

SECONDARY SEXUAL DIMORPHISM AND PHYLOGENETIC CONSTRAINTS IN BATS: A MULTIVARIATE APPROACH

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We develop a method to evaluate the degree to which particular morphological characteristics contribute to multivariate group differences in general and to secondary sexual dimorphism for size and shape in particular. In addition, we recommend a correlative approach to assess the degree to which the contribution of characters to group differences is consistent in different taxa. We apply both methods to a suite of 12 cranial characters obtained from populations of 18 species of bats in five families (Emballonuridae, Noctilionidae, Phyllostomidae, Vespertilionidae, and Molossidae) from Caatinga and edaphic Cerrado biomes of northeastern Brazil. As expected, a correlation usually does not exist between profiles of the importance of characters to sexual dimorphism from the two biomes if the taxa are monomorphic with regard to sex (e.g., *Vampyrops lineatus*, *Artibeus lituratus*, and *Myotis riparia*); any differences between the sexes within a biome are a result of chance. In contrast, significant correlations between profiles of importance of characters to intersexual variation in the two biomes usually exist when species are dimorphic (e.g., *Anoura geoffroyi*, *Carollia perspicillata*, *Glossophaga soricina*, *Phyllostomus discolor*, *Molossus molossus*, and *Artibeus planirostris*). Significant constraints on the expression of sexual dimorphism exist between populations of the same species; similar suites of characters are involved in intersexual variation if dimorphism exists. Such constraints appear inoperative at higher taxonomic levels. We hypothesize that once differentiation occurs at the specific level, coadapted gene complexes and genetic dynamics associated with epistasis, pleiomorphism, and linkage disequilibrium no longer constrain dimorphism in the same fashion as in the ancestral condition.

Key words: sexual dimorphism, phylogenetic constraints, morphometrics, Chiroptera, Phyllostomidae, Molossidae, Vespertilionidae, Emballonuridae, Neotropics, Brazil

From as early as the time of Darwin (1859), evolutionary biologists have been intrigued by secondary sexual dimorphism. Indeed, the mechanisms giving rise to secondary sexual dimorphism, as well as its consequences, continue to be of interest to systematists (Mayr, 1942; Wade, 1976; Yablokov, 1974), geneticists (Arnold, 1985; Falconer, 1960; Lande, 1987; Leutenegger and Cheverud, 1985; Wright, 1968, 1977), and ecologists (Bell, 1982; Shine, 1986; Shine and Crews, 1988) alike. The relation between secondary sexual dimorphism and

polygamous mating systems, unequal sex ratios, differential maturation rates, and dissimilar resource utilization is critical to a number of evolutionary theories (Daly and Wilson, 1978; Selander, 1957). Nonetheless, confusion exists as to what characteristics are ultimate factors selecting for dimorphism and which are secondary effects of the dimorphic condition (compare sexual-selection hypothesis—Trivers, 1972; Wilson, 1975; resource-utilization hypothesis—Selander, 1966, 1972; and big-mother hypothesis—Ralls, 1976, 1977). Moreover,

controversy surrounds the quantification of dimorphism. Although secondary sexual dimorphism historically has been considered from a univariate perspective, Willig et al. (1986) and Willig and Owen (1987), like others before them (Cheverud et al., 1985; Jolicoeur, 1959, 1984), have argued that a univariate approach is inadequate unless single character hypotheses are of interest rather than those concerning variation for size and shape in general. In contrast, Corruccini (1987) suggested that the univariate approach, even in a multivariable setting, can be more informative under certain circumstances (i.e., when one or more univariate test is significant, but the multivariate test is not significant).

Systematists often implicitly or explicitly consider dimorphism to be an attribute of a species when used in morphometric studies of geographic variation or secondary sexual variation. Two generally unacceptable approaches are pervasive. The conservative approach has been to analyze geographic variation separately for each sex if significant dimorphism is expected, detected, or documented in the literature for populations of the taxon of interest (Dowler and Genoways, 1979; Genoways, 1973; Hendrickson, 1973; Hollander, 1990; Humphrey and Setzer, 1989; Robertson et al., 1992; Russell, 1968). Conversely, when dimorphism is slight or undetected by statistical methods, variation attributable to sex has been ignored in subsequent analyses of geographic variation because data are combined without regard to sex (Carleton and Eshelman, 1979; Cooper et al., 1993; Dragoo et al., 1990; Engstrom and Choate, 1979; Moncrief, 1993; Riddle and Choate, 1986; Van Cura and Hoffmeister, 1966). In either approach, statistical power may be sacrificed and hypotheses of interest ignored because of reduced sample size or a failure to appropriately incorporate considerations of secondary sexual variation and its interaction with geographic variation into analyses.

