

## MORPHOLOGICAL AND ECOLOGICAL CORRELATES OF COEXISTENCE IN MALAYSIAN FRUIT BATS (CHIROPTERA: PTEROPODIDAE)

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Niche theory predicts that coexisting species should differ ecologically, morphologically, or behaviorally in ways that minimize competition. We used an ecomorphological approach to determine how coexisting species in the Old World fruit bat genus, *Cynopterus*, assort in morphological and ecological space. The study was conducted in peninsular Malaysia where 4 species of *Cynopterus* are broadly sympatric. Interspecific separation in resource use was estimated along 3 main axes: habitat, based on abundance across a habitat gradient at 2 sites; trophic niche, inferred from a suite of cranial and postcranial characters; and locomotory behavior and efficiency, inferred from wing morphology. Habitat associations, overall size, and the size and shape of the trophic apparatus were all important in separating 2 or more species, whereas interspecific differences in wing morphology were minor. In combination, the results of this study suggest that relatively minor separation among *Cynopterus* species pairs along single axes of resource use is sufficient to counteract overlap on other axes, and permit the coexistence of potential competitors.

Key words: body size, competition, *Cynopterus*, ecomorphology, frugivore, resource partitioning, trophic niche

How much overlap in resource use can ecologically similar species tolerate in sympatry? This question underlies a large body of theoretical (Abrams and Holt 2002; MacArthur and Levins 1967; May and MacArthur 1972), empirical (Hutchinson 1959; Schluter and McPhail 1992; Schoener 1968, 1984) and experimental (Bolnick 2004; Connell 1961; Grant 1972; Pfennig and Murphy 2002) studies in evolution and ecology. Although causative relationships between present-day patterns of resource partitioning and past competitive interactions are difficult to establish with certainty (Connell 1980; Simberloff and Boecklen 1981), identifying the characteristics that permit coexistence among ecologically similar species is an essential 1st step toward understanding the evolutionary processes that have shaped their differences. The high taxonomic and trophic diversity of bats, combined with the constraints on body size imposed by flight, make them a particularly interesting and challenging group in which to address this goal. For example, the remarkably high species richness and close species packing recorded from insectivorous bat assemblages in both the Old

and New World tropics (Findley and Black 1983; Kingston et al. 2003; Simmons and Voss 1998) suggests that subjectively minor, and in some cases cryptic (Kingston et al. 2001), differences in morphology and echolocation call frequency are sufficient to permit the coexistence of more than 50 species at a single site.

Ecomorphological analyses focusing on characters important in trophic and locomotor functions have proved particularly useful in defining the ecological relevance of morphological differences among bat species. A strong relationship between wing morphology, habitat structure, and foraging strategy (Hodgkison et al. 2004a; McKenzie et al. 1995; O'Shea and Vaughan 1980), and between trophic characters and dietary niche (Dumont 1997; Findley and Black 1983; Freeman 1981, 1995) has been demonstrated in multiple taxonomic groups and local assemblages. Recent functional analyses of frugivorous species also have emphasized the importance of the relationship between body size, bite force, gape width, and the physical properties of fruits (Aguirre et al. 2003; Dumont and Herrel 2003; Dumont and O'Neal 2004).

The phenotypic correlates of resource partitioning have been widely studied in insectivorous bats in the Old and New World tropics, and in the plant-visiting members of the New World family, Phyllostomidae (Aguirre et al. 2002; Fleming 1991; Heller and von Helversen 1989; Kalko et al. 1996; Kingston

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et al. 2000). In contrast, few studies have investigated ecomorphological relationships among paleotropical fruit bats (Pteropodidae—Dumont and O'Neal 2004; Hodgkison et al. 2004a; McKenzie et al. 1995). Fleming et al. (1987) proposed that the diets of frugivorous bats in the Old World tropics may be less specialized and may exhibit greater interspecific overlap than those of neotropical frugivores. This suggestion is supported by the more generalized cranial morphology of pteropodid fruit bats relative to their phyllostomid counterparts (Dumont 2004), and by dietary comparisons (Utzurum 1995; Willig et al. 1993). However, the extent of overlap in trophic characters has rarely been examined in coexisting paleotropical species (Kitchener et al. 1990).

Although the assumption that 2 or more species cannot coexist stably on the same limiting resource is axiomatic to competition theory (Gause 1934; Lotka 1925; Volterra 1926), resource limitation is difficult to establish in practice. No study to date has demonstrated present-day or historic resource limitation in Old World fruit bats. However, 2 lines of indirect evidence suggest that dietary resource limitation may have played an important role in the morphological and ecological diversification of pteropodid bats in Southeast Asia. First, forest fruits are generally less abundant in the Paleotropics than in the Neotropics, and more widely dispersed and patchily distributed in space and time (Fleming et al. 1987). This effect is amplified by the supra-annual fruiting cycles of the dipterocarp species that dominate forests in Malaysia and parts of Indonesia (Appanah 1985; Janzen 1974). Second, the much greater range in within-assembly body size with fewer species per size class than that observed in plant-visiting phyllostomids suggests greater interspecific variance in niche space, in terms of differences in foraging distances and resource partitioning by fruit size (Heideman and Heaney 1989; Kalko et al. 1996).

In this study, we combine analysis of ecological and morphological data to explore mechanisms of coexistence among 4 nominal species in the Old World fruit bat genus, *Cynopterus*. Although 7 *Cynopterus* species are currently recognized throughout the range of the genus in India and Southeast Asia (Simmons 2005), recent phylogenetic analysis revealed 6 divergent mitochondrial lineages within a single widespread species, *C. brachyotis*, suggesting that several additional species remain to be described (Campbell et al. 2004). Two evolutionary relationships inferred in this study are important to the current analysis. First, in peninsular Malaysia and in parts of Indonesia, *C. brachyotis* is split into 2 mitochondrial lineages that segregate across habitat types and can be distinguished in the field by minor differences in overall body size and adult pelage coloration (Campbell et al. 2004). Concordance between mitochondrial, nuclear, and ecotypic differentiation, and substantial geographic range overlap, strongly suggests that species status is warranted for both lineages (Campbell et al. 2006a, 2006b, 2006c). Pending taxonomic revision, we refer to the smaller forest-associated species as *C. brachyotis* Forest, and to the slightly larger open habitat species as *C. brachyotis* Sunda. Second, based on mitochondrial DNA, the largest of the Malaysian species, *C.*

*horsfieldii*, is recently derived from the smallest, *C. brachyotis* Forest. Low genetic divergence between *C. horsfieldii* and *C. brachyotis* Forest indicates a relatively recent speciation event; based on both mitochondrial and nuclear markers, the genetic distance between these 2 species is approximately half that of other interspecific comparisons in the *C. brachyotis* complex (Campbell et al. 2004, 2006b).

Our study was conducted in peninsular Malaysia where, collectively, *C. brachyotis* Forest, *C. brachyotis* Sunda, *C. sphinx*, and *C. horsfieldii* account for the majority of captures of fruit bats in habitats ranging from urban parks to primary rain forest (Francis 1990, 1994; Hodgkison et al. 2004b; Lim 1966; Tan et al. 1997). Examination of available data indicates that *Cynopterus* species occupy a broad dietary niche that includes fruit, floral parts, nectar, pollen, and leaves (Bhat 1994; Bumrungsri 2002; Funakoshi and Zubaid 1997; Lim 1970; Marimuthu et al. 1998; Tan et al. 1998).

From smallest to largest, *C. brachyotis* Forest, *C. brachyotis* Sunda, *C. sphinx*, and *C. horsfieldii* describe a continuum in overall body size that is rare in assemblages of Southeast Asian fruit bats (Heideman and Heaney 1989). In peninsular Malaysia, only 1 other sympatric frugivorous bat (*Penthetor lucasi*) falls within the size range of *Cynopterus* (Corbet and Hill 1992). Given that body size is usually strongly correlated with diet in frugivorous bats (Bumrungsri 2002; Heithaus et al. 1975; Wendeln et al. 2000; but see Utzurum 1995), these observations suggest that the potential for overlap in dietary resource use is high within *Cynopterus*.

