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Published in *Biological Journal of the Linnean Society* 72:1 (January 2001), pp. 17–31; doi 10.1111/j.1095-8312.2001.tb01298.x

http://www.wiley.com/bw/journal.asp?ref=0024-4066

Submitted January 20, 2000; accepted August 9, 2000.

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Abstract
Geographic variation in body size and sexual dimorphism of the short-nosed fruit bat *(Cynopterus sphinx)* was investigated in peninsular India. Bats were sampled at 12 localities along a 1,200 km latitudinal transect that paralleled the eastern flanks of the Western Ghats. The geographic pattern of variation in external morphology of *C. sphinx* conforms to the predictions of Bergmann's Rule, as indicated by a steep, monotonic cline of increasing body size from south to north. This study represents one of the first conclusively documented examples of Bergmann's Rule in a tropical mammal and confirms that latitudinal clines in body size are not exclusively restricted to temperate zone homeotherms. Body size was indexed by a multivariate axis derived from principal components analysis of linear measurements that summarize body and wing dimensions. Additionally, length of forearm was used as a univariate index of structural size to examine geographic variation in a more inclusive sample of bats across the latitudinal transect. Multivariate and univariate size metrics were strongly and positively correlated with body mass, and exhibited highly concordant patterns of clinal variation. Stepwise multiple regression on climatological variables revealed that increasing size of male and female *C. sphinx* was associated with decreasing minimum temperature, increasing relative humidity, and increasing seasonality. Although patterns of geographic size variation were highly concordant between the sexes, *C. sphinx* also exhibited a latitudinal cline in the magnitude and direction of sexual size dimorphism. The size differential reversed direction across the latitudinal gradient, as males averaged larger in the north, and females averaged larger in the south. The degree of female-biased size dimorphism across the transect was negatively correlated with body size of both sexes. Canonical discriminant analysis revealed that male- and female-biased size dimorphism were based on contrasting sets of external characters. Available data on geographic variation in the degree of polygyny in *C. sphinx* suggests that sexual selection on male size may play a role in determining the geographic pattern of sexual size dimorphism.

Keywords: Bergmann's Rule, Chiroptera, India, geographic variation, morphological variation, Pteropodidae, sexual selection, Western Ghats

Introduction

Variation in animal body size has functional consequences for a diverse array of life history attributes, and is therefore subject to an equally diverse array of selection pressures (Clutton-Brock & Harvey, 1983; Lindstedt & Swain, 1988). The multifaceted nature of adaptive variation in body size suggests that consistent spatial correlations with particular ecological variables are generally not to be expected. Nonetheless, geographic trends in size variation of many homeothermic species are well-characterized by empirical generalizations such as Bergmann's (1947) Rule. Mayr (1963: 320) interpreted Bergmann's Rule exclusively within the context of intraspecific variation: "… body size in geographically variable species averages larger in the

cooler parts of the range of a species." The original physiological explanation for this pattern was that surface/volume ratio decreases as body size increases, so larger size reduces the rate of heat loss per unit body mass. Although the mass-specific rate of metabolism is inversely related to body mass, the total rate of metabolism (and hence, resource requirements) increases as a positive function of mass (McNab, 1971, 1999). Thus, the classical thermoregulatory explanation for Bergmann's Rule is valid only if the total rate of energy intake more than offsets the increased metabolic demands of large body size.

Empirical assessments of Bergmann's Rule primarily have been based on geographic surveys of temperate zone species at latitudes >20° (Zink & Remsen, 1986; Zeveloff & Boyce, 1988). However, altitudinal and latitudinal clines in body size have also been documented in many non-migratory tropical birds (Mayr, 1944; Mayr & Vaurie, 1948; Ripley, 1950; Traylor, 1950; Moreau, 1957; Handford, 1983; Graves, 1991; Slowtow & Goodfriend, 1996), suggesting that the adaptive basis of size variation may often involve factors other than (or in addition to) cold-tolerance.

In hot aridlands and tropical environments, geographic variation in the size of small-bodied homeotherms may often reflect an adaptive response to the challenges of conserving metabolic water and/or maximizing heat dissipation (Hamilton, 1958, 1961; Brown & Lee, 1969 Power, 1969; James, 1970). Because the evaporative surface area/volume ratio is inversely proportional to body size, this hypothesis predicts that larger size is advantageous in hot arid environments, and smaller size is advantageous in hot humid environments. Intraspecific variation in birds of the genus *Vireo* provides supporting evidence, as birds are smallest in the humid lowland tropics of Central America, and largest in the hot, arid deserts of northern Mexico (Hamilton, 1958, 1961). Likewise, in the 12 species of North American birds studied by James (1970), body size (as indexed by wing length) was smallest in the hot, humid southeast and exhibited a progressive increase across a westward gradient of increasing aridity and a northward gradient of decreasing temperature.

Opinions vary with respect to the statistical validity of Bergmann's Rule in continental populations of birds (Wooler *et al.*, 1985; Zink & Remsen, 1987; Aldrich & James, 1991) and mammals (McNab, 1971; Yom-Tov & Nix, 1986; Zeveloff & Boyce, 1988; Dayan *et al.*, 1991). Rodents have been especially well-studied and often exhibit a considerable degree of clinal variation in body size (Brown & Lee, 1969; Straney & Patton, 1980; Owen, 1989; Baumgardener & Kennedy, 1993; Smith *et al.*, 1995). However, the direction of change across climatic gradients is not always consistent with the classical interpretation of Bergmann's Rule (McNab, 1971; Sullivan & Best, 1997; Weigl *et al.*, 1998). The adaptive basis of clinal variation in mammalian body size has most often been explained by invoking selection for thermoregulatory capabilities (Brown & Lee, 1969) or selection for fasting endurance in climatically severe environments (Boyce, 1979; Searcy, 1980; Lindstedt & Boyce, 1985; Millar & Hickling, 1990). Alternatively, clinal variation in body size may reflect an ecophenotypic response to geographic variation in the nutritional resource base (*e.g.*, Patton & Brylski, 1987). In bats, empirical support for the validity for Bergmann's Rule is marginal (reviewed by Bogdanowicz, 1990). Even among tropical species that maintain thermal homeostasis, bats may be expected to depart from the pattern typical of homeotherms on the basis of both biophysical and ecological considerations. The highly vascularized, naked wing-membranes of bats increase the surface area/volume ratio relative to birds and non-volant mammals of similar body mass. Thus, geographic variation in overall body and wing dimensions may have important consequences for susceptibility to desiccation in hot, arid environments, and the capacity for heat dissipation in hot, humid environments.