The maintenance of dimorphism, at least

in part, is predicated on differential regulation of gene activity in males and females and should be constrained by the boundaries established within species to the extent that coadapted gene complexes are involved and characters are pleiotropic (Lande, 1987; Raff and Kaufman, 1983). Consistent with this view is the idea that phenotypic variation between sexes may be limited to particular characters in one species, which differ from those involved in dimorphism in another species. As a consequence, "closely related species differ most in secondary sexual characters of males, which are therefore among the most rapidly evolving and taxonomically important morphological traits," in higher animals (Lande, 1987:84). Following the same reasoning, populations within a species more likely would express dimorphism via a consistent suite of morphometric characters because the groups are linked to the degree to which they share gene pools. Hence, even if groups within a population differ in the balance among selective forces that result in dimorphism, certain characteristics may be more predisposed toward lability whereas others may be more invariant. The objectives of this study are threefold: to present a general quantitative method whereby the importance of a particular character in the discrimination of groups can be ascertained; to suggest a quantitative approach that measures the degree to which the characters that are indicative of group differences are consistent; to apply these techniques to the question of whether secondary sexual dimorphism is constrained by phylogeny in bats from two different biomes from northeastern Brazil.

MATERIALS AND METHODS

The Caatinga of northeastern Brazil is a large (650,000 km²), heterogeneous, semiarid region with a characteristically unpredictable precipitation regime. In areas unaffected by post-Cretaceous erosion, the original sandstone substrate persists as isolated plateaus or chapadas dominated by woodland-savanna vegetation (edaphic

TABLE 1.—Description of the suite of cranial characters used to examine secondary sexual variation in bats from Caatinga and edaphic Cerrado habitats of northeastern Brazil.

| Morphometric character (acronym) | Description |
|---|--|
| Greatest length of skull (GLS) | Distance from most anterior part of rostrum (excluding teeth) to posteriormost point of skull |
| Condylbasal length (CBL) | Distance from anteriormost edge of premaxillae to the posteriormost projection of the occipital condyles |
| Postorbital constriction (POC) | Least distance across top of skull posterior to postorbital process |
| Mastoid breadth (MB) | Greatest width of skull, including mastoids |
| Breadth of braincase (BBC) | Greatest width across braincase posterior to zygomatic arches |
| Rostral breadth (RB) | Width of rostrum at suture between premaxilla and maxilla |
| Breadth across upper molars (BUM) | Maximum width of outer alveolus of one molar to outer alveolus of opposite molar |
| Breadth across upper canines (BUC) | Width from outer alveolus of canine to outer alveolus of other canine |
| Length of maxillary toothrow (LMT) | Length from anterior edge of alveolus of first tooth present in maxillae to posterior edge of alveolus of last molar |
| Length of upper molariform toothrow (UMT) | Maximum length from anterior edge of alveolus of first premolar to posterior edge of alveolus of last molar |
| Greatest length of mandible (GLM) | Length from anteriormost point on ramus (excluding teeth) to posteriormost point on coronoid process |
| Length of mandibular toothrow (LLT) | Length from anterior edge of alveolus of canine to posterior edge of alveolus of last molar in mandible |

Cerrado). A Precambrian crystalline basement is exposed in extensive lowland areas where semi-deciduous thorn-scrub vegetation characterizes the landscape (Caatinga). Bats were obtained by mist-netting in Caatinga habitats (Exu, Pernambuco, Brazil) as well as from edaphic Cerrado habitats on the Chapada do Araripe (Crato, Ceara, Brazil). Caatinga and edaphic Cerrado sites were only 45 km apart, and all collection localities within each site were restricted to a circular area of ca. 80 km². Mares et al. (1981, 1985) and Willig (1983, 1986) provide a more detailed account of the study area and collection procedures.

Mensural data were obtained from 20 adult males and 20 adult females from each site for each species whenever possible; otherwise, all collected specimens of a taxon (Willig, 1983; Willig et al., 1986) were included in samples. Twelve cranial characters, each measured to the nearest 0.1 mm with dial calipers, constituted the variable suite (Table 1). We follow the nomenclatural recommendations of Willig and Mares (1989) in assigning bats from northeastern Brazil to species, except in the case of *Myotis*, where we follow Woodman (1993) and correctly use the feminine specific epithet, *riparia*, in place of *riparius* (the masculine gender). Based

on a multivariate phenetic evaluation of large *Tonatia* from northeastern Brazil (Williams et al., 1995), specimens provisionally allocated to *Tonatia childreni*, by Willig and Mares (1989) are assigned to *Tonatia saurophila* herein.