Niche theory predicts that, if resources are limited, stable coexistence of potentially competing species should be facilitated by resource partitioning (MacArthur and Levins 1967; Schoener 1974). We tested for evidence of resource partitioning in Malaysian *Cynopterus* species, focusing on 3 main axes of niche space that are relevant to foraging and diet. First, we assessed the degree of local spatial overlap among the 4 species based on relative abundance across habitat types. Second, we used a suite of morphological characters that summarize body size and trophic adaptation to infer the extent of trophic separation among the 4 species. Third, we tested for interspecific differences in wing morphology. In bats, wing shape (aspect ratio) and the ratio of body mass to wing area (wing loading) are tightly linked to the energetic efficiency of flight and to relative maneuverability in cluttered airspace such as forest understory (Norberg and Rayner 1987). Thus, wing morphology describes both the functionality of a given phenotype across structurally different habitats, and the potential for spatial partitioning of resources within habitats.

## MATERIALS AND METHODS

*Study sites.*—Fieldwork was conducted in peninsular Malaysia between June 2002 and January 2004 at 2 main sites: Perlis State Park (Perlis State, 06°42–39'N, 100°11'E) and Taiping (Perak State, 04°50–51'N, 100°45–46'E). Both sites feature tracts of partially logged primary forest, bordered by secondary growth, small fruit orchards, and human settlements. Perlis State Park (50 km<sup>2</sup>) is characterized by

**TABLE 1.**—Sampling effort and total captures for *Cynopterus brachyotis* Forest (CbF), *C. brachyotis* Sunda (CbS), *C. horsfieldii* (Ch), and *C. sphinx* (Cs), by habitat and locality. Net hours = hours × number of nets.

Habitat	Locality	Nights	Hours	Net hours	CbF	CbS	Ch	Cs
Forest	Perlis	21	85	255	123	0	40	29
	Taiping	22	116	267	58	0	19	12
Ecotone	Perlis	18	83	249	46	0	79	217
	Taiping	25	142	301	12	11	104	167
Disturbed	Perlis	9	26	77	0	64	30	95
	Taiping	18	71	213	0	75	32	198
Totals		113	523	1,362	239	150	304	718

limestone hill forest (Latiff et al. 2001). Villages and small agricultural holdings lie along the park's boundaries. At the Taiping site, Larut Hills Forest Reserve comprises 72 km<sup>2</sup> of mixed lowland dipterocarp forest (Putz 1978). The town of Taiping is bordered by a series of landscaped parks planted with ornamental palms and shrubs, giving way to fruit orchards along the forest edge. Our study areas at both sites encompassed 3 main categories of habitat type, defined as follows: forest (forest containing old growth, ≥0.5 km from the nearest edge), ecotone (orchards or young secondary forest, ≤1.0 km from mature forest edge), and disturbed (cultivated or landscaped habitat containing human structures, ≥2.0 km from a forest edge). The Taiping study area was approximately 10 km<sup>2</sup>. In Perlis, the approximately 8-km<sup>2</sup> forest–ecotone study area within Perlis State Park was separated from the disturbed site outside the park boundaries by 15 km of open agricultural habitat dominated by rice cultivation. The disturbed site (Bukit Jernih, 06°33'N, 100°15'E) was approximately 3 km<sup>2</sup> and featured a small rural settlement with widely dispersed houses whose yards contained fruit trees and stands of coconut palms.

**Sampling and species identification.**—Bats were captured in 9-m mist nets (Avinet Inc., New York) set at ground level. Sampling effort at each site ranged from 77 to 301 net hours per habitat type (Table 1). Sampling only in the understory most likely reduced our overall capture rate for *Cynopterus* in forest habitats (e.g., Francis 1990), and may have created a downward bias in estimates of intraspecific abundance for forest relative to open habitats (see Table 1 for species capture totals). However, we have no reason to believe that this approach biased the interspecific capture rate: a study of vertical stratification in Malaysian fruit bats found that capture rates for *C. brachyotis* and *C. horsfieldii* did not differ significantly with respect to net height (Hodgkison et al. 2004a).

All captured *Cynopterus* were marked with individually numbered 2.9-mm Monel forearm bands (Lambournes Ltd., Birmingham, United Kingdom). Lengths of forearm, tibia, and ear were measured using dial calipers (±0.1 mm) and body mass was measured to the nearest 0.5 g using 60- and 100-g Pesola scales (Pesola AG, Baar, Switzerland). Adults were distinguished from juveniles by closure of the phalangeal epiphyses (Anthony 1988). The right wings of live adult males

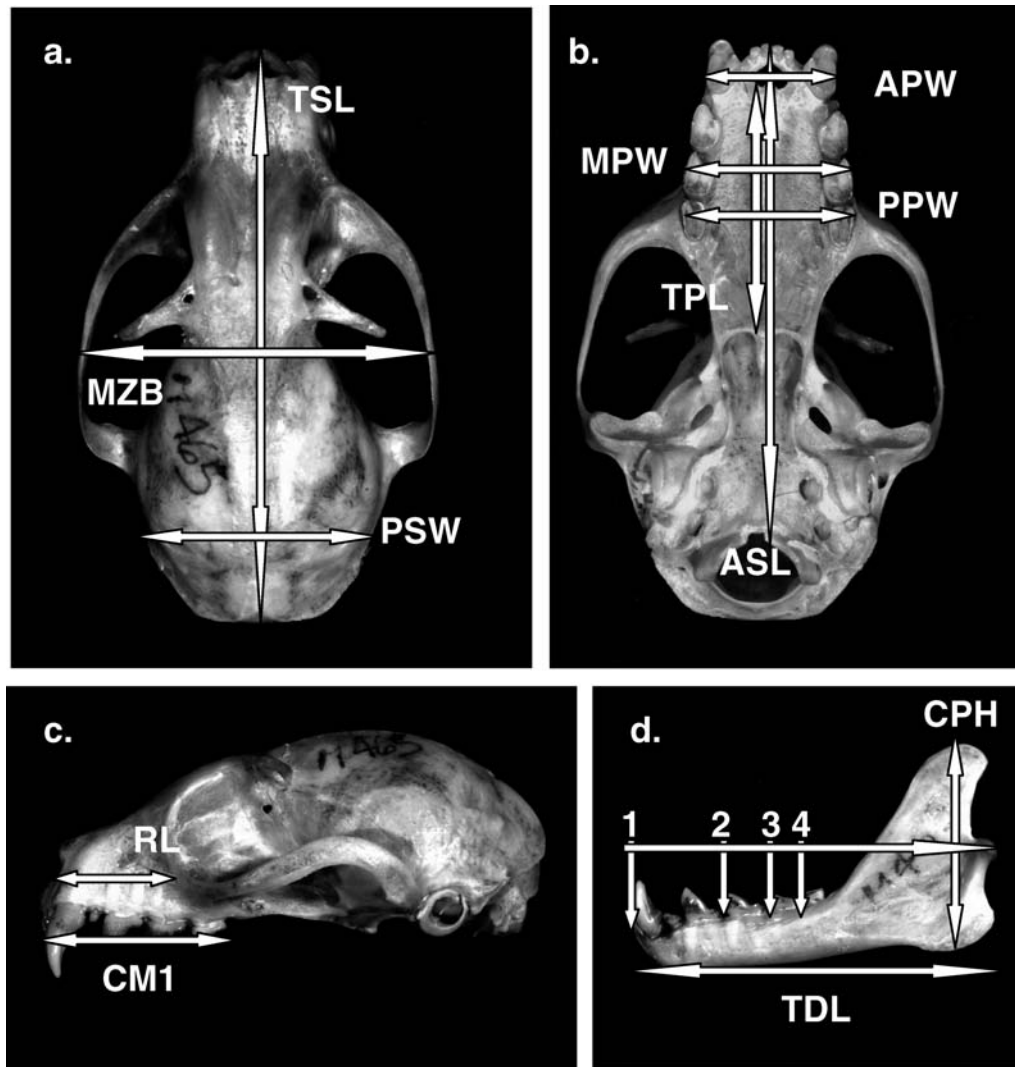
and nonpregnant females were traced with the bat positioned ventrally on a piece of graph paper, with the wing fully extended so that the leading edge of the plagiopatagium formed a straight line from shoulder to thumb (Norberg and Rayner 1987). Bats retained for analysis of craniodental characters were sacrificed using halothane inhalation. All procedures involving live animals were in accordance with guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). Additional Malaysian specimens were obtained on loan from the collections of the Malaysian Department of Wildlife and National Parks. Locality data for all specimens are provided in Appendix I.