Because body size is such a critical determinant of reproductive rates (Clutton-Brock & Harvey, 1983), size variation may often have highly divergent consequences for males and females. Within the constraints imposed by genetic correlation between the sexes (Lande, 1980), the direction and magnitude of sexual dimorphism expressed in a given population may often reflect the interplay between fecundity selection on females and sexual selection on males (Ralls, 1977; Price, 1984). In bats, both male-biased and female-biased size dimorphism have been documented (Myers, 1978; Williams & Findley, 1979; Findley & Wilson, 1982; Ruedas *et al.*, 1994; Willig & Hollander, 1995), although the underlying causes of sex-limited selection pressures have not been demonstrated for any species. Myers (1978) suggested that female-biased size dimorphism in vespertilionid bats reflects an adaptive response to the aerodynamic challenges of flight during pregnancy (and lactation, if it involves aerial transport of suckling young). According to this hypothesis, larger size of females is an allometric effect of selection for reduced wing-loading. By contrast, Williams & Findley (1979) argued that increased female size in vespertilionid bats reflects an adaptive response to the metabolic demands of maintaining thermal homeostasis during pregnancy. Both of these hypotheses are potentially applicable to a wider range of bat species beyond the Vespertilionidae. In addition to fecundity selection on females, sexual selection on males may also be an important driving force in the evolution of sexual dimorphism in bats. If body size influences suc-

cess in territory acquisition and/or mating access to receptive females, the opportunity for sexual selection on male size is expected to be greatest in species characterized by highly polygynous mating systems (*e.g.*, McCracken & Bradbury, 1981; Storz *et al.*, 2000b).

Here we report results of a field-based study of morphological variation in the short-nosed fruit bat, *Cynopterus sphinx* Vahl (Chiroptera: Pteropodidae). The primary objective of this study was to examine ecogeographic correlates of variation in overall body size within and between the sexes, and to test whether the observed patterns conform to Bergmann's Rule. *Cynopterus sphinx* has an extensive continental distribution across South Asia and is peripherally distributed along the western margin of the Malay Archipelago (Storz &Kunz, 1999). This species exhibits an extensive degree of variation in body size, although the nature and geographic pattern of this variation has not been investigated previously. This analysis of size variation in *Cynopterus sphinx* permits an evaluation of the validity of Bergmann's Rule in a tropical mammal, and provides the opportunity to test predictions about patterns of clinal variation in body size across temperature and humidity gradients.

Methods

Area of Study and Sampling Design

The Western Ghats span a linear distance of approximately 1,600 km along the western coast of peninsular India, from the Tapti River (21°N) to the southern tip of the subcontinent (8°N). The crestline averages 900-1,500 m in elevation and intercepts the southwest monsoon, thereby creating a rainshadow across the semi-arid plains to the east. At lower elevations along the eastern flanks of the Ghats, tropical moist-deciduous and dry-deciduous forest typically grade into tropical thorn-scrub vegetation at the mountain/plains interface (Mani, 1974b; Subramanyam & Nayar, 1974). Peninsular India is characterized by a smooth north-to-south gradient of increasing daily minimum temperature and increasing humidity (Mani, 1974a; Ramdas, 1974). The annual range of ambient temperature also varies with latitude, decreasing from the more seasonal Deccan Plateau to the more equable temperature regime of the Tamilnad Plains.

Bats were sampled along a latitudinal transect that spanned a distance of approximately 1,200 km along the eastern flanks of the Western Ghats, from 18°32′N, 73°51′E (Pune) to 8°11′N, 77°30′E (Nagercoil; Figure 1). Bats were sampled at a total of 12 localities along this transect at elevations ranging from 30 to 900 m, in habitats ranging from semi-arid tropical thorn forest to tropical deciduous forest at the mountain/plains interface.

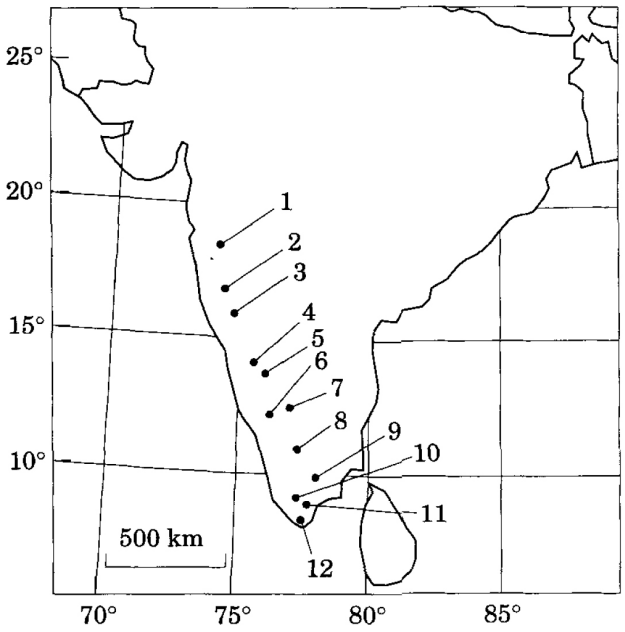

Figure 1. Map of peninsular India showing localities where *Cynopterus sphinx* was sampled. Names of sampling localities, geographic coordinates, and elevation (recorded to the nearest 10 m) are as follows:

1. Pune	18°32′N, 73°51′E, 600 m
2. Kolhapur	16°42′N, 74°13′E, 560 m
3. Belgaum	15°54′N, 74°36′E, 900 m
4. Sorab	14°05′N, 75°24′E, 620 m
5. Shimoga	13°56′N, 75°35′E, 650 m
6. Thithimathi	12°05′N, 76°00′E, 860 m
7. Mysore	12°18′N, 76°37′E, 780 m
8. Metupalayam	11°18′N, 76°59′E, 450 m
9. Othakadai	9°56′N, 78°07′E, 150 m
10. Kuttalam	8°58′N, 77°18′E, 170 m
11. Palayamkottai	8°44′N, 77°42′E, 50 m
12. Nagercoil	8°11′N, 77°30′E, 30 m

Sampling localities were located in the states of Maharashtra (1-2), Karnataka (3-7), and Tamil Nadu (8-12).

The transect spanned the Nilgiri Hills, a transverse range that forms the point of convergence between the Western and Eastern Ghats and demarcates the Deccan Plateau from the uplands and coastal plains of Tamil Nadu to the South.

Bats were trapped on foraging grounds using 2 m × 6m nylon mistnets that were deployed in areas with fruit-bearing trees. In Pune and Palayamkottai, bats were also trapped in diurnal foliage-roosts as described in Storz *et al.* (2000a,b). Each individual was classified as juvenile or adult based on the degree of fusion of the metacarpal-phalangeal epiphyses (Anthony, 1988). Only adults were used in the subsequent analysis of morphological variation. With the exception of those retained as voucher specimens, bats were released at the site of capture after processing.

Analysis of Morphometric Variation

Morphometric variation was assessed in *C. sphinx* by examining eight external characters defined in Kitchener & Maharadatunkamsi (1991) that jointly summarize overall body dimensions and wing area: length of tibia, length of forearm, length of metacarpal of digits 2-5 (DIG2-DIG5), proximal phalanx of digit 3 (DIG3P1), and body mass. External characters were measured to the nearest 0.1 mm using dial calipers and body mass was measured using a 100 g spring balance. All measurements were taken by JFS. All variables were $\log_{10}$-transformed and screened for normality, equality of variances, and equality of variance-covariance matrices. Body mass was considered separately from other external characters. Morphological variation within and between the sexes was initially examined by means of multivariate analysis of variance (MANOVA) and univariate ANOVA with two-way factorial design. Sex and geographic locality were included as fixed-effect factors (model I ANOVA). The factorial design provided tests of three null hypotheses: (1) no effect of geographic locality, (2) no sexual dimorphism, and (3) no geographic variation in sexual dimorphism (as indicated by locality × sex interaction).

