growth forest habitats. Generally, nets were set at least 300 m from the edge of the forest. Mist nets were set from dusk to midnight and checked at least every half-hour. Mean ($\pm$ SD) netting effort in each month was 91 $\pm$ 51 mist-net hours, range 24–255. Netting was suspended for seven nights at full moon. Canopy nets were occasionally set when *Ceiba pentandra* was in flower, or when *Ficus benjamina* was fruiting. Specifically, about 90 percent of the netting effort (2267 net hours) took place within 2 km of an 18-km stretch of road that transected the north of the wildlife sanctuary. In this northern area, 73 percent is old-growth forest, and 27 percent is early successional forest. A total of 801 bats were captured, and placed initially in cloth bags. Bats defecated in

the mist net or in the cloth bags and the feces were collected and given the identification number of the bat. The length of forearm and ear was measured using dial calipers, and body mass determined using a 100 g Pesola spring balance.

Bats were identified to species using the length of forearm and ear. Juvenile, immature, and mature individuals whose dimensions overlapped between *C. brachyotis* and *C. sphinx* were identified by discriminant function analysis (Bumrungsri 2002). Fifty-nine immature and mature bats from a total of 482 individuals caught were in the size overlap zone between the two species and these together with 33 individuals with forearm lengths within 0.5 cm of the overlap zone were included in the analysis. A total of 318 juveniles caught were not easily separable into species on the basis of forearm and wing measurements (Hill & Thonglongya 1972, Kofron 1997), and 144 of these were subject to quadratic discriminant function analysis. Sex, age, and reproductive status were categorized following Racey (1988). Mature individuals were marked with a numbered ring carried on a ball-chain necklace and juveniles by nail varnish applied to toe claws or by tattooing the wings (Barclay & Bell 1988).

The diet of *C. brachyotis* and *C. sphinx* was established by identifying seeds, fruit pulp, pollen, and leaf stomata in the feces by comparing them with a reference collection. For feces containing no seeds or pollen, several alternative methods were applied to identify plant species such as odor and/or pulp morphology or chemical tests. These techniques were validated using identified rejected fruit parts below day roosts, and feces containing identifiable seeds. Some plants such as *Acronychia pedunculata* have a typical mint odor, and feces containing pulp of *Diospyros* sp. darkened rapidly when mixed with NaOH. This color change was not apparent with the pulp of other fruit species. Microscopic examination of feces containing *Chionanthus ramiflorus* reveals small red colloid droplets. Star-like spines occur in feces containing *Solanum* sp. Food plants were scored as presence–absence (Thomas 1988). The relative importance of food items in the diet was expressed as frequency of occurrence over all food items (McAney *et al.* 1991). Diet overlap between the bat species was established using Morisita's index of similarity (Krebs 1989). Interspecific diet variation was examined by χ^2 contingency tests. To investigate the relationship between the size of the bats and the size of the fruit consumed, 10–30 mature fruits from each species were weighed using a 10-g Pesola spring balance. Fruits were categorized into four size classes: <2, 2–5, 5–8, and >8 g (mean fresh weight).

The relative abundance of fruit bats in different habitats and seasons was inferred from the number captured per net hour each month (one net hour = one 6-m mist-net set for 1 h; Heideman & Heaney 1989). The relative degree of site fidelity was established through the recapture rate. Recaptured bats were arbitrarily defined as individuals that were recaptured more than 10 d after marking, following Heideman and Heaney (1989).

RESULTS

Four hundred and eighty two mature and immature bats were caught in 2267 net hours. Of these, 206 were immediately identified

as *C. brachyotis* and 184 as *C. sphinx*. Of those subject to discriminant function analysis, 54 were identified as *C. brachyotis*, and 42 as *C. sphinx*. Of the 318 juvenile bats caught, 99 were immediately identified as *C. brachyotis* and 75 as *C. sphinx*. Of those subject to quadratic discriminant function analysis, 89 were identified as *C. brachyotis* and 55 as *C. sphinx*. Mature *C. brachyotis* had a mean forearm length of ($\pm$ SD) 62.2 $\pm$ 1.8 mm (range 58.3–66.7 mm, $N =$ 131) and a mean weight of 34.79 $\pm$ 3.96 g, while mature *C. sphinx* had a mean forearm length of 68.7 $\pm$ 1.9 mm (range 64.13–73.2, $N =$ 119) and a mean weight of 46.89 $\pm$ 4.57 g. These two species account for 95 percent of 1460 captures, the other species being *Eonycteris speleae, Megaerops ecaudatus,* and *Macroglossus sobrinus.* The mean monthly capture rate was 58 $\pm$ 33 bats (range 6–144).