Despite interspecific overlap in body size, most *Cynopterus* captured were readily identified to species in the field using morphological characters. *C. horsfieldii* is characterized by cusps on the lower premolars that are absent in the other 3 species (Medway 1983; Payne et al. 1985). *C. sphinx* is distinguished by ear length (≥18 mm—Bates and Harrison 1997; Payne et al. 1985). The 2 *C. brachyotis* lineages, Forest and Sunda, were discriminated based on length of forearm (Forest,  $\bar{X} = 59.5 \text{ mm} \pm 1.7 \text{ SD}$ ,  $n = 52$ ; Sunda  $\bar{X} = 63.8 \pm 1.6 \text{ mm}$ ,  $n = 57$ ) and coloration of nuchal collar (Forest = dark orange-red; Sunda = pale orange-yellow). Wing biopsy punches for genetic analyses were collected from all adult individuals. For cases in which *C. sphinx* and *C. horsfieldii* could not be distinguished with certainty in the field, approximately 640 base pairs of the mitochondrial control region were sequenced to confirm species identity (methods in Campbell et al. 2004). *C. brachyotis* Sunda is characterized by an approximately 78-base pair deletion near the 5' end of the control region (Campbell et al. 2004); this difference in sequence length was readily visualized by running amplified polymerase chain reaction product with a size marker on an agarose gel.

**Collection of morphometric data.**—Eleven cranial and 8 dentary characters were measured to the nearest 0.01 mm using Mitutoyo digital calipers (Mitutoyo, Kawasaki, Japan). Characters were selected based on their use in previous studies to define trophic morphology in frugivorous and nectarivorous bats (Dumont 1997; Freeman 1995). Length of forearm and tibia for the same individuals were included in the data set as measures of overall body size. Repeatability was ascertained by examining coefficients of variance for each character measured 30 times nonconsecutively on a single specimen. Measurements with coefficients ≤0.01 were considered to be repeatable. The 16 repeatable characters retained for statistical analysis are shown in Fig. 1.

Maximum gape angle was calculated as the ratio of the distance from the craniomandibular joint to the origin of the masseter muscle, to the distance from the craniomandibular joint to the insertion of the masseter muscle at the base of the angular process (Barlow et al. 1997; Herring and Herring 1974). Gape angle increases with the length of the dentary apparatus; a negative relationship between gape angle and bite force is found in bats (Dumont and Herrel 2003).

Wing tracings were scanned and measured digitally using the program Image J (<http://rsb.info.nih.gov/ij>). The flight pa-



**FIG. 1.**—The 16 repeatable craniodental measurements used in this study, illustrated on the cranium and dentary of *Cynopterus brachyotis* Sunda. a) Dorsal cranium: total skull length (TSL), maximum zygomatic breadth (MZB), posterior skull width (PSW). b) Ventral cranium: anterior skull length (ASL), total palate length (TPL), palate width at canines (APW), palate width at P2 (MPW), palate width at M1 (PPW). c) Lateral cranium: rostral length (RL), canine to M1 length (CM1). d) Lateral dentary: total dentary length (TDL), coronoid process height (CPH), 1 = condyle to canine length (Cc), 2 = condyle to p3 length (Cp3), 3 = condyle to m1 length (Cm1), 4 = condyle to m2 length (Cm2).

rameters aspect ratio (AR) and wing loading (WL) were calculated according to Norberg and Rayner (1987), where  $AR = \text{wingspan}^2 / \text{wing area}$ , and  $WL = \text{body mass} \times \text{acceleration of gravity} / \text{wing area}$ . In bats, aspect ratio and wing loading are typically positively correlated: long, narrow wings (high aspect ratio) increase the energetic efficiency of flight at the cost of reduced turning ability in cluttered airspace, whereas a high ratio of body mass to wing area (high wing loading) increases flight speed and reduces maneuverability and load-carrying capacity. Conversely, low values for both indices favor slow, maneuverable flight in cluttered environments and high load-carrying capacity (Norberg and Rayner 1987).

**Ecological analysis.**—Relative interspecific abundance was calculated separately for the 2 sites as the percent of total *Cynopterus* captures accounted for by each species, within each of the 3 habitat types. To obtain pairwise estimates of

interspecific overlap in habitat use at each site, we 1st calculated relative intraspecific abundance across the 3 habitat types from capture rate per net hour for each species. These values were used to calculate the percentage similarity measure of niche overlap (Schoener 1970):

$$P_{jk} = \left[ \sum_{i=1}^n (\text{minimum } p_{ij}, p_{ik}) \right] 100$$

where  $P_{jk}$  is the percentage of overlap in between species  $j$  and species  $k$ ,  $p_{ij}$  and  $p_{ik}$  are the proportion that resource  $i$  (in this case, habitat type) is of the total resources used by species  $j$  and  $k$ , and  $n$  is the total number of resource states (in this case, the 3 habitat types). Overall measures of habitat overlap between each species were obtained by averaging pairwise estimates of niche overlap across the 2 sites.

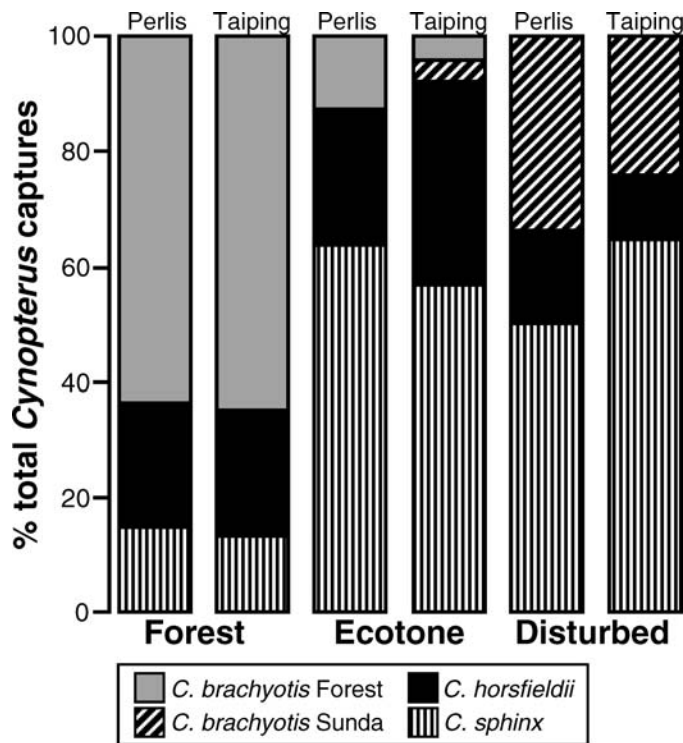


FIG. 2.—The relative abundance of 4 species of *Cynopterus* across habitat types at two sites in peninsular Malaysia.

*Statistical analysis.*—All variables were ln-transformed except the flight indices and estimated gape angle, which were arcsine-transformed. We used multivariate analysis of variance to test for sexual dimorphism within species, and for the effect of sex on character variance across species. Because sex had a significant effect on 1–6 characters within species and 3 characters across species, subsequent analyses were run both with and without the sexes pooled.