Significant microgeographic or intersexual variation in morphology was assessed via multivariate analysis of variance on the suite of cranial characters in Table 1; detailed results appear in Willig et al. (1986), with descriptive statistics summarized in Willig (1983). Stepwise discriminant-function analysis (Program Discriminant; SPSS Inc., 1986) was used to determine the linear combination of variables that best distinguished between the morphologies of males and females. Separate analyses were conducted for each site (Caatinga versus edaphic Cerrado). The loading of each variable on the discriminant-function axis is a measure of the importance of each variable in discriminating between sexes. However, some variables that are important in differentiating between sexes may have low loadings on the discriminant axes if they have high communality with other variables but little unique discriminatory ability. As a consequence, variables that significantly differ between sexes may not appear as important discriminators based on factor loadings or may not

even appear in the final equation based on step-wise, step-up, or step-down algorithms. To avoid this problem, the importance of the original characters in discriminating between sexes was ascertained by separately correlating each character to the discriminant-function score for each individual. The magnitude of the square of the correlation coefficient quantifies the importance of the variable in distinguishing between sexes and provides a measure of the proportion of the variation in the discriminant-function scores that is accounted for by variation in the original morphometric character. In all cases, we have standardized the polarity of discriminant-function axes so that males have higher loadings than do females. The sign of the correlation coefficient thereby reveals the direction of dimorphism: positive correlation between an original character and the discriminant-function score indicates that males are larger than females with respect to that character.

This quantitative method is applicable to situations involving more than two groups or more than one discriminant axis. In general, the importance (I_i) of a variable (i) in discriminating among a number of a priori groups (n) is given by:

$$I_i = \sum_{j=1}^{n-1} \lambda_j^2 r_{ij}^2$$

where λ^2 is the proportion of the variation among groups accounted for by discriminant-function j , and r_{ij}^2 is the square of the correlation coefficient between original character i and discriminant-function j . The importance of a variable thereby varies from 0 to $n - 1$, where 0 indicates no discriminatory value in a character and $n - 1$ represents maximal discriminatory ability. Dividing the importance value by $n - 1$ scales the index to a range from 0 to 1 and facilitates comparisons between analyses involving a different number of discriminant-function axes. In the special case of sexual dimorphism, $n = 2$ and a single discriminant axis exists, with I_i equaling r_{ij}^2 and varying from 0 to 1.

Bar diagrams, in which the height of the bar for a particular character i is equal to I_i , then provide convenient mechanisms for viewing the relative importance of particular characters in discriminating among groups. A comparison of bar diagrams for the same species in different areas, or for different species in the same higher taxon (e.g., species within a genus) provides a

means of evaluating character-specific phylogenetic constraints on the expression of secondary sexual dimorphism. The degree of concordance between character suites, in terms of the importance profile of variables as intergroup discriminatory agents, can be evaluated by correlating the importance values of each character between groups (Pearson's product moment correlation—Sokal and Rohlf, 1981). A high correlation can exist between the importance values for sexual dimorphism in two different localities, even if males are larger than females in one locality and females are larger than males in the other locality. The direction of dimorphism is obscured when the correlation coefficient is squared in the formula for importance. The correlation of importance values thereby measures the similar involvement of characters in discriminating between sexes regardless of the polarity of the contribution.

RESULTS

Eighteen species of bats in five families (Emballonuridae, 1 species; Noctilionidae, 1 species; Phyllostomidae, 12 species; Vespertilionidae, 2 species; Molossidae, 2 species) were obtained in adequate numbers for multivariate analyses of secondary sexual dimorphism. In a number of cases, a species only occurred in a single site (Caatinga or edaphic Cerrado), and, as a consequence, an analysis of phylogenetic constraints on the expression of dimorphism was not possible at the specific level. Nonetheless, it was possible to identify the cranial characters that contributed most to morphometric distinction between males and females.