INTERSPECIFIC DIET VARIATION BETWEEN *C. BRACHYOTIS* AND *C. SPHINX*.—*Cynopterus brachyotis* and *C. sphinx* are mainly frugivorous, with fruit contributing more than 90 percent of their diet, and the remainder consisting of pollen and leaves. The diet of these sympatric *Cynopterus* differed significantly in both years, although both species shared most of the same set of food plants. In the first year, *C. brachyotis* ingested a higher proportion of *Muntingia calabura, Solanum torvum,* and *Chionanthus ramiflorus* but less *Solanum erianthum, Diospyros lanceifolia, Ziziphus mauritiana,* and *Ficus* than *C. sphinx* ($\chi^2 = 63.3$ df $= 10$, $P < 0.001$). Consistently, in the second year, *C. brachyotis* consumed a greater proportion of these three fruit species but also *Z. mauritiana,* whereas *C. sphinx* still favored *S. erianthum* and *Ficus* ($\chi^2 = 27.3$, df $= 10$, $P = 0.001$). Overall, *C. brachyotis* favored *M. calabura* and *S. torvum* whereas a higher proportion of *S. erianthum, D. lanceifolia, Ficus,* and *Z. mauritiana* were ingested by *C. sphinx* ($\chi^2 = 71.7$, df $= 11$, $P < 0.001$; Table 1). Note that *M. calabura, S. torvum, S. erianthum,* and *Z. mauritiana* are exotic to Thailand. Diet overlap between both fruit bats was high (Morisita's index: 0.89).

Cynoperus brachyotis ate a significantly greater proportion of fruits from successional plants while *C. sphinx* favored fruits from old-growth forest ($\chi^2 = 24.0$, df $= 2$, $P = 0.001$). The size of fruit eaten was positively related to the size of the mature bat. *Cynopterus brachyotis*, the smaller species (mean $\pm$ SD $= 34.66 \pm 4.15$ g, $N = 211$), feeds proportionally more on small fruit (<2 g) whereas *C. sphinx* (46.44 ± 4.28 g, $N = 176$) showed a significantly higher consumption of large (5–8 g) fruits ($\chi^2 = 9.2$, df $= 2$, $P = 0.01$; Fig. 1).

SPATIOTEMPORAL VARIATION IN HABITAT USE.—Although both species were present together in every month, a greater number of *C. brachyotis* were captured per net hour in early successional forest than *C. sphinx* in almost every month (Fig. 2A). In contrast, a greater number of *C. sphinx* were captured in selectively logged forest especially in dry seasons (Fig. 2B). In terms of temporal variation, the number of captured *C. sphinx* consistently increased in early successional forest during the mid-dry season (December–January in both years; Fig. 2A), although its relative abundance was lower in the second year compared to the first year. On the other hand, the number of captured *C. brachyotis* was higher from July to September (rainy season) in both years, possibly due to the addition of two cohorts of weaned bats to the population.

A significantly higher proportion of *C. brachyotis* was recaptured in early successional forest (0.374, $N = 438$) than *C. sphinx* (0.224, $N = 210$; χ^2 with Yates' correction $= 38.7$, df $= 1$, $P < 0.001$). However, in old-growth forest, the recapture rate of the former was significantly lower than the latter (0.033, $N = 30$ and 0.151, $N = 53$ respectively; χ^2 with Yates' correction $= 9.69$,

TABLE 1. *Frequency percentage of food plants in the feces of* C. brachyotis *and* C. sphinx *between April 1998 and March 2000.*