In studies of geographic variation, a variety of different multivariate and univariate approaches have been used to measure animal body size. In morphological studies of vertebrates, overall body size is typically indexed by a multivariate axis derived from external, osteometric, and/or craniometric characters (Mosimann & James, 1979; Grant *et al.*, 1985; Rising & Somers, 1989; Freeman & Jackson, 1990; Patton & Smith, 1992). In bats, a multivariate axis that summarizes body and wing dimensions should provide a functionally relevant measure of structural size for the purpose of testing predictions related to Bergmann's Rule. Accordingly, principal components analysis was performed on the variance-covariance matrix of $\log_{10}$-transformed variables to extract an allometric size vector. The analysis was conducted separately for each sex. Variation in the first principal component (PC1) was analyzed for a subset of the total sample of bats. Length of forearm was used as a univariate index of structural size to examine geographic variation in the full sample of bats across the transect. If PC1 and length of forearm do, in fact, provide accurate and functionally meaningful representations of overall structural size, both metrics should covary with body mass in a positive, linear fashion (Rising & Somers, 1989). This relationship was tested by means of bivariate correlation analysis. Body mass combines information about overall structural size in addition to a more variable component that reflects nutrient-reserve storage (Piersma & Davidson, 1991). Thus, in order to control for seasonal and interannual variation in reproductive condition and nutrient stores, the analysis of body mass was restricted to males and nonpregnant females sampled during a single 8 week period following the dry-season parturition period (March 4 through May 2, 1998).

Variation among localities in PC1 and length of forearm was examined using single-classification ANOVA. The geographic pattern of size variation among particular localities was investigated using Hochberg's GT2-method for multiple comparisons (Sokal & Rohlf, 1995: 247-252). The results of correlation analyses are presented as Pearson's product-moment correlation coefficients. Stepwise multiple regression analysis was used to examine the relationship between body size of males and females (as indexed by PC1) and the following climatological variables: mean annual temperature, mean maximum daily temperature, mean minimum daily temperature, annual range in temperature, mean annual rainfall, mean maximum rainfall during the wettest month, mean minimum rainfall during the driest month, and annual range in total rainfall. Climatological data were obtained from meteorological stations located within 30 km of each sampling locality. Weighted mean values of ecogeographic variables for each locality were used for pooled samples. To control for multicolinearity, temperature and precipitation variables were reduced to a smaller set of orthogonal vectors by means of principal components analysis on the correlation matrix. Climatic principal components were used as independent variables in the multiple regression analysis.

Both multivariate and univariate tests of sexual dimorphism were conducted on samples from each general locality. The degree of sexual dimorphism in body size was quantified as the difference between females and males in PC1 factor scores, obtained by conducting the principal components analysis on the pooled sample of both sexes. Canonical discriminant analysis was used to determine the relative contributions of each linear combination of morphometric variables to the observed pattern of multivariate differentiation between the sexes. Factor loadings on the first canonical variate axis provided a measure of the relative discriminatory power of individual characters. However, high communalities among variables can produce factor loadings that belie the true discriminatory power of individual characters that differ between the sexes. Following Willig & Hollander (1995), the relative importance of each character in discriminating between the sexes was ascertained by the magnitude of correlation between the original variable and individual scores on the canonical variate axis. The square of the correlation coefficient (importance value) measures the fraction of the variation in discriminant-function scores accounted for by variation in the original morphometric character. The consis-

Table 1. Statistics describing length of forearm of adult *Cynopterus sphinx* sampled from peninsular India. Statistics are reported for general localities used in the univariate ANOVA. The southern Tamil Nadu group comprises samples from Kuttalam, Palayamkottai, and Nagercoil.

	Males				Females			
Locality	Mean ± 1 SD (mm)	Range	Variance	*n*	Mean ± 1 SD (mm)	Range	Variance	*n*
Pune	74.3 ± 2.1	70.5–79.3	4.51	37	73.9 ± 2.0	68.2–80.1	4.01	249
Kolhapur/Belgaum	71.7 ± 1.9	67.2–74.5	3.52	16	71.6 ± 2.2	66.3–75.7	4.62	48
Sorab/Shimoga	69.6 ± 2.5	65.8–74.4	6.38	21	69.6 ± 1.8	66.8–73.5	3.19	9
Thithimathi/Mysore	69.7 ± 2.0	64.5–72.5	4.16	14	69.9 ± 2.0	65.5–74.6	4.00	26
Metupalayam	68.4 ± 2.5	64.4–72.8	6.46	11	69.2 ± 2.2	63.0–72.5	4.82	19
Othakadai	68.2 ± 1.8	65.0–72.1	3.25	20	69.7 ± 1.7	67.1–72.4	2.95	11
Southern Tamil Nadu	67.5 ± 2.1	61.8–74.4	4.40	122	68.0 ± 2.1	60.2–73.9	4.52	154
Total	69.3 ± 3.2	61.8–79.3	10.42	241	71.4 ± 3.3	60.2–80.1	10.89	516

tency with which a particular set of characters contributes to the expression of secondary sexual dimorphism can then be examined by comparing profiles of trait-specific importance values among different populations. A highly positive correlation between profiles of importance values in different populations is interpreted as evidence for geographical uniformity in the morphological basis of sexual dimorphism. The analyses were conducted separately on latitudinal subdivisions of transect point samples.

Results

A total of 757 adult *C. sphinx* were sampled along the transect. The multivariate analysis of external morphology was based on a subset of 256 bats while length of forearm was analyzed for the full sample. In all analyses, samples of *C. sphinx* from Sorab and Shimoga were pooled. Additionally, when males and females were considered separately in multivariate and univariate analyses, adjacent point samples were pooled as follows: Kolhapur/Belgaum, Thithimathi/Mysore, and the three southernmost localities (Kuttalam/Palayamkottai/Nagercoil). These pooled samples compensated for unbalanced representation of the sexes at individual localities. Variance component analysis confirmed that each grouping of adjacent localities constituted a statistically homogeneous subset of transect point samples.

The multivariate analysis was based on $\log_{10}$-transformed values of all external characters except body mass. Univariate normality and equality of error variances was confirmed for each variable. No inequality of variance-covariance matrices was detected in samples of *C. sphinx* (Box's test: $M = 414.627$; $F = 1.089$; d$f = 308, 15444$; $P = 0.139$). With regard to $\log_{10}$-length of forearm for the full sample of bats, no statistically significant departures from normality were detected (one-sample Kolmogorov-Smirnov test: $Z = 1.305$; $n = 757$; $P = 0.066$) and no inequality of variances among point samples was evident (Levene's test: $F = 0.675$; d$f = 11, 745$; $P = 0.763$). Length of forearm of males ranged from 61.8 mm to 79.3 mm, a difference of 28%. In females, length of forearm ranged from 60.2 mm to 80.1 mm, a difference of 33% (Table 1). Variation in body mass for the 1998 subset of males and nonpregnant females also conformed to a log-normal distribution (one-sample Kolmogorov-Smirnov test: $Z = 0.994$; $n = 329$; $P = 0.277$) and exhibited a relatively greater range of variation: 75% in males (38.7 g–67.9 g) and 78% in non-pregnant females (39.0 g–69.5 g).