The major morphological differences among the 4 species were established with a principal component analysis on the correlation matrix of the 16 repeatable craniodental characters, plus gape angle and lengths of forearm and tibia. Stepwise discriminant function analysis was used to reduce the craniodental data set to the combination of trophic characters that best predicted species membership. The performance of selected characters in correctly assigning individuals to species was evaluated using a jackknifed classification matrix. We chose discriminant function analysis because the utility of this method has been demonstrated in morphometric analysis of ecologically relevant characters in frugivorous and nectarivorous species (Dumont 1997).

Because we were interested in potential differences in the shape of trophic characters, independent of size, we minimized the effects of size by regressing all linear characters selected in the previous analysis against total length of skull. Total length of skull was chosen as a proxy for skull size because of its high correlation with all other craniodental characters ( $R^2 = 0.99$ ). Residuals from individual regressions were used in canonical discriminant function analysis.

TABLE 2.—Estimates of pairwise species overlap in habitat use, within localities (Perlis and Taiping) and across localities ( $\bar{X}$ ), calculated using the percentage similarity measure of niche overlap (Schoener 1970).

Species pairs	% overlap		$\bar{X}$
	Perlis	Taiping	
<i>CbF</i> – <i>CbS</i>	0	9.4	4.7
<i>CbF</i> – <i>Cs</i>	32.8	42.0	37.4
<i>CbF</i> – <i>Ch</i>	43.4	28.1	35.7
<i>CbS</i> – <i>Cs</i>	55.6	55.4	55.5
<i>CbS</i> – <i>Ch</i>	39.0	35.9	37.4
<i>Cs</i> – <i>Ch</i>	75.8	66.5	71.2

*CbF* = *Cynopterus brachyotis* Forest, *CbS* = *C. brachyotis* Sunda, *Ch* = *C. horsfieldii*, *Cs* = *C. sphinx*.

An initial discriminant function analysis of the 2 flight parameters was run to evaluate interspecific differences in flight adaptations independent of trophic morphology. In an attempt to minimize the possible effects of measurement error amplified in composite characters, we ran additional analyses with the 2 indices decomposed into wingspan, wing area, and body mass. Finally, because of significant differences in body mass between all species ( $P < 0.001$ ), we reduced the effect of size on wing-loading values by recalculating the index as: relative wing loading =  $\text{mass}^{0.67}/\text{wing area}$  (Norberg 1998).

Principal component analysis of the full craniodental data set plus aspect ratio and wing loading was used to examine the relative contribution of trophic and locomotor characters to among-species variation. We also ran a stepwise discriminant function analysis for the same data set to assess the discriminatory power of trophic versus locomotor characters in correctly assigning species membership. All statistical analyses were carried out in SYSTAT version 11 (SYSTAT Software Inc., Richmond, California).

## RESULTS

*Ecology.*—Although capture rates for each species in ecotone and disturbed habitats differed between sites, interspecific differences in habitat associations were consistent across sites (Fig. 2). *C. brachyotis* Forest was predominantly associated with forest and never captured in highly disturbed habitats. Conversely, *C. brachyotis* Sunda was common in highly disturbed habitats and absent from forest. *C. sphinx* and *C. horsfieldii* co-occurred across habitats but at different abundances: *C. sphinx* dominated in disturbed and ecotone habitats but was relatively uncommon in forest, whereas *C. horsfieldii* was slightly more common at the ecotone than in forest and least abundant in disturbed habitats.

Percent overlap in habitat use, averaged across sites, was moderately high between *C. sphinx* and *C. horsfieldii* (71.2%); intermediate between *C. brachyotis* Sunda and *C. sphinx* (55.5%), *C. brachyotis* Sunda and *C. horsfieldii* (37.4%), *C. brachyotis* Forest and *C. sphinx* (37.4%), and *C. brachyotis* Forest and *C. horsfieldii* (35.7%); and minimal between *C. brachyotis* Forest and *C. brachyotis* Sunda (4.7%; Table 2).

**TABLE 3.**—Sample sizes for *Cynocephalus* (*n*: males [M], females [F]) and species means (*SD*) for characters measured in this study. Linear measures are in millimeters unless otherwise noted. FA = forearm, TIB = tibia, GAPE = gape angle; see Fig. 1 caption for key to all other character abbreviations.

	<i>C. brachyotis</i> Forest	<i>C. brachyotis</i> Sunda	<i>C. sphinx</i>	<i>C. horsfieldii</i>
<i>n</i> (M, F)	19 (11, 8)	31 (16, 15)	23 (14, 9)	27 (14, 13)
FA	59.90 (1.46)	63.98 (1.25)	68.65 (1.52)	73.24 (1.79)
TIB	22.06 <sup>*a</sup> (0.50)	24.72 (1.20)	26.96 (0.83)	27.04 (1.20)
MZB	18.35 (0.41)	18.52 (0.51)	20.50 (0.56)	22.64 (0.85)
PSW	12.36 (0.31)	12.59 (0.36)	13.72 (0.42)	14.39 (0.38)
TSL	27.61 (0.63)	28.40 (0.61)	31.02 <sup>*b</sup> (0.64)	32.36 (0.76)
RL	6.35 (0.35)	6.69 (0.26)	7.21 (0.34)	7.01 (0.32)
ASL	24.46 (0.57)	25.12 (0.57)	27.67 <sup>*b</sup> (0.64)	28.91 (0.83)
TPL	14.15 (0.55)	14.59 (0.43)	16.07 (0.44)	17.01 (0.53)
CM1	9.09 (0.33)	9.19 (0.34)	10.42 <sup>*b</sup> (0.44)	10.74 (0.31)
PPW	8.26 (0.36)	8.26 (0.27)	9.35 (0.33)	9.67 (0.32)
MPW	7.26 (0.33)	7.19 (0.28)	8.00 (0.35)	8.55 (0.33)
APW	5.91 (0.36)	5.89 <sup>*b</sup> (0.29)	6.48 <sup>*b</sup> (0.33)	6.88 <sup>*b</sup> (0.27)
CPH	10.38 (0.58)	10.75 (0.48)	11.73 (0.50)	13.18 (0.51)
TDL	20.88 (0.48)	21.37 (0.51)	23.68 <sup>*b</sup> (0.62)	24.81 (0.58)
Cc	20.32 (0.54)	20.80 (0.51)	23.06 (0.58)	24.15 (0.59)
Cp3	15.56 (0.42)	16.0 (0.41)	17.59 <sup>*b</sup> (0.44)	18.73 (0.53)
Cm1	13.38 (0.38)	13.73 (0.40)	15.08 (0.41)	16.16 (0.48)
Cm2	11.25 (0.41)	11.51 (0.34)	12.62 (0.41)	13.53 (0.45)
GAPE	2.26 (0.12)	2.23 (0.12)	2.30 (0.13)	2.13 (0.08)
<i>n</i> (M, F)	27 (15, 12)	32 (15, 17)	31 (17, 14)	31 (18, 13)
Mass (kg)	0.0293 (0.0022)	0.0367 (0.0024)	0.0470 (0.0033)	0.0579 (0.0048)
Wing area (m <sup>2</sup> )	0.024 (0.001)	0.028 (0.002)	0.030 (0.002)	0.036 (0.002)
Wingspan (m)	0.387 (0.012)	0.413 (0.014)	0.433 (0.013)	0.465 (0.017)
Aspect ratio	6.20 (0.16)	6.15 (0.18)	6.24 (0.19)	6.08 (0.19)
Wing loading (Nm <sup>-2</sup> )	11.95 (0.87)	13.03 (1.23)	15.37 (1.04)	15.98 (1.26)

<sup>a</sup> Females > males.

<sup>b</sup> Males > females.

\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ .

The same order of species overlap was retained within sites with the exception of *C. brachyotis* Forest–*C. horsfieldii*. Overlap was higher between these 2 species in Perlis because of the relatively higher abundance of *C. brachyotis* Forest in ecotonal habitat at this site.