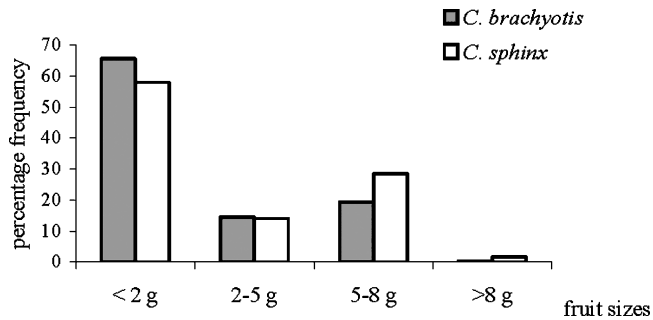| Taxa	Mean fresh weight (g)	Cynopterus brachyotis		Cynopterus sphinx	
		Apr 1998–March 1999 ($N = 416$)	Apr 1999–March 2000 ($N = 351$)	Apr 1998–March 1999 ($N = 206$)	Apr 1999–March 2000 ($N = 96$)
Muntingia calabura L.	1.59	33.65	24.75	16.02	13.54
Chionanthus ramiflorus Roxb.	5.17	8.89	19.37	4.37	29.17
Ziziphus mauritiana Lamb.	7.70	11.78	15.95	20.87	9.38
Acronychia pedunculata Miq.	1.50	8.89	7.69	9.71	6.25
Solanum torvum Sw.	1.51	9.62	6.55	2.91	1.04
Solanum erianthum D. Don	1.76	2.64	1.99	11.17	8.33
Solanum sp.	–	9.38	7.12	8.74	11.46
Diospyros lanceifolia Roxb.	5.44	6.25	3.13	12.14	2.08
Ficus spp.	–	4.81	6.84	8.74	8.33
Ceiba pentandra Gaertn.[a]	–	1.20	1.42	1.46	3.13
Leaf (stomata)	–	2.40	2.28	1.46	3.13
Others (*e.g.*, guava)	>8	0.48	2.85	2.43	6.25

[a] Pollen.

FIGURE 1. The percentage frequency of fruits in each size classes in the diet of *C. brachyotis* and *C. sphinx*. This result is based on 731 and 282 feces for *C. brachyotis* and *C. sphinx*, respectively.

df = 1, $P < 0.001$; Fig. 3). Sexual variation in recapture rate was found only in *C. sphinx*. Males had a significantly higher rate of recapture (0.30, $N = 126$) in early successional forest than females (0.11, $N = 84$; χ^2 with Yates' correction = 7.67, df = 1, $P = 0.004$; Fig. 3).

DISCUSSION

Although recent molecular analysis has revealed that *C. brachyotis* is a complex of distinct lineages, specimens from Thailand are monophyletic within the lineage characterized by Campbell *et al.* (2004). In addition, *C. sphinx* haplotypes formed a monophyletic group within the *brachyotis* species. Campbell *et al.* (2004) also point out that the resolution of taxonomic issues in the genus *Cynopterus* awaits combined analysis of morphometric characters and molecular data. Our own morphometric analysis (Bumrungsri & Racey 2005) confirms that the present study compared two distinct taxonomic groups as identified by Campbell *et al.* (2004).

DIET VARIATION BETWEEN *C.BRACHYOTIS* AND *C. SPHINX*.—Although *C. brachyotis* and *C. sphinx* consume the same set of fruit species, it is clear that the smaller species, *C. brachyotis*, feeds more on smaller fruits than the larger species, *C. sphinx*. Size is one of the main factors by which animals such as fruit bats select their food, because of their behavior in carrying fruit to feeding roosts for consumption (Bonaccorso 1979). Among sympatric *Carollia* species, the proportion of large fruits in the diet also increases with body size (Fleming 1991). Similarly, there was a significant correlation between body mass and the average fruit mass of species included in the diet of Palaeotropical frugivorous bats in peninsular Malaysia (Hodgkison 2001). Resource partitioning by food size has also been observed in several Neotropical frugivorous bat communities (Heithaus *et al.* 1975, Bonaccorso 1979, Fleming 1986, Kalko *et al.* 1996), although not among sympatric *Sturnira* in the Andes which are instead separated by elevation (Giannini 1999). In addition to fruit size, the size of the fruit crop, which negatively correlates with the duration of its availability, was also suggested as a factor influencing resource partitioning within the pteropodid bat community in primary lowland

forest in Malaysia (Hodgkison 2001). Large crop size of canopy trees that fruit for short periods (*i.e.*, "big bang" crops) supported species that consistently form large aggregations, whereas small crop sizes of subcanopy plants that are available for more extended time periods (*i.e.*, "steady state" crops) were exploited exclusively by several solitary foraging frugivorous bats (Hodgkison 2001, Hodgkison *et al.* 2004b).