Secondary sexual dimorphism within a site.—Eight species of bats occurred in adequate numbers for reliable statistical analyses of secondary sexual dimorphism within an area. Two of those species (*Trachops cirrhosus* and *Eptesicus furinalis*) were not dimorphic based on multivariate analyses of cranial characters (Willig et al., 1986). In those cases, importance values were consistently low compared with most situations in which secondary sexual dimorphism was significant (Fig. 1a and 1b). Six of the spe-

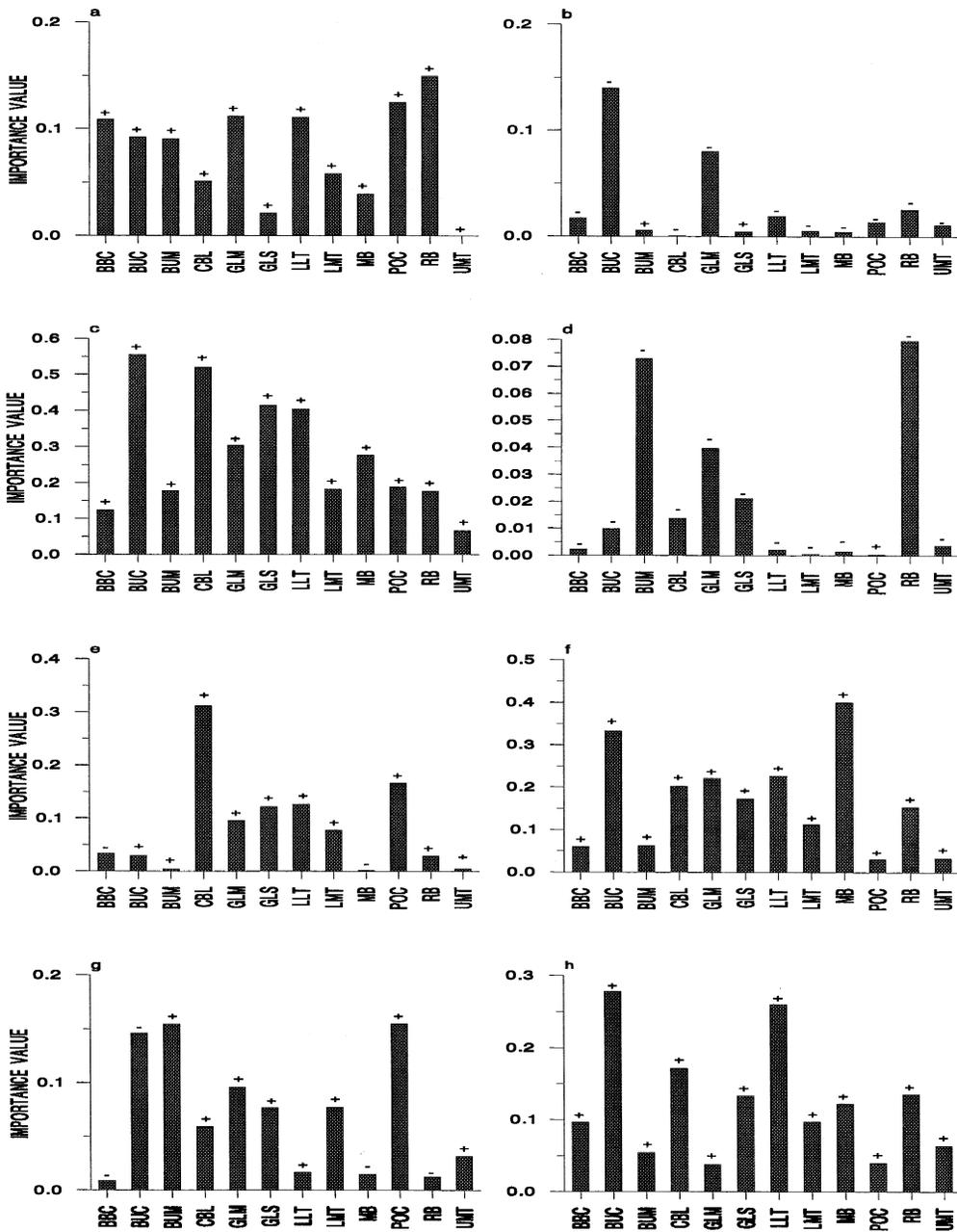


FIG. 1.—Values for profiles of importance for 12 cranial characters that distinguish between sexes in species of bats from a single area (Caatinga or edaphic Cerrado) in northeastern Brazil (a, *Trachops cirrhosus*; b, *Eptesicus furinalis*; c, *Noctilio leporinus*; d, *Peropteryx macrotis*; e, *Tonatia bidens*; f, *Phyllostomus hastatus*; g, *Lonchophylla mordax*; h, *Neoplattymops mattogrossensis*). Acronyms and descriptions of cranial characters are in Table 1. The height of a bar for a particular character equals its importance value (I) and estimates the proportion of variation between sexes that is accounted for by that character. The sign above each bar indicates direction of dimorphism for that character, with males larger than females indicated by a plus (+), and females larger than males indicated by a minus (-).

cies restricted to a single site (*Noctilio leporinus*, *Peropteryx macrotis*, *Tonatia bidens*, *Phyllostomus hastatus*, *Lonchophylla mordax*, and *Neoplaticomys mattogrossensis*; Fig. 1c–h, respectively) were dimorphic based on multivariate analyses of cranial characters (Willig et al., 1986); the profiles of importance values differed considerably among species.