The two-way MANOVA revealed a highly significant effect of locality, a marginally significant effect of sex, and a highly significant locality × sex interaction (Table 2A). Univariate *F*-tests on each external character of *C. sphinx* revealed a uniformly high degree of heterogeneity among localities ($P < 0.001$ for all variables). Single-variable tests also revealed statistically significant differences between the sexes for DIG3, DIG4, and DIG5 ($P < 0.05$) and a significant locality × sex interaction for DIG4 ($P < 0.05$). The geographic pattern of multivariate differences between the sexes is evaluated in more detail below. Univariate analyses of length of forearm also revealed a high degree of heterogeneity among localities, but differences between the sexes were not statistically significant (Table 2B). Males and females were treated separately in subsequent analyses.

Geographic Variation in Body Size

In both sexes of *C. sphinx*, the first axis of the principal components analysis (E1) was clearly interpretable as an overall size vector. Factor loadings for all characters

Table 2. Effects of geographic locality and sex on variation in external morphology of *Cynopterus sphinx* as revealed by MANOVA and univariate ANOVA with two-way factorial design. The multivariate analysis is based on seven external characters for a subset of bats (n = 256). The univariate analysis is based on length of forearm for the full sample of bats (n = 757).

(a) Multivariate analysis	Effect	d*f*	Pillai's trace	*F*	*P*
	Locality	35, 1210	0.958	8.190	<0.001
	Sex	7, 238	0.056	2.021	0.053
	Locality × sex	35, 1210	0.266	1.946	0.001
(b) Univariate analysis	Effect	d*f*	Type III SS	*F*	*P*
	Locality	10	0.138	84.506	<0.001
	Sex	1	3.893×10^{-4}	2.376	0.124
	Locality × sex	10	2.467×10^{-3}	1.506	0.133
	Error	735	0.120		

Table 3. Factor loadings of seven external variables on the first principal component axis (PC1) computed for males and females of *Cynopterus sphinx*. Principal components analysis was conducted on each sex separately, and PC1 was extracted from the variance-covariance matrix of $\log_{10}$-transformed variables. See text for abbreviations of characters.

Variable	Males (n = 100) PC1	Females (n = 156) PC1
Length of forearm	0.920	0.903
Length of tibia	0.907	0.883
Length of DIG2	0.954	0.929
Length of DIG3	0.969	0.938
Length of DIG3P1	0.865	0.914
Length of DIG4	0.961	0.921
Length of DIG5	0.948	0.834
Variance explained (%)	87.0	81.7
Eigenvalue	6.09	5.72

were uniformly high and positive (Table 3). Moreover, PC1 was strongly and positively correlated with body mass in males (r = 0.820, n = 100, P < 0.001) and nonpregnant females (r = 0.741, n = 137, P < 0.001), as illustrated in Figure 2. Single-classification ANOVA revealed a high degree of heterogeneity in mean PC1 among localities for both males (F = 21.963, df = 5, 94, P < 0.001)and females (F = 27.067, df = 5, 150, P < 0.001). Mean PC1 scores for both sexes exhibited a progressive increase from south to north, indicating a latitudinal cline in overall body size (Figure 3).Multiple comparisons using Hochberg's GT2-method revealed similar geographic patterns of size variation in both sexes. The interval between Sorab/Shimoga and Kolhapur/Belgaum represented a statistically significant demarcation between southern and northern subdivisions of the transect (P < 0.05). In females, samples from Kolhapur/Delgaum and Pune were also identified as statistically distinct subsets.

The pattern of clinal variation in body size was further substantiated by analysis of length of forearm for the full sample of bats across the transect. Length of forearm exhibited high factor loadings on PC1 (Table 3) and a low coefficient of variation relative to other external characters, and therefore provided a useful univariate index of overall body size. Length of forearm also was strongly and positively correlated with body mass in males (r = 0.814, P < 0.01, n = 100) and nonpregnant females (r = 0.731, P < 0.01, n = 229), as illustrated in Figure 4. The magnitude of correlations remained similar even when considering the full sample of bats collected in different seasons and different years (males: r = 0.708, P < 0.001, n = 241, and non-pregnant females: r = 0.741, P < 0.001, n = 401). In accordance with the multivariate analysis, single-classification ANOVA revealed a significant degree of heterogeneity among localities in mean length of forearm for males (F = 51.005, df = 6, 234, P < 0.001) and females (F = 136.532, df = 6, 509, P < 0.001). Differentiation among localities in length of forearm was chiefly attributable to a monotonic cline in body size (Figure 5). Mean length of forearm at Pune (73.9 mm), the northernmost locality on the transect, was 9.8% larger than at Nagercoil (67.3 mm), the southernmost locality. Multiple comparisons revealed that Pune exhibited the greatest degree of differentiation in samples of both sexes. The remaining localities were grouped into three statistically homogeneous subsets, all of which were partially overlapping. As illustrated in Figure 6, body mass exhibited a highly concordant pattern of clinal variation relative to PC1 and length of forearm.

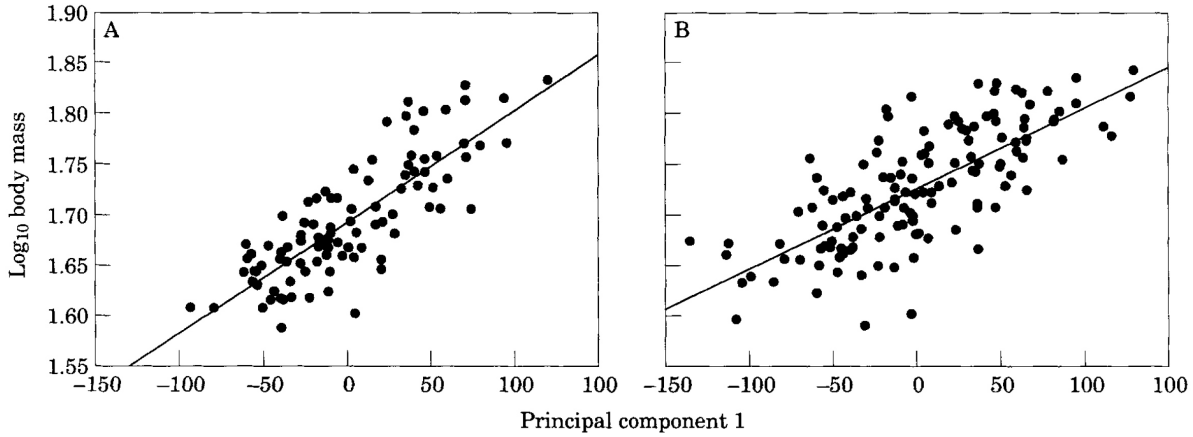

Figure 2. Bivariate plots of $\log_{10}$-body mass *vs*. PC1 for (A) males (n = 100) and (B) nonpregnant females (n = 156) of *Cynopterus sphinx*. All bats were sampled during an 8-week period in the 1998 dry season. Least squares linear regression lines are shown for illustration.