HABITAT USE VARIATION BETWEEN *C. BRACHYOTIS* AND *C. SPHINX*.— Although it has been suggested that habitat within which bats are caught does not necessarily coincide with their feeding habitat (Heithaus *et al.* 1975, Thomas 1988), the consistency of diet, capture rate, and recapture percentage in the present study suggests significant differences in habitat use between sympatric *Cynopterus*. In general, *C. brachyotis* used successional forest more intensively than *C. sphinx* and the reverse was the case in old-growth dry evergreen forest. This is consistent with Fleming's (1991) suggestion that, in Neotropical forests, the smaller species of *Carollia* were more common in successional habitats and were more sedentary than the larger ones. Similarly, the capture rate of *C. brachyotis* in the Philippines was much higher in orchard/secondary forest than in lowland primary forest (Heaney *et al.* 1989, Heideman & Heaney 1989). Likewise, in an African hornbill community, the smaller species *Certogymna fistulator* has the higher density in secondary forest compared to primary forest, and is more sedentary in such habitat than the larger congeners (Whitney & Smith 1998).

Wing morphology constrains habitat use and plays a considerable role in food partitioning in Old World fruit bat communities (McKenzie *et al.* 1995, Hodgkison *et al.* 2004a). *Cynopterus brachyotis* has a slightly higher aspect ratio but lower wing loading than *C. sphinx* and an almost identical tip shape index (Norberg & Rayner 1987). Wing loading and tip shape index are important to Megachiroptera as they relate to the flight speed and the ability to fly in cluttered habitats (McKenzie *et al.* 1995). These combined features suggest slower flying and lower load-carrying ability in *C. brachyotis* than in *C. sphinx*, although both species were capable of flying within vegetation (Norberg & Rayner 1987, S. Bumrungsri, pers. obs.). Compared to old-growth forest in the present study area, fruit is more common and was always available in early successional forest. This is partly due to the presence of fruit trees in orchard remnants, patches of *Muntingia calabura* and planted trees near the sanctuary's headquarters. On the other hand, bat-dispersed fruits in old-growth forest tend to have high seasonal fluctuations in abundance, and are occasionally sparsely available. DeWalt *et al.* (2003) and Levey (1988) also reported that understory fleshy fruit availability was highest in young secondary forest, but fruit size tends to be larger in primary forest (Hamann & Curio 1998). Thus, larger bat species like *C. sphinx* should theoretically forage more efficiently than the smaller species in primary forest habitats as the cost of searching and transportation of food is high (Fleming 1991). This is consistent with the findings of Heithaus *et al.* (1975) who suggested that small frugivore species utilize resources which are more consistently available but larger species use those which are patchy in time and space.
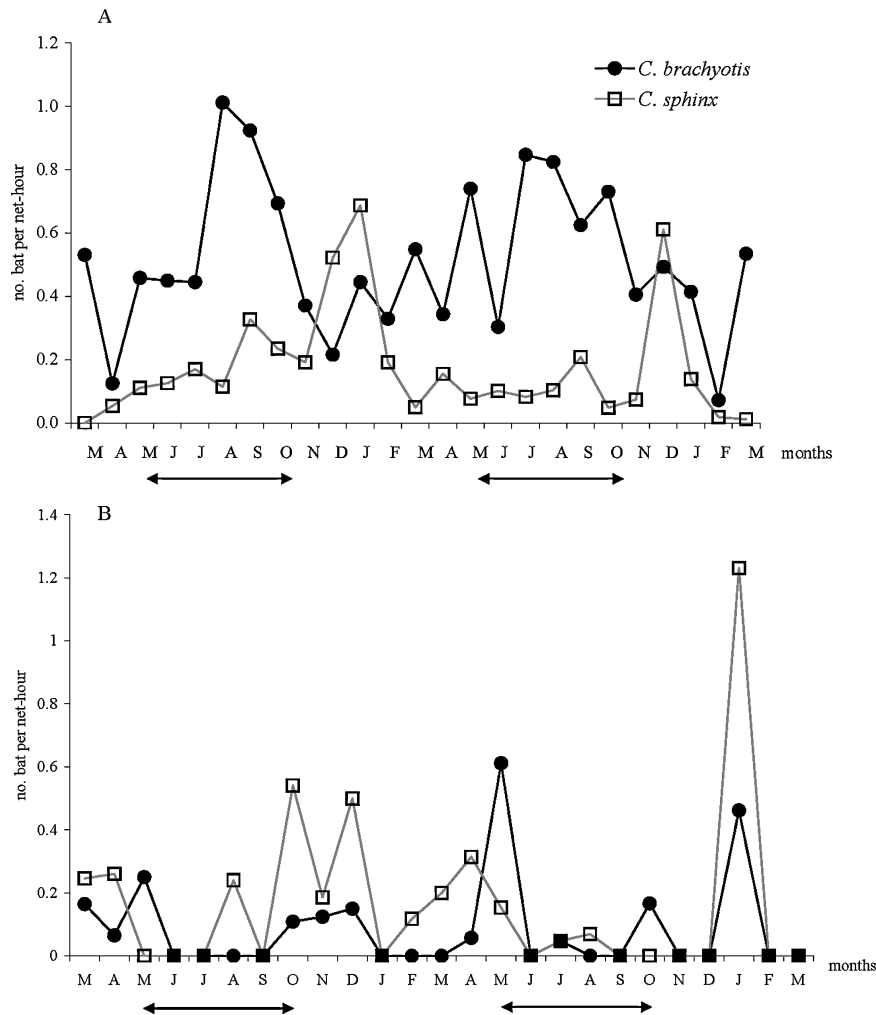
FIGURE 2.   (A) Monthly capture rate of *C. brachyotis* ($N = 995$) and *C. sphinx* ($N = 313$) in early successional forest habitats between March 1998 and March 2000 ($N = 1946$ net hour; ↔ = rainy season). (B) Monthly capture rate of *C. brachyotis* ($N = 40$) and *C. sphinx* ($N = 71$) in old-growth forest habitats between March 1998 and March 2000 ($N = 321$ net hour).