**Morphology.**—No craniodental characters were significantly sexually dimorphic in *C. brachyotis* Forest, but the tibia was significantly longer in females ( $P = 0.05$ ) and length of forearm followed the same trend ( $P = 0.06$ ). Palate width at canines was significantly larger in *C. horsfieldii* and *C. brachyotis* Sunda males ( $P = 0.03$  and  $P = 0.04$ , respectively). Six characters were significantly larger in male *C. sphinx*: total length of skull ( $P = 0.02$ ), anterior skull length ( $P = 0.04$ ), canine to upper molar length ( $P = 0.002$ ), palate width at canines ( $P = 0.009$ ), total dentary length ( $P = 0.01$ ), and condyle to lower 3rd premolar length ( $P = 0.003$ ). Across species, sex had a significant effect on 3 characters: length of forearm ( $P = 0.05$ ), length of tibia ( $P = 0.04$ ), and palate width at canines ( $P < 0.001$ ). Sex did not have a significant effect on flight indices or their components in any species. With the sexes pooled, interspecific differences were significant for all characters (aspect ratio,  $P = 0.005$ ; all others,  $P < 0.001$ ). Mean trait values are summarized in Table 3.

Principal component analysis of 16 repeatable craniodental characters plus gape angle and length of forearm and tibia

clearly identified size as the principal factor distinguishing the 4 species (Fig. 3). All characters except gape angle were strongly loaded on the 1st axis, which accounted for 83% of the overall variance. There was considerable overlap on this axis between *C. brachyotis* Forest and *C. brachyotis* Sunda and, to a lesser degree, between *C. sphinx* and *C. horsfieldii*. Gape angle loaded strongly on the 2nd axis (0.898), along with rostral length (0.386) and coronoid process height (−0.289). Accounting for 6.0% of the total variance, this axis distinguished *C. sphinx* from *C. brachyotis* Forest and *C. horsfieldii* and, to a lesser extent from *C. brachyotis* Sunda, with a wider gape angle, longer rostrum, and reduced coronoid process height. There was no clear separation by sex for any species on either axis.

Stepwise discriminant function analysis of the trophic data set selected 6 cranial and 3 dentary characters, plus gape angle, as the best predictors of species membership (Table 4a). The linear characters could be divided roughly into descriptors of the size and shape of the cranium (maximum zygomatic breadth, total skull length, and rostral length), area of the upper tooththrow and palate shape (canine to molar length and breadth of palate at molar and 2nd premolar) and area of the lower tooththrow (distances from condyle to canine, to the 2nd molar and to the 3rd premolar). The 1st function was clearly related to overall size, explaining 91% of the total variance and

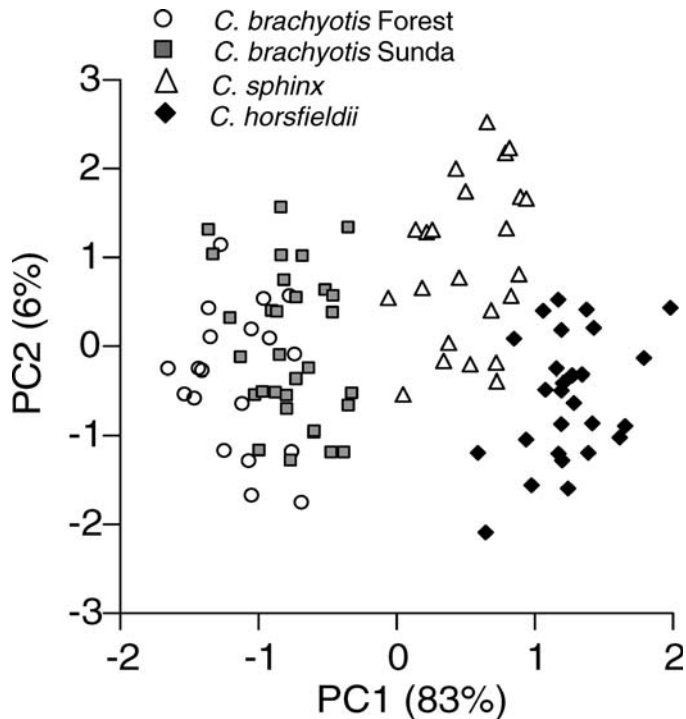


FIG. 3.—Morphological separation and overlap among 4 species of *Cynoptyrus*. Distribution on the first 2 axes of principal component space (PC1 and PC2) based on 16 craniodental characters, gape angle, and lengths of forearm and tibia. PC1 and PC2 explain 83% and 6% of the variance, respectively.

separating all species except *C. brachyotis* Forest and *C. brachyotis* Sunda. The 2nd function explained 7% of overall variance and defined *C. sphinx* relative to the other 3 species in having a narrower, more elongate cranium, a narrower distance across the upper 3rd upper premolars (P3) relative to that at the upper molars (M1), and reduced lower 3rd premolar (p3) and 1st molar (m1), relative to the total length of the lower tooththrow and the distance from the condyle to the 2nd lower molar (m2). The 3rd function partially separated *C. brachyotis* Forest from *C. brachyotis* Sunda, with a blunter cranium, longer upper tooththrow, more-robust p3 and m1, and slightly wider gape angle (Table 4a). The jackknife classification matrix correctly assigned 83% of all individuals to the correct species. Accuracy was 100% in *C. sphinx*, 96% in *C. horsfieldii* (one misassignment to *C. sphinx*), 74% in *C. brachyotis* Sunda (8 misassignments to *C. brachyotis* Forest), and 58% in *C. brachyotis* Forest (8 misassignments to *C. brachyotis* Sunda).

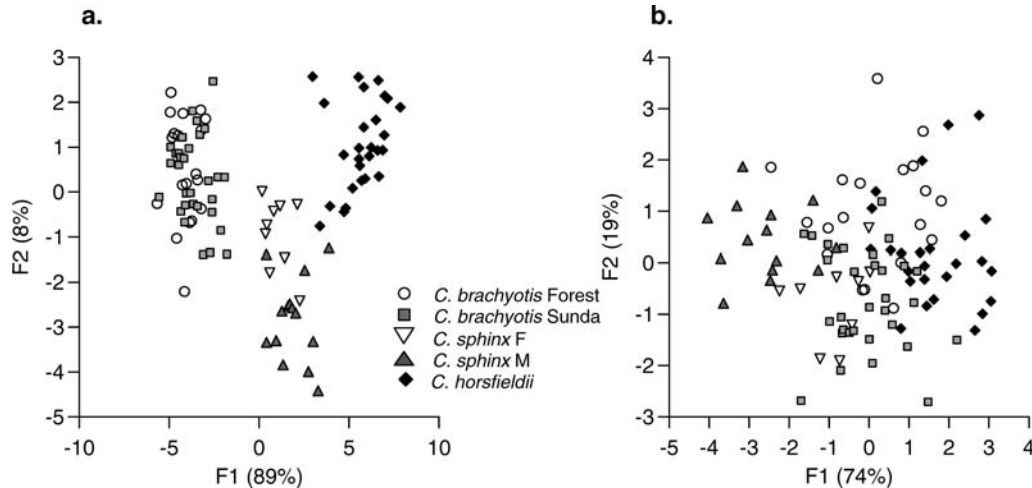
Running the same stepwise procedure with males and females separated yielded similar results for all species except *C. sphinx*. The results of this analysis, with the sexes separated in *C. sphinx* only, are shown in Table 4b and Fig. 4a. The characteristics defining *C. sphinx* on the 2nd function generally were more pronounced in males, whereas females clustered in the upper ranges of *C. brachyotis* Forest and *C. brachyotis* Sunda.

Canonical discriminant function analysis of the reduced, size-adjusted trophic data set distinguished *C. sphinx* from *C.*

TABLE 4.—Results of stepwise discriminant function analysis of 16 craniodental characters plus gape angle (GAPE). All other character abbreviations as in Fig. 1 caption. a) Sexes pooled for all species. b) Male and female *Cynoptyrus sphinx* analyzed separately; results are summarized graphically in Fig. 4a.