Phylogenetic constraints within species.—Ten species of bats occurred in adequate numbers in each area to provide an evaluation of phylogenetic constraints on the expression of dimorphism in distinct populations of a species. Four species were monomorphic in both Caatinga and edaphic Cerrado, three species exhibited consistent dimorphism in both sites, and three species exhibited site-specific dimorphism.

Four species that occurred at both sites (*Vampyrops lineatus*, *Artibeus lituratus*, *Desmodus rotundus*, and *Myotis riparia*) were monomorphic for cranial characters (Willig et al., 1986). All but *D. rotundus* failed to exhibit a significant correlation between profiles of character importance in Caatinga and edaphic Cerrado (compare Fig. 2a–c with Fig. 2d). This observed nonsignificance is expected; the characters identified in the discriminant-function analysis somewhat separate the sexes in each sample, but the suite of characters chosen to discriminate in each area would not be expected to be similar if the sexes are statistically indistinguishable (i.e., any differences are no greater than that attributable to chance alone). Although *D. rotundus* does not exhibit significant secondary sexual variation (Willig et al., 1986) at either site, a significant correlation between profiles of importance values occurred between populations from the Caatinga and edaphic Cerrado ($R = 0.82$; $P < 0.001$). Breadth across the upper canines, condylobasal length, greatest length of mandible, and greatest length of skull differed most between sexes at both sites, but the magnitude of difference was insufficient to affect significant dimorphism, especially in the edaphic Cer-

rado where importance values for all characters were low (Fig. 2d).

Consistent secondary sexual dimorphism in the Caatinga and edaphic Cerrado was exhibited by *Anoura geoffroyi*, *Glossophaga soricina*, and *Carollia perspicillata* (Willig et al., 1986) based on multivariate analyses of cranial characters. The correlation between profiles of importance values was highly significant ($P < 0.001$) for *A. geoffroyi* ($r = 0.97$) and *C. perspicillata* ($r = 0.93$), indicating phylogenetic or intra-specific constraints on the characters that may differ between sexes. Breadth across upper canines and rostral breadth greatly contribute to the difference between males and females in *A. geoffroyi* (Fig. 3a) and in *C. perspicillata* (Fig. 3b). Those characters with high importance values are larger in males than in females. Although intersexual variation in *G. soricina* consistently was significant in Caatinga and edaphic Cerrado, the profiles of importance values were not correlated. In particular, breadth of braincase and greatest length of skull contributed the most to dimorphism in the Caatinga, whereas mastoid breadth and, to a lesser extent, breadth across upper canines and length of upper molariform toothrow, contributed to dimorphism in the edaphic Cerrado (Fig. 3c).

Three species (*Phyllostomus discolor*, *Artibeus planirostris*, and *Molossus molossus*) each exhibited secondary sexual dimorphism, which was habitat-specific, as indicated by significant two-way interactions in multivariate analyses of variance of cranial characters (Willig et al., 1986). Nonetheless, the highly significant correlation ($0.001 < P < 0.01$) between profiles of importance in each area for *P. discolor* ($r = 0.73$) and for *M. molossus* ($r = 0.77$) suggests that the morphological characters involved in dimorphism are similar within each species, regardless of biome (Fig. 3d and 3e, respectively). In the case of *M. molossus*, dimorphism is strong, with condylobasal length, greatest length of mandible, greatest length of skull, length of mandib-