The presence/absence of partitioning in vertical space of both *Cynopterus* species cannot be assumed in the absence of direct study. *Cynopterus brachyotis* was mostly captured at ground level or in sub-canopy level in Malaysia (Francis 1994, Zubaid 1994, Hodgkison 2001, Hodgkison *et al.* 2004a). However, since bats with smaller body mass and lower wing loading appear to have higher maneuverability (Norberg & Rayner 1987), *C. brachyotis* should be more capable of foraging in the more cluttered habitats of the lower forest story than *C. sphinx*. Subtle differences in flight morphology may be ecologically significant in the fine-scale vertical partitioning of structurally complex habitats. For example, *Balionycteris maculata* was unique among other subcanopy frugivorous bats in peninsular Malaysia in that it was the only species that was strongly associated with dense vegetation clutter (Hodgkison 2001). For further studies on partitioning in vertical space between these species, canopy netting is recommended, as most frugivorous bats in this region also forage at canopy level (Francis 1994, Hodgkison *et al.* 2004a)

Alternatively, more intensive use of early successional forest by *C. brachyotis* and old-growth forest habitat by *C. sphinx* can be explained in terms of fasting endurance (reviewed by Millar & Hickling 1990). In this hypothesis, energy reserves last longer in larger animals. When they encounter resource shortage, and all other factors are equal, the smaller animals will deplete their energy reserves first, and will be more susceptible to starvation. The larger species will cope better with fasting, the energy loss of which can be recouped later. On the other hand, smaller frugivores will be better adapted to a generally low food supply that is always available (Millar & Hickling 1990). Furthermore, this reason presumably explains the restriction of *C. brachyotis* in India to tropical evergreen forest whereas *C. sphinx* is found largely in dry deciduous forest (Storz *et al.* 2001).

So far as the temporal variation in habitat use is concerned, *C. sphinx* consistently increased its relative abundance in early successional forest in the mid-dry season in both years. Female bats were
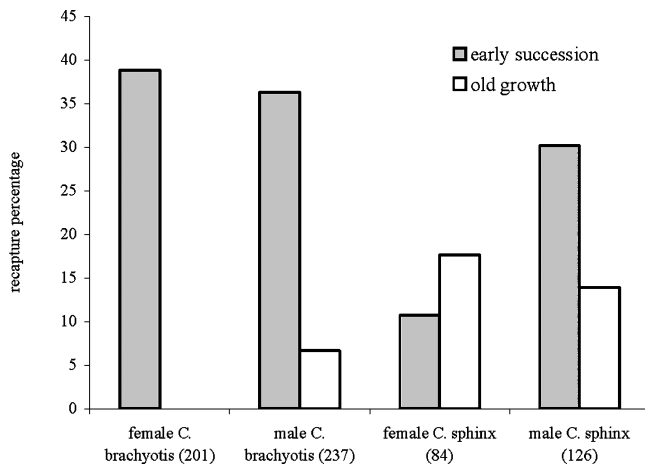
FIGURE 3.   The recapture percentage of each sex in *C. brachyotis* and *C. sphinx* in early successional forest and old-growth forest habitats. The number of marked individuals in each habitat is in parentheses.

mostly responsible for this phenomenon, since male *C. sphinx* are more faithful to early successional forest. The shifting of females from old-growth forest habitats to early successional forest may be the result of food scarcity in the former and/or the greater availability of preferred food in the latter. *Ziziphus mauritiana*, a favorite fruit of *C. sphinx*, was most abundant in early successional forest in the mid-dry season. Similar tracking of fruit resources, such as occurred in female *C. sphinx*, was also reported in African hornbills and Neotropical frugivorous birds, and the shift of many resident frugivores from primary forest to secondary forest corresponds with increased fruit availability (Levey 1988, Whitney & Smith 1998). In some frugivorous bat communities, some species from mature forest move seasonally to other habitats (Thomas 1982, Bonaccorso & Humphrey 1984).