Predictor	Canonical discriminant functions (F)		
	F1	F2	F3
a) Sexes pooled for all species			
MZB	0.37	0.549	0.281
TSL	0.726	-0.126	-0.659
RL	-0.772	-0.359	-0.612
CM1	0.401	-0.105	0.953
PPW	0.269	-0.856	0.195
MPW	-0.122	0.763	0.125
Cc	-0.594	-1.798	0.334
Cp3	0.533	2.085	-1.261
Cm2	0.236	-0.561	0.737
GAPE	-0.038	-0.287	0.441
Eigenvalue	16.99	1.36	0.41
% variance explained	90.6	7.2	2.2
Species means			
<i>C. brachyotis</i> Forest	-4.065	0.66	1.072
<i>C. brachyotis</i> Sunda	-3.554	0.262	-0.743
<i>C. sphinx</i>	1.461	-2.029	0.145
<i>C. horsfieldii</i>	5.696	0.963	-0.025
b) Male and female <i>C. sphinx</i> analyzed separately			
MZB	0.402	0.368	0.501
TSL	0.644	0.133	-0.829
RL	-0.765	-0.305	-0.616
CM1	0.378	-0.153	0.819
PPW	0.2	-0.557	-0.273
MPW	-0.122	0.668	0.303
Cc	-0.301	-2.319	0.657
Cp3	0.54	2.018	-0.762
GAPE	0.023	-0.443	0.496
Eigenvalue	17.42	1.65	0.46
% variance explained	88.9	8.4	2.4
Species means			
<i>C. brachyotis</i> Forest	-4.112	0.534	1.102
<i>C. brachyotis</i> Sunda	-3.596	0.304	-0.665
Female <i>C. sphinx</i>	1.033	-0.927	-0.744
Male <i>C. sphinx</i>	1.927	-2.82	0.329
<i>C. horsfieldii</i>	5.679	1.046	0.065

*horsfieldii* on the 1st function based on reduced lower cheek teeth (p3 and m1), reduced palate breadth at P3 relative to M1, a narrower cranium, longer rostrum, and wider gape angle (Table 5a). Scores for *C. brachyotis* Forest and *C. brachyotis* Sunda on this function were roughly intermediate and largely overlapping. The 2nd function partially discriminated these 2 species, with a relatively blunter rostrum, longer upper tooththrow, more-robust lower cheek teeth, and wider gape angle in *C. brachyotis* Forest (Table 5a). Character loadings on the 3rd function were largely due to intraspecific variance that was not explained by sexual dimorphism. Rerunning the analysis with the sexes separated produced very similar results to those obtained using the unadjusted data set: in *C. sphinx*, character loadings on the 1st function were generally higher in



**FIG. 4.**—a) Discrimination among 4 *Cynopterus* species and between male and female *C. sphinx*, based on the first 2 functions (F1 and F2) from stepwise discriminant function analysis of 16 craniodental characters plus gape angle. F1 and F2 explain 89% and 8% of the variance, respectively. Loadings for the characters that were the strongest predictors of species membership with and without sexes separated in *C. sphinx* are provided in Tables 4a and 4b. b) Discrimination among species and between male and female *C. sphinx*, based on the first 2 functions from size-adjusted canonical discriminant function analysis of the reduced trophic data set. F1 and F2 explain 74% and 19% of the variance, respectively. Character loadings with and without sexes separated in *C. sphinx* are provided in Tables 5a and 5b.

males, whereas females overlapped with *C. brachyotis* Sunda (Table 5b; Fig. 4b).

Discriminant function analysis of the 2 flight indices partially distinguished *C. sphinx* and *C. horsfieldii* from *C. brachyotis* Sunda and *C. brachyotis* Forest based on wing loading, with the 4 species ordered by body size (results not shown). Wing loading was strongly loaded on the 1st function (1.009), which accounted for 96% of the variance. Aspect ratio was uninformative because of minimal interspecific differentiation and considerable intraspecific variation (Table 3). Decomposing aspect ratio and wing loading into wingspan, wing area, and body mass also returned a size-based result: on the 1st function, loadings were large and positive for body mass (0.856), smaller for wingspan (0.399), and weak for wing area (0.015). The strong loading for wing area on the 2nd function (2.057) was due almost entirely to variation within species. Running the same analysis using the size-adjusted index, relative wing loading, effectively eliminated species differences.

Principal component analyses with aspect ratio and wing loading added to the original unadjusted craniodental data set increased differences among species on the size axis, whereas interspecific separation on the 2nd axis was reduced by high intraspecific variance in aspect ratio. Neither of the flight indices was selected as a predictor of species membership using stepwise discriminant function analysis.

## DISCUSSION

In this study, we tested the prediction that the coexistence of 4 species of ecologically and morphologically similar Old World fruit bats would be facilitated by separation along 1 or more axes of niche space. We used 3 interrelated estimates of resource use: relative abundance across habitat types, morpho-

logical characters relevant to trophic adaptation, and wing-shape parameters associated with flight performance. Overall, we did not find a consistent relationship between interspecific divergence in ecomorphological characters and degree of spatial overlap. Rather, our study suggests several alternative solutions to the problem of coexistence, involving relatively minor separation along single axes of resource use among *Cynopterus* species pairs. Three main factors were important in separating 2 or more species: distribution across habitat types, body size, and craniodental morphology. Wing morphology contributed surprisingly little to differences among species.

*Spatial separation and overlap.*—Consistent differences in the relative abundances of the 4 species in forest, ecotonal, and disturbed habitats at 2 sites in peninsular Malaysia suggest that spatial partitioning of resources is important in reducing potential competitive interactions. This pattern was most striking in *C. brachyotis* Forest and Sunda, which are sympatric throughout Malaysia and in parts of Indonesia and southern Thailand, but rarely are syntopic (Campbell et al. 2004, 2006b). The local segregation of these 2 species strongly suggests competitive exclusion across habitat types, an inference that is supported by the absence of evidence for ecological specialization in either. For example, although *C. brachyotis* Sunda typically forages in agricultural and suburban environments that are uncluttered relative to the forest understory and midcanopy utilized by *C. brachyotis* Forest (Hodgkison et al. 2004a), interspecific differences in wing morphology are minimal, suggesting comparable flight efficiency in cluttered airspace. Likewise, at sites from which *C. brachyotis* Forest is absent, *C. brachyotis* Sunda forages in secondary forest (Bumrungsri 2002; Tan et al. 1998).

Although the 2 larger species, *C. sphinx* and *C. horsfieldii*, cross readily between forest and disturbed habitats, marked differences in between-habitat abundance suggest that *C.*



**TABLE 5.**—Results of canonical discriminant function analysis of size-adjusted variables selected from the trophic data set by stepwise discriminant analysis. Character abbreviations as in Fig. 1 caption, plus gape angle (GAPE). a) Sexes pooled for all species. b) Male and female *Cynopterus sphinx* treated separately; results are graphically summarized in Fig. 4b.

Predictor	Canonical discriminant functions (F)	
	F1	F2
a) Sexes pooled for all species		
MZB	-0.516	0.228
RL	0.364	-0.496
CM1	0.03	0.708
PPW	0.731	0.291
MPW	-0.64	0.046
Cc	1.192	0.279
Cp3	-1.614	-1.074
Cm2	0.446	0.738
GAPE	0.345	0.393
Eigenvalue	1.49	0.42
% variance explained	74.4	20.9
Species means		
<i>C. brachyotis</i> Forest	-0.293	0.963
<i>C. brachyotis</i> Sunda	0.099	-0.823
<i>C. sphinx</i>	1.869	0.242
<i>C. horsfieldii</i>	-1.5	0.062
b) Male and female <i>C. sphinx</i> analyzed separately		
MZB	0.372	0.453
RL	-0.321	-0.508
CM1	-0.076	0.627
PPW	-0.482	-0.204
MPW	0.575	0.23
Cc	-1.565	0.522
Cp3	1.605	-0.655
GAPE	-0.476	0.466
Eigenvalue	1.787	0.462
% variance explained	74.4	19.2
Species means		
<i>C. brachyotis</i> Forest	0.165	1.009
<i>C. brachyotis</i> Sunda	-0.055	-0.744
Female <i>C. sphinx</i>	-0.823	-0.685
Male <i>C. sphinx</i>	-2.616	0.432
<i>C. horsfieldii</i>	1.578	0.148

*sphinx* is primarily associated with nonforest habitat, whereas *C. horsfieldii* is more reliant on forest and adjacent ecotone. However, the extent to which competitive interactions between these 2 species may modify their distributions across habitat types is uncertain. Lower within-habitat abundance of *C. horsfieldii* relative to other *Cynopterus* species is reported from areas where *C. sphinx* does not occur (Francis 1994; Hodgkison et al. 2004b; Zubaid 1993), suggesting that other factors may act to maintain relatively low population densities in this species.