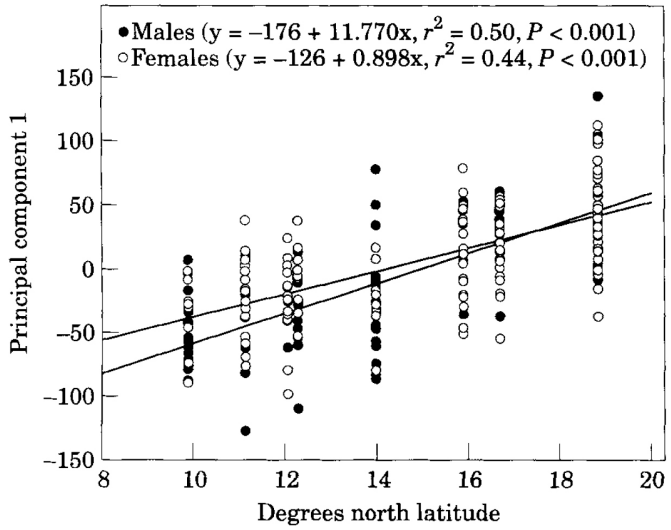

Figure 3. Model I linear regression of PC1 against latitude for males (n = 100) and females (n = 156) of *Cynopterus sphinx* sampled in peninsular India.

Influence of Ecogeographic Factors on Body Size

The first axis of the principal components analysis on temperature variables (PC1-T) explained 79.2% of the variance among localities (eigenvalue = 3.96). Correlations between the original variables and PC1-T factor scores were high and positive (maximum temperature, r = 0.523; minimum temperature, r = 0.985; average temperature, r = 0.741; wet-bulb temperature, r = 0.943), except for annual range of temperature (an index of seasonality), which exhibited a strong negative correlation (r = –0.677). PC1-T was interpreted as an overall temperature/equability vector. The first axis of the principal components analysis on rainfall variables (PC1-R) explained 73.1% of the variance among localities (eigenvalue = 2.92). Correlations between original variables and PC1-R factor scores were uniformly high and positive (maximum rainfall, r = 0.986; minimum rainfall, r = 0.942; average rainfall, r = 0.971; annual range of rainfall, r = 0.848). PC1-R was therefore clearly interpretable as an overall rainfall vector. The second axis of the principal components analysis on rainfall variables (PC2-R) explained 26.0% of the variance among localities (eigenvalue = 1.04). This vector contrasted minimum rainfall (r = –0.277) and average rainfall (r = –0.167), against maximum rainfall (r = 0.212) and annual range of rainfall (r = 0.573). PC2-R was interpreted as a measure of seasonality of rainfall. Principal components analysis of temperature and rainfall variables thus produced an ordination of sampling localities across a north-to-south gradient of increasing minimum, maximum, and mean temperature, increasing relative humidity (as indexed by wet-bulb temperature), and decreasing seasonality of temperature and precipitation.

Associations between PC1 and ecogeographic variables were highly concordant between the sexes (Table 4). The inverse correlation between latitude and longitude reflects the northwest to southeast orientation of the transect. Similarly, elevation along the transect increases as a positive function of latitude. Partial correlation analysis revealed that when latitude was held constant, longitude and elevation were not significantly associated with PC1 scores of males (longitude, r = -0.227, P = 0.824; elevation, r = –0.141, P = 0.165) or females (longitude, r = 0.071, P = O.381; elevation, r = –0.064, P = 0.426). With regard to climatological variables, PC1 scores of males and females were most strongly correlated with the temperature vector (PC1-T)and the second rainfall vector (PC2-R). These same variables emerged as the best predictors of size variation in the stepwise multiple regression analysis (Table 5). The magnitude and sign of

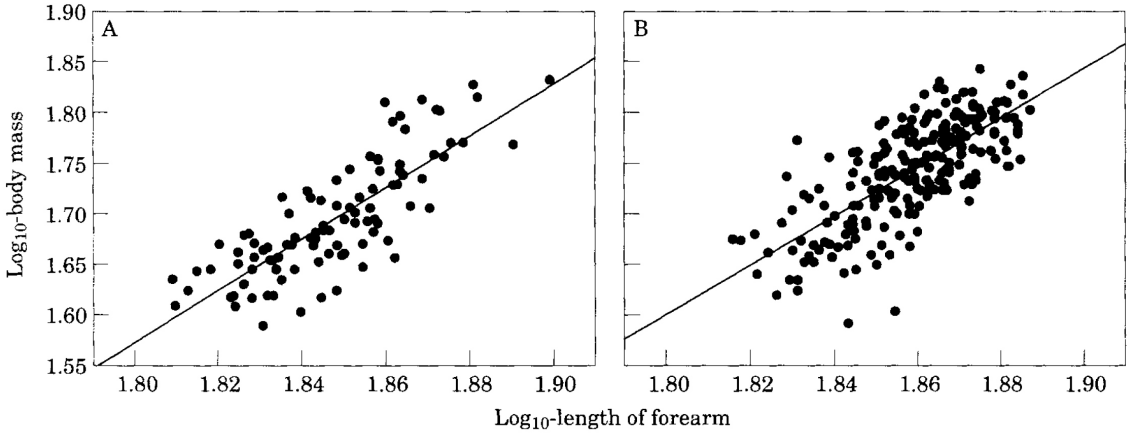

Figure 4. Bivariate plots of $\log_{10}$-body mass vs. $\log_{10}$-length of forearm for (A) males (n = 100) and (B) nonpregnant females (n = 229) of *Cynopterus sphinx* . All bats were sampled during an 8 week period in the 1998 dry season. Least squares linear regression lines are shown for illustration.

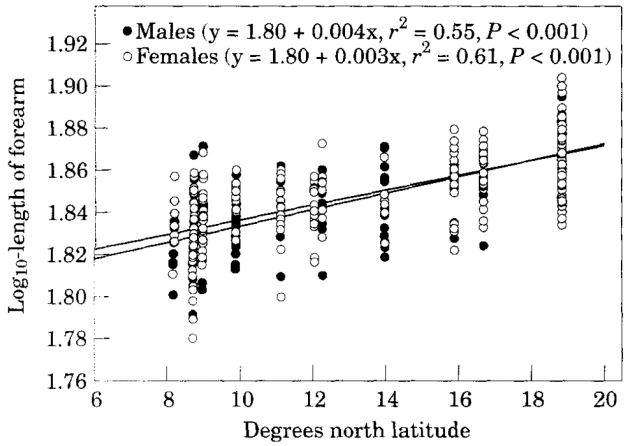

Figure 5. Model I linear regression of $\log_{10}$-length of forearm against latitude for males (n = 100) and females (n = 156) of *Cynopterus sphinx* sampled in peninsular India.