The relative foraging range can be inferred from the recapture percentage (Heithaus *et al.* 1975; Fleming 1988, 1991). Higher recapture rates suggest a relatively smaller foraging range at least corresponding to the area in which mist nets were set. In general, *C. brachyotis* probably has a smaller home range size than *C. sphinx*. Similarly, based on the recapture data, the average nightly foraging movement of the subcanopy frugivorous bats in peninsular Malaysia increases in relation to body mass (Hodgkison 2001). A positive relationship between bat size and home range size was also indicated in Neotropical frugivorous bat communities (Heithaus *et al.* 1975). Using radio tracking techniques, Funakoshi & Zubaid (1997) also showed that the larger *C. horsfieldi* had about double the home range size of the smaller *C. brachyotis*. Sexual variation in home range size of *C. sphinx* could be expected from its recapture rate in the present study. Previous studies showed that in several fruit bat species, males travel shorter distance than females to forage (Heideman & Heaney 1989, Nair *et al.* 1999, Winkelman 2000).

In conclusion, it is clear that *C. brachyotis* and *C. sphinx* partition their resources by means of diet differences and habitat use.

Further simultaneous investigation of foraging behavior using radio tracking especially during critical periods of food shortage of both frugivorous bats could shed further light on how they partition these resources. In addition the extent to which habitat selection differs between sexes in *C. sphinx* warrants further investigation. From a conservation perspective, both fruit bat species act as "mobile links" between early successional forest and old-growth forest, particularly female *C. sphinx*. Fruit bats are well recognized as effective seed dispersers in tropical forest since they can retain seeds for many hours in their gut, without affecting their viability (Shilton *et al.* 1999). Seedlings of pioneer bat-dispersed plants were common in open areas and along forest trails in the study area, indicating that the fruit bat population plays an important role in the restoration of disturbed forest.

ACKNOWLEDGMENTS

LITERATURE CITED

ARLETTAZ, R. 1999. Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. J. Anim. Ecol. 68: 460–471.

ARITA, H. T. 1997. Species composition and morphological structure of the bat fauna of Yucatan, Mexico. J. Anim. Ecol. 66: 83–97

BATES, P., AND D. L. HARRISON. 1997. Bats of Indian Subcontinent, p. 258, Harrison Zoological Museum, London. UK.

BARCLAY, R. M. R., AND G. P. BELL 1988. Marking and observational techniques. *In* T. H. Kunz (Ed.). Ecological and behavioural methods for the study of bats, pp. 59–76. Smithsonian Institutional Press, Washington.

BEGON, M., J. L. HARPER, AND TOWNSEND. 1996. Ecology: Individuals, populations and communities. Blackwells Science, Oxford, UK.

BHAT, H. R. 1994. Observations on the food and feeding behavior of *Cynopterus sphinx* Vahl (Chiroptera, Pteropodidae) at Pune, India. Mammalia 53: 363–370.

BONACCORSO, F. J. 1979. Foraging and reproductive ecology in a Panamian bat community. Bull. Florida State Mus. Biol. Sci. 24: 359–408.

BONACCORSO, F. J., AND S. R. HUMPHREY. 1984. Fruit bat niche dynamics: their role in maintaining tropical forest diversity. *In* A. C. Chadwick and S. L. Sutton (Eds.). Tropical rain forest: The Leeds symposium, pp. 169–183. Philosophical and Literary Society, Leeds, UK.

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 Thesis, University of Aberdeen, UK.

BUMRUNGSRI, S., AND P. A. RACEY. 2005. Field discrimination between lesser short-nosed fruit bat (*Cynopteris brachyotis* Muller, 1838) and greater short-nosed fruit bat (*C. sphinx* Vahl 1797) (Chiroptera: Pteropodidae) in Southeast Thailand. Nat. Hist. Bull. Siam Soc. 53: 111–121.

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: 764–787.