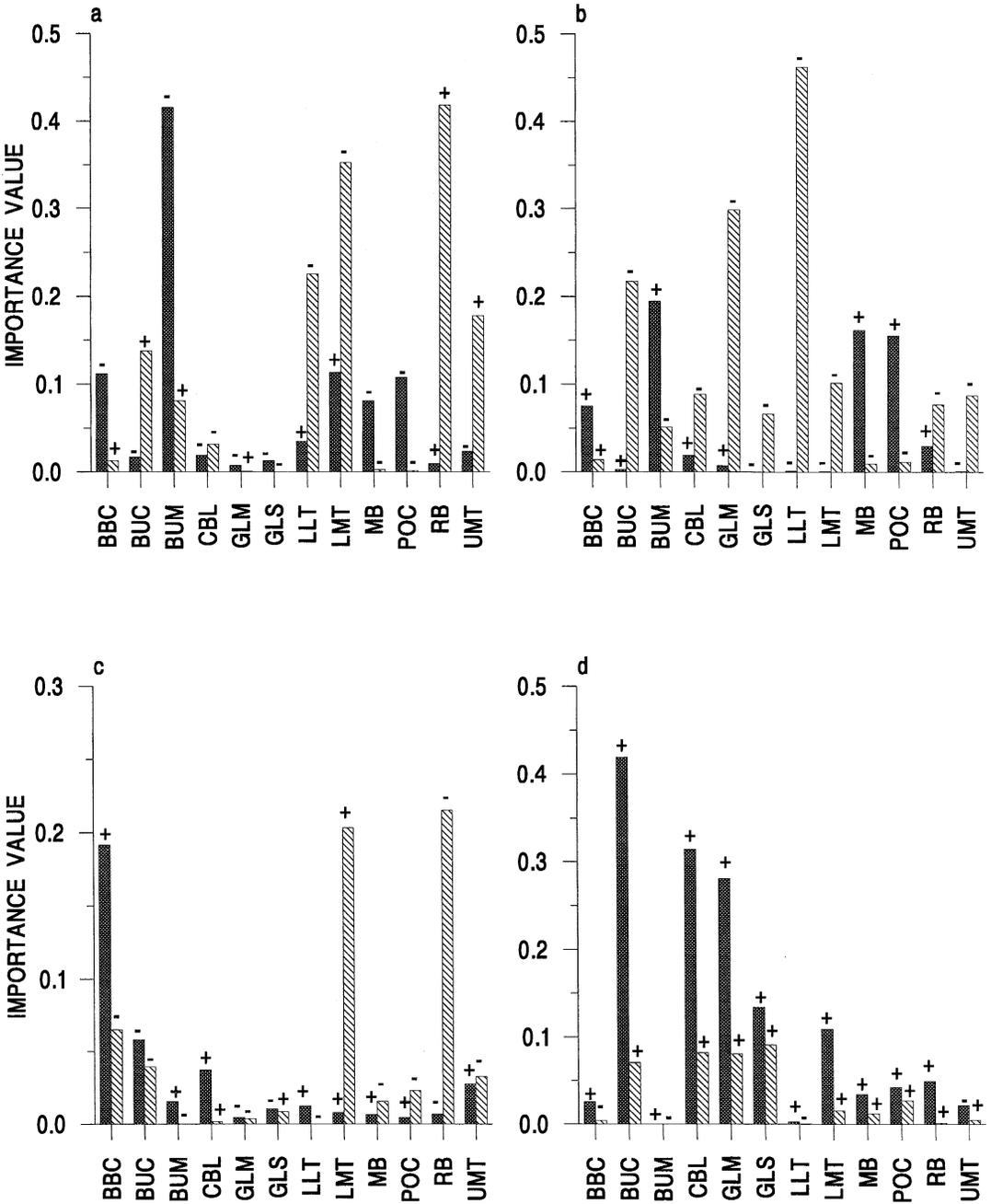


FIG. 2.—Values for profiles of importance for 12 cranial characters that distinguish between sexes in species of bats from Caatinga (cross-hatching) and edaphic Cerrado (hatching) of northeastern Brazil (a, *Vampyrops lineatus*; b, *Artibeus lituratus*; c, *Myotis riparia*; d, *Desmodus rotundus*). None of these species exhibited significant secondary sexual dimorphism at either site. Acronyms and descriptions of cranial characters are in Table 1. The height of a bar for a particular character equals its importance value (I) and estimates the proportion of variation between sexes that is accounted for by that character. The sign above each bar indicates direction of dimorphism for that character, with males larger than females indicated by a plus (+), and females larger than males indicated by a minus (-).