Although pairwise habitat overlap between *C. sphinx* and *C. brachyotis* Sunda was only moderate, the potential competitive effect of *C. sphinx* on the smaller species is considerable because *C. brachyotis* Sunda is essentially restricted to disturbed habitats where *C. sphinx* is most abundant. While

differences between the 2 species in body size and diet (discussed below) may be important in promoting coexistence, the effects of interspecific competition also may be reduced by the instability of highly disturbed habitats (e.g., Connell 1978; Huston 1979), or by a superabundance of dietary resources in agricultural and suburban areas.

*Ecological effects of size.*—Hutchinson (1959) was among the 1st to point out that differences in size should be important in facilitating the coexistence of ecologically similar species. This expectation is supported in a broad range of taxonomic assemblages (desert rodents [Bowers and Brown 1982], bird-eating hawks [Schoener 1984], and New World bats [Stevens and Willig 1999]). The segregation across habitat types of the most similarly sized species in this analysis, *C. brachyotis* Forest and Sunda, and the evolutionarily rapid acquisition of large body size in *C. horsfieldii*, suggest that *Cynopterus* is no exception: size likely does play an important role in mediating the potential for interspecific competition.

Given the relatively recent common ancestry of *C. brachyotis* Forest and *C. horsfieldii*, and assuming that relatively small body size is the ancestral state in *Cynopterus*, the evolutionarily rapid increase in size in *C. horsfieldii* suggests response to strong directional selection (Campbell et al. 2004). Despite the often tenuous nature of the relationship between observed patterns and past competitive processes (e.g., Connell 1980), it seems reasonable to suggest that interspecific interactions may have played an important role in driving morphological divergence in *C. horsfieldii*. The prevalence of size differences among coexisting, closely related vertebrate species (Foote and Larkin 1988; Nagel and Schluter 1998; Ratcliffe and Grant 1983) suggests that change in size is a common response to strong ecological selection, requiring an overall increase in growth rather than unique changes in single structures. Functionally, if similar food items are available in a range of sizes, change in size can reduce interspecific competition for dietary resources in the absence of a major shift in diet.

In Malaysia, the diversity of figs (*Ficus*) is extremely high, with as many as 39 species reported at a single primary forest site (Hodgkison et al. 2003). The fruits of *Ficus* species that constitute a significant proportion of the diets of *C. horsfieldii*, *C. brachyotis* Forest, and *C. brachyotis* Sunda vary considerably in mass, ranging from 3.0 to 45.5 g (Boon and Corlett 1989; Fletcher 2001; Funakoshi and Zubaid 1997; Tan et al. 1998; P. Campbell, in litt.). It has been suggested that adaptation to consuming fruits of different textures plays an important role in resource partitioning in frugivorous bats (Dumont 1999; Dumont and O'Neal 2004). Bite force scales positively with body mass (Aguirre et al. 2002) and a positive correlation exists between fruit size and hardness (Aguirre et al. 2003). Thus, *C. horsfieldii* should tend to exploit larger and therefore harder fruits than its smaller, lighter congeners. This expectation is supported by a comparative study of diet and foraging patterns in syntopic populations of *C. brachyotis* Forest and *C. horsfieldii*, which found that the wet mass of individual figs carried by *C. horsfieldii* averaged twice that of figs carried by *C. brachyotis* Forest (Funakoshi and Zubaid

1997). Likewise, the soft fruits of *Piper aduncum* accounted for a significant proportion of the diet of *C. brachyotis* Forest but were not eaten by *C. horsfieldii*.

**Trophic differentiation.**—The suite of trophic characters that differentiate *C. sphinx*, particularly with regard to males, suggests that nectar may be a relatively more important component of this species' diet. In bats, nectarivory is correlated with elongation and narrowing of the rostrum and palate, concomitant increase in gape angle and decrease in bite force, and is typically associated with reduction in molar size (Dumont and Herrel 2003; Freeman 1995). Reductions in the height of the coronoid process and the robustness of premolars are characteristics that distinguish nectarivorous from primarily fruit-eating pteropodids (Dumont 2004; Freeman 1995). In India, *C. sphinx* typically is described as frugivorous (Bhat 1994; Marimuthu et al. 1998), but has been observed feeding extensively on the nectar of several species of plants (Elangovan et al. 2000; Singaravelan and Marimuthu 2004). Although dietary studies of *C. horsfieldii*, *C. brachyotis* Forest, and *C. brachyotis* Sunda in Malaysia indicate that nectar accounts for a relatively small proportion of a mainly frugivorous diet (Lim 1970; Fletcher 2001; Tan et al. 1998), no comparably detailed data are available for *C. sphinx* in this region. However, a comparison of the diets of *C. sphinx* and *C. brachyotis* Sunda in Thailand found similarly low levels of nectarivory in both species (Bumrungsri 2002). Determining whether the differences in trophic morphology that distinguish *C. sphinx* actually translate to a higher degree of nectarivory relative to the other 3 Malaysian *Cynopterus* awaits comparative analysis of the diets of all 4 species in sympatry.

*Cynopterus sphinx* was the only species that exhibited significant sexual dimorphism in several characters. The 6 characters that were significantly larger in males are descriptors of the relative elongation of the cranium and dentary, the area of cheek teeth, and palate shape. Interestingly, no significant differences were found in the larger measures of body size and wing dimensions, for which geographically variant sexual dimorphism has been described in Indian populations of *C. sphinx* (Storz et al. 2001). The size-adjusted analysis demonstrated that sexual dimorphism in *C. sphinx* was primarily due to differences in the shape of trophic structures. This type of differentiation is suggestive of trophic resource partitioning as a consequence of intraspecific competition (Shine 1989). Evidence that competition between the sexes may play a role in the evolution and maintenance of sexual dimorphism in trophic characters has been found in several carnivore species (Dayan et al. 1989, 1990; Johnson and Macdonald 2001) and a temperate species of bat (*Antrozous pallidus*—T. Perry, pers. comm.). However, larger sample sizes and dietary data are required to evaluate this intriguing hypothesis in *C. sphinx*.

It is uncertain whether the minor differences between *C. brachyotis* Forest and Sunda in the shape of the trophic apparatus correspond to functional ecological differences. Although the diets of the 2 species certainly differ as a consequence of the distinct floristic compositions of anthropogenic and forest habitats, both exhibit considerable

geographic and seasonal variation in dietary preferences (Fletcher 2001; Funakoshi and Zubaid 1997; Hodgkison et al. 2004b; Tan et al. 1998). It is notable, however, that the characters that partially discriminate *C. brachyotis* Forest from *C. brachyotis* Sunda (relatively broad cranium, blunt rostrum, and robust cheek teeth) are amplified in *C. horsfieldii*. This observation supports the proposition that divergence between *C. horsfieldii* and *C. brachyotis* Forest has occurred mainly along an axis of size, with little concomitant change in shape.