CORBET, G., AND J. E. HILL. 1992. The mammals of the Indomalayan region: A systematic review, p. 488. Oxford University Press, Oxford. UK.

DEWALT, S. J., S. K. MALIAKAL, AND J. S. DENSLOW. 2003. Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife. For. Ecol. Manage. 182: 139–151.

FLEMING, T. H. 1986. Opportunism versus specialization: the evolution of feeding strategies in frugivorous bats. *In* A. Estrada and T. H. Fleming (eds.). Frugivores and seed dispersal, pp. 105–117. Dr. W. Junk Publishers, Dordrecht.

FLEMING, T. H. 1988. The short-tailed fruit bat: A study in plant-animals interactions, p. 365. University of Chicago Press, Chicago, Illinois.

FLEMING, T. H. 1991. The relationship between body size, diet and habitat use in frugivorous bats, genus *Carollia* (Phyllostomidae). J. Mammal. 72: 493–501.

FRANCIS, C. M. 1994. Vertical stratification of fruit bats (Pteropodidae) on lowland dipterocarp rainforest in Malaysia. J. Trop. Ecol. 10: 523–530.

FINDLEY, J. 1993. Bats, a community perspective. Cambridge University Press, Cambridge, UK.

FUNAKOSHI, K., AND A. ZUBAID. 1997. Behavioural and reproductive ecology of the dog faced fruit bats, *Cynopterus brachyotis* and *C. horsefieldi*, in a Malaysian rainforest. Mammal Study 22: 95–108.

GASTON, K. J. AND T. M. BLACKBURN. 1996. Range size-body size relationships: evidence of scale dependence. Oikos 75: 479–485.

GIANNINI, N. P. 1999. Selection of diet and elevation by sympatric species of *Sturnira* in an Andean rainforest. J. Mammal. 80: 1186–1195.

HAMANN, A., AND E. CURIO. 1998. Interactions among frugivores and fleshy fruit trees in a Philippine submontane rainforest. Conservation Biology 13: 766–773.

HEANEY, L. R., P. D. HEIDEMAN, E. A. RICKART, R. C. B. UTZURRUM, AND J. S. H. KLOMPEN. 1989. Elevation zonation of animals in the central Phillipines. J. Trop. Ecol. 5: 259–280.

HEIDEMAN, P. D., AND L. R. HEANEY. 1989. Population biology and estimates of abundance of fruit bats (Pteropodidae) in Philippine submontane rainforest. J. Zool. (Lond.) 218: 565–586.

HEITHAUS, E. R., T. H. FLEMING, AND P. A. OPLER. 1975. Foraging patterns and resources utilization in seven species of bats in a seasonal tropical forest. Ecology 56: 841–854.

HILL, J. E., AND K. THONGLONGYA. 1972. Bats from Thailand and Cambodia. Bull. Br. Mus. (Nat. Hist.) 22: 171–196.

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, Aberdeen, Scotland.

HODGKISON, R., S. T. BALDING, A. ZUBAID, AND T. H. KUNZ. 2004a. Habitat structure, wing morphology, and the vertical stratification of Malaysisan fruit bats (Megachiroptera: Pteropodidae). J. Trop. Ecol. 20: 667–673.

HODGKISON, R., S. T. BALDING, A. ZUBAID, AND T. H. KUNZ. 2004b. 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 35: 522–533.

HUTCHINSON, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? Am. Nat. 93: 145–159.

KALKO, E. K. V. 1998. Organisation and diversity of tropical bat communities through space and time. Zoology 101: 281–297.

KALKO, E. K. V., E. A. HERRE, AND C. O. HANDLEY. 1996. Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. J. Biogeogr. 23: 565–576.

KITCHENER, D. J., A. GUNNELL, AND MAHARADATUNKAMSI. 1990. Aspects of the feeding biology of fruit bats (Pteropodidae) on Lombok Island, Nusa Tenggara, Indonesia. Mammalia 54: 561–578.

KOFRON, C. P. 1997. Reproduction of two species of fruit bats (*Cynopterus*) in Borneo. J. Zool. (Lond.) 243: 485–506.

KREBS, C. J. 1989. Ecological methodology, p. 654. Harper Collins Publisher, New York.

LEKAGUL, B., AND J. R. MCNEELY. 1977. The mammals of Thailand. Association for the Conservation of Wildlife. Bangkok, Thailand.

LEVEY, D. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecolog. Monogr. 58: 251–269.