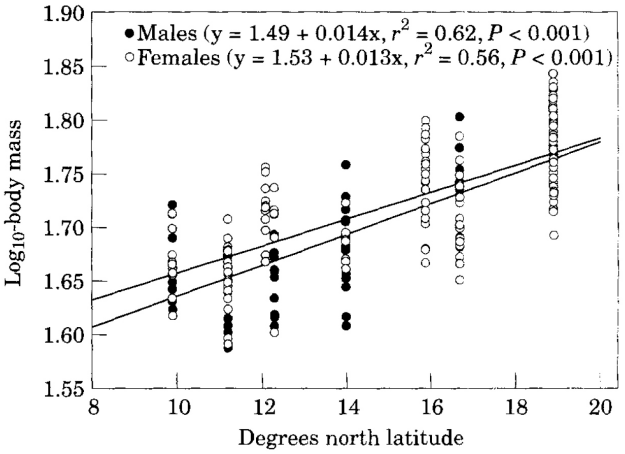

Figure 6. Model I linear regression of $\log_{10}$-body mass against latitude for males (n = 100) and females (n = 229) of *Cynopterus sphinx* sampled in peninsular India during an 8 week period in the 1998 dry season.

the standardized regression coefficients indicated that increasing body size of both sexes was primarily associated with decreasing minimum temperature, decreasing relative humidity, and increasing seasonality.

Geographic Variation in Sexual Dimorphism

A statistically significant degree of sexual dimorphism in overall body dimensions of *C. sphinx* was detected in the northernmost locality (Pune), and in two of the southern localities (Table 6). The size differential reversed direction across the latitudinal gradient, as males averaged slightly larger in the north, and females averaged slightly larger in the south. The degree of female-biased size dimorphism across the transect was negatively correlated with body size (PC1) of both males (r = –0.911, P = 0.011) and females (r = –0.830, P = 0.041). Variation between the sexes in length of forearm mirrored the latitudinal pattern revealed by the multivariate analysis; males averaged larger in the northernmost localities, and females averaged larger in all localities < 15°N. The female- biased size differential in length of forearm was statistically significant in Othakadai (F = 5.302; df = 1, 29; P = 0.029) and approached statistical significance in the southern Tamil Nadu localities (F = 3.419; df = 1, 274; P = 0.066). The degree of female-biased size dimorphism in length of forearm across the transect was negatively correlated with mean values for males (r = –0.616, P = 0.140) and females (r = –0.777, P = 0.040).

Having revealed a significant locality × sex interaction by means of two-way MANOVA (Table 2A), a canonical discriminant analysis was used to investigate the geographic pattern of sexual dimorphism in *C. sphinx* in more detail. Point samples on the transect were pooled

Table 4. Pearson product-moment correlations among body size of male and female *Cynopterus sphinx* (as indexed by PC1), geographic variables, and principal components of variation in temperature (PC1-T), and rainfall (PC1-R and PC2-R).

	PC1 males	PC1 females	Latitude	Longitude	Elevation	PC1-T	PC1-R	PC2-R
PC1 males	1.00	0.986**	0.691**	–0.642**	0.414**	–0.450**	0.134	0.327**
PC1 females		1.00	0.660**	–0.597**	0.302**	–0.450**	0.037	0.472**
Latitude			1.00	–0.934**	0.520**	–0.780**	0.190*	0.502**
Longitude				1.00	–0.582**	0.773**	–0.378**	–0.444**
Elevation					1.00	–0.892**	0.317**	0.039
PC1-T						1.00	–0.262**	–0.036
PC1-R							1.00	0.052
PC2-R								1.00

* $P < 0.05$, ** $P < 0.01$

Table 5. Results of stepwise multiple regression analyses of body size of male and female *Cynopterus sphinx* (as indexed by PC1) against climatic variables. The following stepwise criteria were employed probability of *F*-to-enter < 0.050, and probability of *F*-to-remove > 0.100. The standardized regression coefficients express the importance of particular independent variables in determining the value of PC1, when other variables are held constant. The coefficients of multiple determination (R^2 and adjusted R^2) for all entered variables are given in parentheses below. These coefficients express the fraction of the total variability of PC1 attributable to the effects of the independent variables, as defined by the regression model fit to the data.

	PC1 (Males)	PC1 (Females)
Climatological variables	Standardized regression coefficient	Standardized regression coefficient
PC1-Temperature	–0.615 ($P < 0.001$)	–0.462 ($P < 0.001$)
PC1-Rainfall	0.018 ($P = 0.817$)	–0.108 ($P = 0.094$)
PC2-Rainfall	0.524 ($P < 0.001$)	0.461 ($P < 0.001$)
	($R^2 = 0.451$, adjusted $R^2 = 0.433$)	($R^2 = 0.421$,adjusted $R^2 = 0.410$)

Table 6. Degree of sexual dimorphism of *Cynopterus sphinx* as revealed by two-sample MANOVA for six general localities. Direction of the size differential indicates which sex averages larger in size across all external characters.

Localities (North to South)	Direction	d*f*	Hotelling's T^e	Exact *F*	*P*
Pune	♂ > ♀	7, 53	0.242	2.417	0.032
Kolhapur/Belgaum	♂ > ♀	7, 56	0.133	1.222	0.306
Sorab/Shimoga	♂ < ♀	7, 22	0.233	0.953	0.488
Thithimathi/Mysore	♂ < ♀	7, 32	0.386	2.879	0.019
Metupalayam	♂ < ♀	7, 22	0.574	4.227	0.004
Othakadai	♂ < ♀	7, 23	0.316	1.516	0.211

into three latitudinal subdivisions: northern (>15°N), central (11–15°N), and southern (<11°N). Each of the three analyses included ≥ 30 individuals of each sex. The canonical discriminant analysis revealed statistically significant differences between the sexes in the southern subdivision (eigenvalue = 0.322, Wilks' $\Lambda = 0.756$, df = 7, $P = 0.030$), but not in the central (eigenvalue = 0.171, Wilks' $\Lambda = 0.854$, df = 7, $P = 0.178$) or northern subdivisions (eigenvalue = 0.096, Wilks' $\Lambda = 0.912$, df = 7, P = 0.140). Within each subdivision, the direction of the size differential was uniform across all characters (Figure 7). Males averaged larger in all external characters in the northern subdivision, and females averaged larger in all characters in the central and southern subdivisions. Profiles of importance values in the northern subdivision were negatively correlated with those of the central (r = –0.228, $P = 0.622$) and southern subdivisions (r = –0.572, $P = 0.179$). This pattern indicated that male- and female-biased size dimorphism were based on contrasting sets of external characters. Female-biased size dimorphism