**Generalization of wing morphology.**—The contribution of characters relevant to flight performance to total morphological differences among species was minimal, suggesting that different performance capabilities in closed forest versus open anthropogenic habitats, or within the strata of the forest, are not primary mediators of species coexistence. Although wing loading differed significantly among species, the lack of interspecific differentiation in the size-adjusted index, relative wing loading, indicated that species values for wing loading were strongly related to differences in body mass, not wing area. Examination of experimental data demonstrates that bats' ability to negotiate obstacles in their environment is negatively correlated with body mass, regardless of wing shape (Stockwell 2001). As a heavy bat that is relatively common in the forest understory, *C. horsfieldii* seems somewhat ill-equipped to negotiate the clutter it is likely to encounter in this environment. This apparently suboptimal aspect of phenotype suggests that although body size, possibly in relation to trophic adaptation, appears to have been the target of strong selection in *C. horsfieldii*, selection on flight performance has been comparatively weak.

In general, constraints on wing morphology are likely to be less stringent in species that do not pursue and capture mobile prey. Norberg and Rayner (1987) suggested that wing morphology in bats may be influenced as much by the breadth of environmental conditions a given species experiences, as by the extremes of those conditions. Despite differences in abundance across habitat types, the range of structurally different environments encountered by the 4 species treated in this study is evidently quite broad. Relative to other pteropodid fruit bats, the values for aspect ratio and wing loading reported for *Cynopterus* species in this and other studies are intermediate, describing a generalist phenotype that is moderately well suited to foraging in relatively cluttered airspace and not specialized for either long-distance or highly maneuverable flight (Hodgkison et al. 2004a; McKenzie et al. 1995; Norberg and Rayner 1987).

**Conclusions.**—In comparison with the well-studied assemblages of insectivorous bats in both the Old and New World tropics, and frugivorous phyllostomids in the Neotropics (Bernard 2001; Bonaccorso 1979; Heller and von Helversen 1989; Kalko et al. 1996; Kingston et al. 2000; McKenzie and Rolfe 1986), community studies of Old World fruit bats are rare, and typically have focused on single niche dimensions (Hodgkison et al. 2004a; Kitchener et al. 1990; McKenzie et al. 1995; Uzzurum 1995). Consequently, the number of axes of resource use available to pteropodid species is not well defined. The results of our study suggest that at least 3 niche dimensions

are important in facilitating coexistence in pteropodids: habitat association, body size, and size and shape of the trophic apparatus. We did not measure vertical stratification, a dimension that is likely to be important in structuring resource use in frugivorous bats at the assemblage level (Francis 1994; Henry et al. 2004; Hodgkison et al. 2004a). However, the minimal differentiation in wing morphology found among species in this study and the previously reported lack of vertical separation between *Cynopterus* species (Hodgkison et al. 2004a), suggest that spatial resource partitioning within this genus occurs at a broader scale across habitat types, rather than within the vertical strata of the forest.

Schoener (1974) proposed that potentially competing species should partition resources in a complementary manner, such that the similarity of 2 species along 1 niche dimension is counterbalanced by dissimilarity along another. We found this to be the case for Malaysian *Cynopterus* species. *C. brachyotis* Forest and Sunda differ little morphologically but segregate by habitat, strongly suggesting that these 2 species fall below the margin of limiting similarity compatible with coexistence for members of this genus. *C. sphinx* overlaps in habitat use with *C. brachyotis* Sunda and *C. horsfieldii*, and with the latter in size, but is distinguished by divergent trophic morphology, indicative of dietary resource partitioning. *C. brachyotis* Forest and *C. horsfieldii* overlap in trophic morphology and habitat associations but differ substantially in size. Morphological divergence that permits exploitation of a different set of key resources in the same environment is a strong indicator of the role of ecological selection in the maintenance of species boundaries, and in their origin (Schluter 1998, 2001). The rapid evolution of large body size in *C. horsfieldii*, and consequent opportunity for exploitation of fruits in a different size class, is suggestive of an ecological niche shift associated with recent speciation.

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## APPENDIX I

Peninsular Malaysian *Cynopterus* specimens measured in this study. Specimens with the prefix, MCZ, are housed in the Harvard Museum of Comparative Zoology. All other specimens are identified by individual collector numbers and are housed at the Department of Wildlife and National Parks, Kuala Lumpur, Malaysia. Males (♂) and females (♀) are separated within collection localities in peninsular

Malaysia. *Cynopterus brachyotis* nomenclature follows Campbell et al. (2004).

*Specimens at MCZ*

*Cynopterus brachyotis* Forest.—Perlis State Park, Perlis State: MCZ64565–64569, MCZ64574 (♂), MCZ64572–64573, MCZ64757, MCZ64578 (♀), Taiping, Perak State: MCZ64570–64571, MCZ64576, MCZ64581 (♂), Gombak, Selangor State MCZ64577 (♀). Taman Negara, Pahang State: NP033 (♂), C1185, NP043, NP034 (♀).

*Cynopterus brachyotis* Sunda.—Bukit Jernih, Perlis State: MCZ64586–64589 (♀), Taiping, Perak State: MCZ64580, MCZ64590–64591, MCZ64582, MCZ64584 (♂), MCZ64589, MCZ64583, MCZ64585 (♀). Bangi, Selangor State: P1, P3, P4, P6, P7, P8, P10 (♂), P12, P13, P14, P15, P18, P19 (♀), Melaka, Melaka State: M156, M123, M136, M125 (♂), M139, M135 (♀).

*Cynopterus sphinx*.—Perlis State Park, Perlis State: MCZ64615–64616, MCZ64618–64619, MCZ64625–64626, MCZ64612–64614 (♂), MCZ64633, MCZ64617, MCZ64630–64632 (♀), Taiping, Perak State: MCZ64620–64624 (♂), MCZ64627–64629, PC.Ms218 (♀).

*Cynopterus horsfieldii*.—Perlis State Park, Perlis State: MCZ64611, MCZ64592, MCZ64594, MCZ64596 (♂), MCZ64595, MCZ64607, MCZ64609 (♀). Bukit Jernih, Perlis State: MCZ64606, MCZ64608 (♂), MCZ64610 (♀). Taiping, Perak State: MCZ64597, MCZ64602–64605 (♂), MCZ64593, MCZ64598–64601 (♀). Taman Negara,

Pahang State: NP042, NP036, NP038 (♂), NP040, NP037, NP039, NP041 (♀).

*Specimens at Department of Wildlife and Natural Parks, Kuala Lumpur*

*Cynopterus brachyotis* Sunda.—Bukit Jernih, Perlis State: PC.M575, PC.M577, PC.M580, PC.M581 (♀), Taiping, Perak State: PC.M292, PC.M458, PC.M460, PC.M465, PC.M501 (♂), PC.M286, PC.M496, PC.M503 (♀). Bangi, Selangor State: P1, P3, P4, P6, P7, P8, P10 (♂), P12, P13, P14, P15, P18, P19 (♀). Melaka, Melaka State: M156, M123, M136, M125 (♂), M139, M135 (♀).

*Cynopterus sphinx*.—Perlis State Park, Perlis State: PC.Ms070, PC.Ms074, PC.Ms095, PC.Ms105, PC.Ms184, PC.Ms185, PC.Ms239, PC.Ms240, PC.Ms241 (♂), PC.Ms080, PC.Ms087, PC.Ms224, PC.Ms233, PC.Ms234 (♀). Taiping, Perak State: PC.Ms131, PC.Ms140, PC.Ms143, PC.Ms141, PC.Ms142 (♂), PC.Ms209, PC.Ms216, PC.Ms217, PC.Ms218 (♀).

*Cynopterus horsfieldii*.—Perlis State Park, Perlis State: PC.Mh033, PC.Mh038, PC.Mh109, PC.Mh111 (♂), PC.Mh110, PC.Mh174, PC.Mh206 (♀). Bukit Jernih, Perlis State: PC.Mh170, PC.Mh204 (♂), PC.Mh207 (♀). Taiping, Perak State: PC.Mh144, PC.Mh149, PC.Mh150, PC.Mh151, PC.Mh152 (♂), PC.Mh089, PC.Mh145, PC.Mh146, PC.Mh147, PC.Mh148 (♀). Taman Negara, Pahang State: NP042, NP036, NP038 (♂), NP040, NP037, NP039, NP041 (♀).