MARINHO-FILHO, J. A. 1991. The coexistence of two frugivorous bat species and the phenology of their food plants in Brazil. J. Trop. Ecol. 7: 59–67.

MCANEY, C. M., C. B. SHIEL, C. M. SULLIVAN, AND J. S. FAIRLEY. 1991. The analysis of bats droppings, p. 48. Mammal Society, London.

MCKENZIE, N. L., A. C. GUNNELL, M. YANI, AND M. R. WILLIAMS. 1995. Correspondence between flight morphology and foraging ecology in some Palaeotropical bats. Austr. J. Zool. 43: 241–257.

MILLAR, J. S., AND G. J. HICKLING. 1990. Fasting endurance and the evolution of mammalian body size. Funct. Ecol. 4: 5–12.

NAIR, N. G., V. ELANGOVAN, K. SRIPATHI, G. MARIMUTHU, AND R. SUBBARAJ. 1999. Foraging behaviour of the Indian short-nosed fruit bat, *Cynopterus sphinx*. Z. Saugetierkd. 64: 187–191.

NORBERG, U. M., AND J. M. V. RAYNER. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. Philos. Trans. Zool. Soc. Lond. B 316: 335–427.

PYRON, M. 1999. Relationship between geographical range size, local abundance, and habitat breadth in North American suckers and sunfishes. J. Biogeogr. 26: 549–558.

RACEY, P. A. 1988. Reproductive assessment in bats. *In* T. H. Kunz (ed.). Ecological and behavioural methods for the study of bats, pp. 31–45. Smithsonian Institution Press, Washington, D. C.

RICKLEFS, R. E. 1990. Ecology, 3rd edition, Freeman, New York.

SAUNDERS, M. B., AND R. M. R. BARCLAY. 1992. Ecomorphology of insectivorous bats: A test of predictions using two morphologically similar species. Ecology 73: 1335–1345.

SCHMITT, L. H., D. J. KITCHENER, AND R. A. HOWE. 1995. A genetic perspective of mammalian variation and evolution in the Indonesian Archipelago: Biogeographic correlates in the fruit bat genus *Cynopterus*. Evolution 49: 399–412.

SHILTON, L. A., J. D. ALTRINGHAM, S. G. COMPTON AND R. J. WHITTAKER 1999. Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. Proc. R. Soc. Lond. B 266: 219–223.

STORZ, J. F., AND T. H. KUNZ. 1999. *Cynopterus sphinx*. Mammalian Species 613: 1–8.

STORZ, J. F., J. BALASINGH, H. R. BHAT, P. T. NATHAN, D. P. S. DOSS, A. A. PRAKASH, AND T. H. KUNZ. 2001. Clinal variation in body size and sexual dimorphism in an Indian fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae). Biol. J. Linn. Soc. 72: 17–31.

TAN, K. H., A. ZUBAID, AND T. H. KUNZ. 1998. Food habits of *Cynopterus brachyotis* (Muller) (Chiroptera: Pteropodidae) in peninsular Malaysia. J. Trop. Ecol. 14: 299–307.

THOMAS, D. W. 1982. The ecology of an African savanna fruit bat community: resource partitioning and seed dispersal. PhD Dissertation. University of Aberdeen, UK.

THOMAS, D. W. 1988. Analysis of diets of plant-visiting bats. *In* T. H. Kunz (ed.) Ecological and behavioural methods for the study of bats, pp. 211–220. Smithsonian Institution Press, Washington, D. C.

WHITNEY, K. D., AND T. B. SMITH. 1998. Habitat use and resource tracking by African *Certogymna* hornbills: Implications for seed dispersal and forest conservation. Anim. Conserv. 1: 107–117.

WICH, S. A., AND C. P. VAN SCHAIK. 2000. The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malaysia. J. Trop. Ecol. 16: 563–577.

WILLIG, M. R., AND M. P. MOULTON. 1989. The role of stochastic and deterministic processes in structuring Neotropical bat communities. J. Mammal. 70: 323–329.

WINKELMAN, J. R., F. J. BONACCORSO, AND T. L. STRICKLER. 2000. Home range of the southern blossom bat, *Syconycteris australis*, in Papua New Guinea. J. Mammal. 81: 408–414.

WRIGHT, S. J., C. CARRASCO, O. CALDERON, AND S. PATTON. 1999. The El Niño Southern Oscillation variable fruit production, and famine in a tropical forest. Ecology 80: 1632–1647.

ZUBAID, A. 1994. Vertical stratification of pteropodid bats in a Malysian lowland forest. Mammalia 58: 309–311.