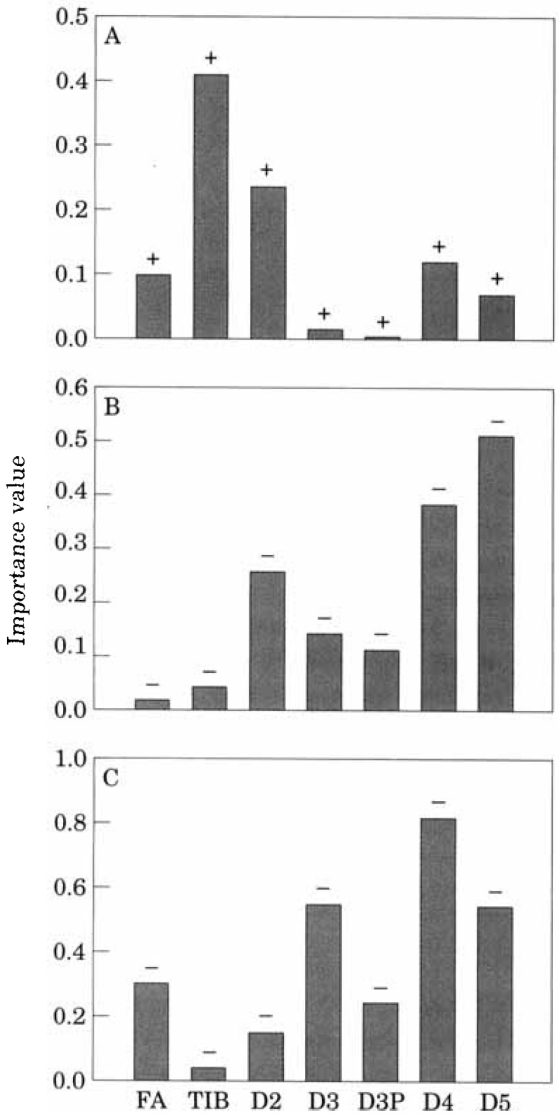

Figure 7. Profiles of importance values for seven external characters that distinguish between the sexes in *Cynopterus sphinx*. Point samples on the transect were pooled into three latitudinal subdivisions: A, northern (>15°N); B, central (11–15°N); and C, southern (<11°N). Importance values are estimates of the fraction of morphometric variance between the sexes attributable to a particular character. The sign above each bar indicates direction of the size differential for each character; a plus (+) indicates that males are larger than females, and a minus (−) indicates that females are larger than males. See text for abbreviations of characters.

was primarily attributable to a proportional increase in the area of the hand-wing, as indicated by the high importance values for DIG3, DIG4, and DIG5 in the southern subdivision. By contrast, male-biased dimorphism in the northern subdivision was primarily attributable to length of tibia and DIG2, although importance values were low for most characters. Although direction of the size differential was similar in the central and southern subdivisions, profiles of importance values were not strongly correlated ($r = 0.630$, $P = 0.129$). Lack of statistical significance likely reflects the fact that the overall degree of sexual size dimorphism was relatively subtle.

Discussion

Geographic Variation in Body Size

The pattern of geographic variation in the external morphology of *Cynopterus sphinx* conforms to Bergmann's Rule, as indicated by a monotonic cline of increasing body size from south to north. Multivariate and univariate indices of structural size were strongly and positively correlated with body mass, and exhibited highly concordant patterns of clinal variation. This study represents one of the first conclusively documented examples of Bergmann's Rule in a tropical mammal and provides further confirmation that latitudinal clines in body size are not exclusively restricted to temperate zone homeotherms (Graves, 1991).

In pteropodid bats, basal metabolic rate is highly size-dependent and medium-sized frugivorous species such as *C. sphinx* are typically characterized by precise regulation of body temperature (McNab, 1989; McNab & Bonaccorso, 1995). Because the energetics of temperature regulation have important consequences for fecundity, gestation period, and rates of postnatal growth in bats (McNab, 1982; Kunz, 1987), the ecologically optimal body size of non-migratory species may be expected to vary geographically in response to broad-scale climatic gradients. However, pteropodid bats are also known to employ a diverse array of physiological and behavioral strategies to maintain heat and water balance in extreme environments (McNab & Bonaccorso, 1995; Ochoa-Acuña & Kunz, 1999), so adaptive adjustments to environmental challenges may not necessarily entail changes in gross morphology. Although many pteropodid species occupy day-roosts in highly exposed situations such as tree canopies, roosting groups of *C. sphinx* typically aggregate in confined spaces such as tree hollows or modified foliage roosts (Bhat & Kunz, 1995; Balasingh *et al.*, 1995; Storz *et al.*, 2000a,b). *Cynopterus sphinx* has a polyestrus reproductive cycle and adult females are either pregnant or lactating throughout most of the year (Storz & Kunz, 1999). Aggregation into tightly clustered groups can significantly alter the microclimate of diurnal roosts, thereby minimizing energetic costs to reproductive females and mitigating the effects of adverse temperature and humidity conditions in the outside environment (Kunz, 1982). With regard to the thermoregulatory capacities of birds and mammals, Scholander (1955) argued that such behavioral adjust-

ments, in addition to changes in insulation and mechanisms of vascular control, largely preclude an adaptive role for body size. However, as stated by Mayr (1963: 321), "Multiple solutions for biological needs are the general rule in evolution. Selective advantages are independent and strictly additive. The fact that a thicker fur or denser plumage reduces heat loss does not eliminate completely the selective advantage of an improved body surface/volume ratio." The same logic applies to physiological explanations of Bergmann's Rule that are based on the scaling relationship between body mass and total metabolic rate.

Causal explanations for the underlying basis of Bergmann's Rule have traditionally invoked the adaptive significance of body size in connection with temperature regulation or conservation of metabolic water (Hamilton, 1961; Mayr, 1963; Brown & Lee, 1969; Power, 1969; James, 1970). An alternative hypothesis is that geographic patterns of size variation primarily reflect selection for fasting endurance during episodic periods of food scarcity in seasonal environments (Boyce, 1979; Lindstedt & Boyce, 1985; Millar & Hickling, 1990). In contrast to explanations based on surface/volume ratios, the fasting endurance hypothesis is based on a relationship between starvation time and body mass that is derived from total units, and therefore can be interpreted with respect to both total and mass-specific rates of metabolism (McNab, 1999). This hypothesis has received correlative support from studies of intraspecific variation in temperate zone rodents (Boyce, 1978; Owen, 1989), marsupials (Quin *et al.*, 1996), and passerine birds (Murphy, 1985). The fasting-endurance hypothesis deserves serious attention in nonmigratory tropical frugivores and nectarivores that rely on the sequential overlap of fruiting and flowering peaks in different plant species throughout the annual cycle. The latitudinal cline in body size of *C. sphinx* is consistent with each of the major adaptive hypotheses, due to parallel variation in multiple climatic factors across peninsular India. The increase in body size of *C. sphinx* parallels a latitudinal gradient of increasing minimum daily temperature, decreasing relative humidity, and increasing seasonality of temperature and precipitation. Each of the relevant climatic factors covary to such an extent that their independent effects cannot be readily discerned. A broader geographic scale of sampling may be required to elucidate the causal basis of clinal variation. Furthermore, calculating an index of seasonality that is biologically relevant to tropical frugivores would require information on the phenology of key food plants on a macrogeographic scale.