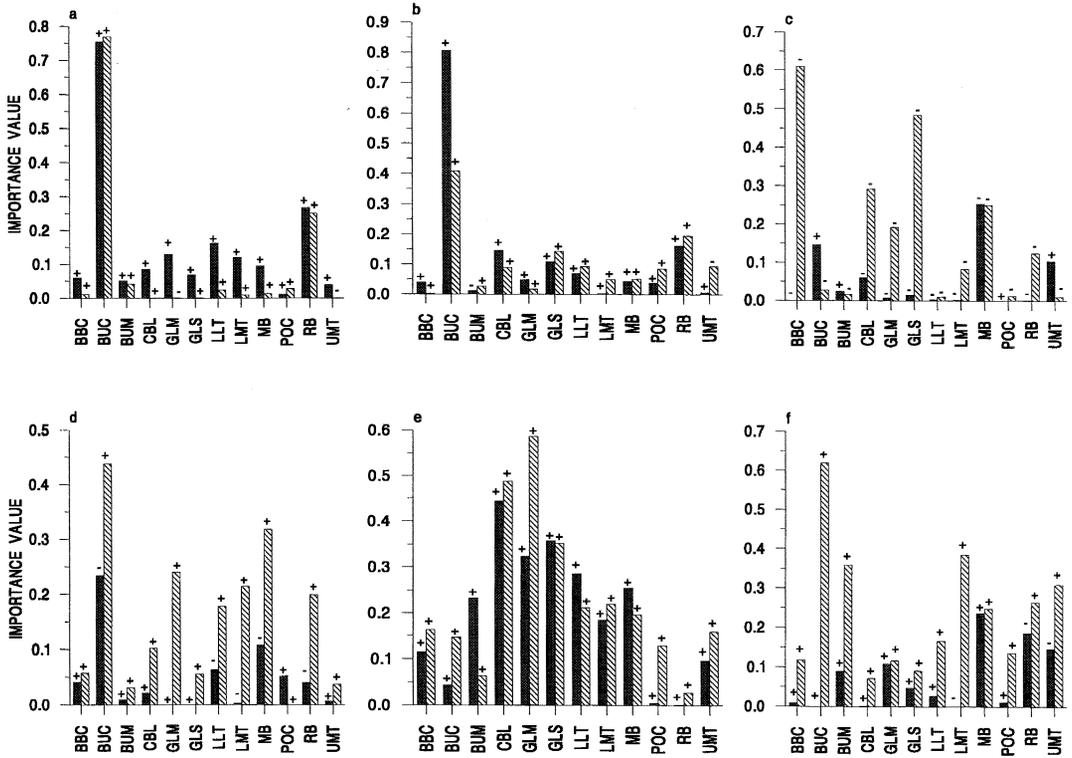


FIG. 3.—Values for profiles of importance for 12 cranial characters that distinguish between sexes in species of bats from Caatinga (cross-hatching) and edaphic Cerrado (hatching) of northeastern Brazil (a, *Anoura geoffroyi*; b, *Carollia perspicillata*; c, *Glossophaga soricina*; d, *Phyllostomus hastatus*; e, *Molossus molossus*; f, *Artibeus planirostris*). The first three species (a–c) exhibited secondary sexual dimorphism in a consistent fashion in both sites, whereas the last three species (d–f) exhibited dimorphism that was site-specific. Acronyms and descriptions of cranial characters are in Table 1. The height of a bar for a particular character equals its importance value (I) and estimates the proportion of variation between sexes that is accounted for by that character. The sign above each bar indicates direction of dimorphism for that character, with males larger than females indicated by a plus (+), and females larger than males indicated by a minus (-).

ular toothrow, length of maxillary, and mastoid breadth, each contributing appreciably to the difference between sexes in both sites. The significant two-way interaction in *M. molossus* is likely a result of positive synergism; that is, males are consistently larger than females, equivalent character profiles are involved in the dimorphism, but the size differential is exaggerated in one biome compared with the other. In contrast, the significant two-way interaction in *P. discolor* involves negative synergism. The sexes are dimorphic, but males are larger than females in the Caatinga

and females are larger than or indistinguishable from males in the edaphic Cerrado. Similar profiles of characters are involved in the dimorphism, as indicated by the highly significant, positive correlation ($0.001 < P < 0.01$), but the direction of the size differential between the sexes differs, as indicated by the sign of the correlation coefficients used to produce importance values. In particular, breadth across the upper canines, mastoid breadth, and rostral breadth are larger in males than in females from the edaphic Cerrado, but larger in females than in males from Caatinga (Fig.