With regard to the multiple regression analysis, the explanatory power of the complete set of ecogeographic variables was comparable to that observed in previous studies of geographic variation in continental populations of vespertilionid bats (Burnett, 1983; Bogdanowicz, 1990). In North America, *Eptesicus fuscus* exhibits a progressive increase in size across a gradient of decreasing ambient temperature, in agreement with the classical form of Bergmann's Rule. In contrast to the pattern observed in Indian populations of *C. sphinx,* wing size of *E. fuscus* exhibited a proportional decrease across a gradient of increasing aridity. However, interpretation of this trend was complicated by the fact that patterns of variation in craniometric and external characters were not entirely concordant (Burnett, 1983). In the absence of data on body mass, it is not clear whether craniometric characters provide a meaningful index of overall structural size. Also consistent with Bergmann's Rule, Eurasian populations of *Myotis daubentoni* exhibit a progressive increase in size (as indexed by craniometric and dental characters) across a gradient of decreasing temperature and increasing precipitation. Negative correlations between ambient temperature and size (or positive correlations between latitude and size) have been reported for several microchiropteran bat species (Findley & Jones, 1967; Stebbings, 1973; Bogan, 1975; Owen *et al.*, 1984; Tidemann, 1986; Hand & York, 1990), though exceptions exist (Strelkov, 1972). Still other species exhibit complex patterns of geographic variation that defy a clear explanation in terms of climatic adaptation (Findley & Traut, 1970; Nagorsen & Tamsitt, 1981; McLellan, 1984; Kitchener & Caputi, 1985). In the Lesser Sunda Islands of the Malay Archipelago, *Cynopterus nusatenggara* (Pteropodidae) and *Hipposideros diadema* (Hipposideridae) exhibit longitudinal clines of increasing size across a west-to-east gradient of increasing aridity and climatic severity (Kitchener *et al.*, 1992; Kitchener & Maharadatunkamsi, 1996). These same patterns of geographic size variation are paralleled by a number of co-distributed Indo-Australian mammals (Kitchener & Suyanto, 1996), which strongly suggests a common evolutionary response to a shared set of spatially varying ecogeographic factors. The generality of clinal variation in body size of Indian mammals and birds remains to be investigated, although information compiled by Ali & Ripley (1980) indicates that many nonmigratory birds of the Indian plains (including pigeons, parakeets, trogons, mynas, and bulbuls) exhibit a south-to-north trend of increasing size. The remarkably steep cline in body size of *Cynopterus sphinx* suggests that variation of equal or greater magnitude can be expected in other small-bodied homeotherms that are distributed across the same climatic gradients.

Geographic variation in body size may also reflect the influence of character displacement in areas of range overlap between ecologically similar species that com-

pete for the same food resources (Grant, 1965; Brown, 1975; Heaney, 1978). Of the four other species of frugivorous bats that occur in peninsular India, only *Rousettus leschenaulti* and *Pteropus giganteus* could reasonably be expected to represent close competitors of *C. sphinx,* and both species have equally cosmopolitan distributions (Bates & Harrison, 1997). *Cynopterus brachyotis* (a smaller-bodied congener) and *Latidens salimalii* are largely restricted to tropical evergreen forest habitat in higher elevations of the Western Ghats (Storz *et al.*, unpublished data; J. Koilraj, pers. comm.). More refined information on the ecological distribution, relative abundance, and degree of dietary overlap among avian and mammalian frugivores (Ganesh & Davidar, 1999) are needed to assess whether competitive interactions have any significant role in determining body size variation of *C. sphinx* in peninsular India.

Geographic Variation in Sexual Dimorphism

Although patterns of size variation were highly concordant between the sexes, *C. sphinx* also exhibited a latitudinal cline in the magnitude and direction of sexual size dimorphism. Geographic variation in sexual dimorphism has been documented in several mammalian taxa, including pocket gophers (genus *Thomomys*; Patton & Smith, 1992), North American weasels (genus *Mustela*; Ralls & Harvey, 1985), and Australian sugar gliders (genus *Petaurus*; Quin *et al.*, 1996). With regard to causal explanations for the pattern of sexual dimorphism in *C. sphinx,* Myers' (1978) hypothesis makes clear predictions about the nature of morphological differences between the sexes. Specifically, selection on females for reduced wing-loading should result in females having proportionally greater wing area relative to males. The hypothesis of Williams & Findley (1979) provides an equally clear prediction about variation in sexual dimorphism in response to climatic variation; selection on females for enhanced thermal inertia should result in a greater degree of female-biased size dimorphism in colder environments. The pattern of sexual dimorphism in *C. sphinx* appears to support Myers' (1978) wing-loading hypothesis. In the southernmost localities, where the degree of female-biased size dimorphism was most pronounced, characters that exhibited the greatest size differential were skeletal elements of the hand-wing. It is unclear, however, why the female-biased size differential is negatively correlated with overall body size. The pattern of geographic variation in sexual dimorphism of *C. sphinx* is in direct contrast to the prediction of the Williams & Findley (1979) hypothesis. If the adaptive value of increased female size is related to thermal homeostasis during pregnancy, the degree of female- biased dimorphism should be inversely correlated with mean minimum daily temperature. The opposite pattern was observed, as males were larger than females in the northernmost localities where minimum temperatures are lowest (18.2–19.2°C). The hypothesis of Williams & Findley (1979) was originally formulated in terms of the relationship between body size and the energetics of temperature regulation in vespertilionid bats. Perhaps this hypothesis is not generally applicable to pteropodid bats in tropical environments.

The increase in relative size of males in the northernmost localities may also reflect the pressure of sexual selection. Available evidence suggests that the degree of polygyny may be subject to a considerable degree of geographic variation in *C. sphinx* . Information on the mode of social organization and mating system is available for Pune (northern locality; Storz *et al.*, 2000b) and Palayamkottai (southern locality; Storz *et al.*, 2000a). In both localities, the clustering of breeding females in confined roosting spaces facilitates a male mating strategy of resource defense polygyny (Storz *et al.*, 2000a,b). Comparative census data revealed striking differences between the two sites with regard to patterns of female dispersion during the postpartum estrus period. Compared to Palayamkottai, the mean number of breeding females per roost in Pune was 16.4-fold greater, the proportion of available roosts defended by territorial males was 5.8-fold greater, the overall level of female aggregation (as indicated by the variance/mean ratio of harem size) was 4.7-fold greater, and the average harem sex ratio was 4.2-fold greater. Interpreting the harem sex ratio as an empirical measure of the potential for polygyny, the expected variance in male mating success (and concomitant opportunity for sexual selection) appears to be much higher in Pune than in Palayamkottai. Information on the mating system of *C. sphinx* from a greater number of localities and habitat types will be required to determine whether the degree of polygyny does in fact covary with the magnitude of male-biased size dimorphism.

Acknowledgments

For assistance in the field, we thank S. Isaac, J. Ronald, K. Emmanuel, N. Gopukumar Nair, V. Elangovan, J. Koilraj, and E. Rajan. For logistical support we thank G. Marimuthu, R. Subbaraj, G. Desai, K. N. More, D. N. Deobagkar, S. R. R. Reddy, S. L. Shinde, R. Patel, and the personnel at St. John's College, St. Xavier's College, Madurai Kamaraj University, Mysore University, Vaccine Institute of Belgaum, Shivaji University, and Pune University. For comments on the manuscript, we thank B. K. McNab, T. Kingston, C. J. Schneider, F. E. Wasserman, and two anonymous reviewers for the *BJLS*. Field expeditions by JFS and HRB in 1997–1998 were funded by a Research and Exploration Grant from the National

Geographic Society. Additional funding was provided by grants to JFS from the National Science Foundation (Dissertation Improvement Grant DEB 97-01057), Sigma Xi, the American Society of Mammalogists, Bat Conservation International, and the Society for Integrative and Comparative Biology, and a grant to THK and JFS from the Lubee Foundation, Inc. JFS received additional support from the Albert R. and Alma Shadle Fellowship in Mammalogy during preparation of the manuscript.

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