3d). Dimorphism in *A. planirostris* is complex. Intersexual variation is not independent of biome (a significant sex-by-area interaction—Willig et al., 1986), and the profiles of importance values are uncorrelated as well (Fig. 3f). Males are larger than females for all characters in the Cerrado, with breadth across upper canines, breadth across upper molars, length of maxillary toothrow, and length of upper molariform toothrow contributing most to dimorphism. In contrast, mastoid breadth, rostral breadth, and length of upper molariform toothrow contribute most to dimorphism in the Caatinga, with males having larger mastoid breadths and females having larger rostral breadths and lengths of upper molariform toothrows.

DISCUSSION

Theoretical context.—Comparisons of morphological features within and among populations aid in understanding how and to what extent variation among individuals is molded into differences that separate races and species (Mayr, 1942; Simpson, 1944; Yablokov, 1974). Sexual reproduction reduces genetic and, hence, morphological differences between sexes in an analogous fashion to the manner by which migration between populations reduces interdemographic genetic and morphological variation. Indeed, the degree to which morphologies of males and females are affected by the same genes or segregating factors constrains the evolution of secondary sexual dimorphism. Despite factors favoring dimorphism in populations (e.g., intersexual selection, intrasexual selection, competition for resources, reproductive demands in females), genetic correlations between sexes are reinforced as a consequence of a variety of dynamic genetic processes such as pleiotropism, epistasis, and linkage disequilibrium (Lande, 1987; Raff and Kaufman, 1983). Arnold (1985), Fisher (1930, 1958), and Lande (1987) provide useful insight into the genetic dynamics involved in the evolution of secondary sexual characters. The clear con-

sensus is that morphological characters in males and females cannot evolve independently within populations.

Migration between populations reduces interdemographic variation in gene frequencies and morphology. The existence of coadapted gene complexes should further reduce the likelihood that different suites of characters (genes and their associated morphological consequences) would become involved in dimorphism in two populations between which considerable movement of individuals occurs. Perhaps for these reasons, systematists frequently have considered secondary sexual dimorphism as if it were a species-specific attribute rather than a population-level phenomenon. For the same reasons, closely related species, as a consequence of their shared genetic heritage, may involve similar characters in the expression of dimorphism, when it occurs.

Our results allow us to address two interrelated questions concerning the evolution of secondary sexual dimorphism. First, do different populations of the same species exhibit similar patterns of secondary sexual variation; second, do closely related species exhibit more similar character profiles than do distantly related species?

Intraspecific phylogenetic constraints.—Nine of the 12 species that occurred in both Caatinga and edaphic Cerrado exhibited correlations between patterns of importance values that would be expected if phylogenetic constraints are in operation. One of the four monomorphic species (*D. rotundus*) and four of the six dimorphic species (*A. geoffroyi*, *C. perspicillata*, *P. discolor*, and *M. molossus*) exhibited significantly correlated profiles of importance values. The two dimorphic taxa that do not conform to expectations each exhibit such low correlations between profiles of importance values (*G. soricina*, $r = 0.07$; *A. planirostris*, $r = 0.02$, respectively) that the nonsignificance is unlikely to be an artifact of sample size. Two phenomena could contribute to this: reduced migration between Caatingas and edaphic Cerrado populations of

each species; elevated migration between either of these populations and another population outside the domain of this study.

Constraints at higher taxonomic levels.—If the legacy of shared gene pools in the past limits the degree to which differences in sexes can be expressed in dimorphic taxa, the correlation of profiles of importance values should decrease as one makes comparisons within genera, subfamilies, and families. Of the 28 populations examined (combinations of species and sites), the vast majority did not correspond to this expectation. Discounting conspecific correlations, the highest correlations were infrequently between members of the same genus (only for *Phyllostomus*) or subfamily (none). In fact, most populations had profiles of importance that were uncorrelated with that of any other population (e.g., *Artibeus planirostris*, *G. soricina*, *L. mordax*, and *M. molossus* from the Caatinga and *G. soricina* from edaphic Cerrado) or, at most, maximally correlated with a population from a different subfamily (e.g., *Anoura geoffroyi*, *C. perspicillata*, *G. soricina*, *Noctilio leporinus*, *Neoplatymops matto-grossensis*, *Phyllostomus discolor*, and *Tonatia bidens* from the Caatinga, as well as *A. geoffroyi*, *A. planirostris*, *C. perspicillata*, and *M. molossus* from edaphic Cerrado). Taken together, these data suggest that once differentiation occurs at the specific level, coadapted gene complexes and genetic dynamics associated with epistasis, pleiotrophism, and linkage disequilibrium no longer constrain the expression of dimorphism. For the most part, patterns in the exhibition of intersexual variation appear species-specific and relatively unrelated to systematic arrangements at the generic level or higher.

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