

Functional morphology meets macroecology: size and shape distributions of New World bats

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ABSTRACT

Questions: What is the distribution of sizes of bats when estimated from multivariate analyses conducted on a number of morphological characteristics? Can shapes generated from such analyses inform our understanding of macroecology, in particular how phenotypic characteristics in general vary in nature? Do species-rich functional groups of bats exhibit similar size and shape distributions?

Quantitative methods: Principal components analysis imposed on seven morphometric characteristics. Kolmogorov-Smirnov and bootstrap analyses to determine differences among phenotypic distributions.

Organisms: New World bats.

Conclusions: All distributions were modal, skewed and deviated significantly from the log-normal. Significant differences regarding central tendency of functional groups existed on all phenotypic axes. Functional groups exhibited similar size distributions based on skew and kurtosis, but significantly differed on the log-mass and shape axes. Although similarities in the unimodal and skewed nature of phenotypic distributions suggest universal properties governing the diversification of organisms through space and time, quantitative differences among distributions highlight unique aspects of the evolution of particular phenotypic attributes.

Keywords: body-size distribution, functional morphology, morphometrics, principal components analysis, shape distribution, size–shape decomposition.

INTRODUCTION

Perhaps one of the most conspicuous and variable phenotypic attributes of organisms is their size. Life on earth spans approximately 21 orders of magnitude in size, from microscopic microplasma to the blue whale (Schmidt-Nielsen, 1984). The description of this variation and attempts to identify underlying causative mechanisms has been a paradigm of evolutionary and ecological research for decades (Peters, 1983; Calder, 1984; Brown, 1995). The emphasis on body size is in part because it can be estimated easily for large numbers of

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organisms. Moreover, the distribution of body sizes for a taxonomic, functional or ecological group provides insight into the ecology of constituent organisms. For example, because of allometric relationships, body size is associated intimately with other phenotypic attributes such as morphology and physiology, as well as ecological attributes such as behaviour, home-range size, food-particle size, and the scale at which an organism perceives its environment (Peters, 1983; Brown, 1995).

Empirically, body-size distributions that encompass large groups of related species at large spatial scales tend to be unimodal but not log-normal (Brown and Nicolletto, 1991; Brown, 1995). When attributes such as body size result from the action of a large number of independent traits whose effects compound multiplicatively, random variation in those traits will cause the attribute to be log-normally distributed (May, 1975; Brown, 1995). This provides a null expectation. Deviations from log-normality suggest that something more than random variation determines a particular attribute. Moreover, the consistently right-skewed body-size distribution for most taxonomic groups suggests that the shape of these distributions has a mechanistic basis. Although phylogenetic and ecological constraints likely affect the shape of body-size distributions, few mechanisms have been proposed to account for their non-random properties (Maurer *et al.*, 1992; Brown *et al.*, 1993; Kozłowski and Weiner, 1997; Lovegrove and Haines, 2004). Despite modest differences among studies, body-size distributions appear to be quite general: most studies indicate that the majority of species are relatively small (i.e. arithmetic mean < mode) and right-skewed distributions suggest that phenotypes are more strongly influenced by limits to small size than to limits to large size (Brown and Maurer, 1989; Brown, 1995; Gaston and Blackburn, 1999).

Historically, the estimation of body size has not been consistent. For bats, measures of body size have included mass, forearm length, various dimensions of the skull, and the first principal component derived from analyses of multiple morphological characters (Findley and Black, 1983; Freeman, 1984, 1988; Fleming, 1988; Arita and Figueroa, 1999; Stevens and Willig, 1999; Willig *et al.*, 2003). In macroecological studies, body size typically has been estimated from mass (Brown, 1995). Although each of these measures reflects important aspects of body size, like most estimators each has advantages and disadvantages. For example, mass has disadvantages, such as including variation due to weight change related to ontogeny, senescence, seasonality and pregnancy, to name only a few. Alternatively, mass has advantages of being easy to measure, repeatable, readily available in the literature, and straightforwardly expressed as an independent variable in allometric relationships that relate phenotypic traits to body size (Brown, 1995). Equally important, mass may often be the only comparable metric when studies encompass a large number of disparate taxa. Although body size can be represented by any of a number of morphological characteristics, it is inherently a multivariate attribute that integrates the allometric relationships of many morphological traits. Moreover, body size represents an emergent property of organisms that describes numerous aspects of functional morphology. Because body size is an inherently multivariate attribute, when possible it should be measured using multivariate statistical methods that incorporate measures reflecting various dimensions of the functional morphology of species.

Typically, macroecological studies of body size have focused almost entirely on allometry. When phenotypic variation is treated from a multivariate perspective, non-allometric elements related to shape variation can be explored as well. Moreover, when phenotypic variation is decomposed orthogonally, components of size and shape can be used to represent two independent estimates of phenotypic variation. While shape variation has contributed greatly to understanding systematic relationships among species (Strauss, 1987,

1990), its ecological implications are not as well understood as those for size variation. Nonetheless, shape variation can be related to phenotypic attributes that are associated with ecological performance such as predator avoidance (Walker, 1996), resource utilization (Freeman, 1984, 1988, 1992; James and Boeklen, 1984; Wikramanayake, 1990; Spencer, 1995; Dumont and Herrell, 2003; Dumont, 2003, 2004) and mode of locomotion (Webb, 1984; Norberg and Rayner, 1987; Norberg, 1990; Walker, 1996; Ribera and Foster, 1997). Little is known about the fundamental multivariate distributions of shape for any group of organisms. Moreover, the investigation of shape distributions represents a point of departure from traditional macroecological investigations and may provide improved insights regarding the generality of the shape of phenotypic distributions, and ultimately the way in which the environment affects variation of phenotypes in nature. Here, I compare the log-mass, size and shape distributions characterizing New World bats and explore differences in the distributional characteristics among species-rich functional groups along these phenotypic axes.

METHODS

I followed Koopman (1993) for a comprehensive list of continental New World (North, Central and South America) bats. For each species, I obtained measurements for seven morphological characteristics that reflect variation in body size (e.g. forearm length and greatest length of skull) as well as the shape of the cranium and associated trophic structures (e.g. greatest length of skull, condylobasal length, length of maxillary row of teeth, breadth across upper molars, width across post-orbital constriction, breadth of braincase). These characters are useful descriptors of the functional characteristics of New World bats (Stevens and Willig, 1999). In most cases, mean values were obtained from measurements of four males and four females of each species. Morphological variables were log-transformed before analysis. Species were classified to one of seven functional groups: aerial insectivores, frugivores, carnivores/gleaning insectivores [also classified as gleaning animalivores in Stevens and Willig (1999, 2001) and Stevens *et al.* (2003)], high-flying insectivores, nectarivores, piscivores and sanguinivores. Species from the piscivore and sanguinivore functional groups were included to construct log-mass, size and shape distributions for all bats, but were excluded from other analyses due to the small number of species (piscivore, $n = 2$; sanguinivore, $n = 3$).

I used principal components analysis (PCA) to create composite orthogonal morphological axes that reflected the principal features of size and shape variation. Correlation analyses were used to interpret principal components (PCs); morphological measures with high correlations with particular principal components reflect the pattern of variation accounted for by the derived PC axis. Principal components that have correlations with morphological variables which are all positive and relatively uniform in magnitude reflect variation in body size, whereas principal components with correlations that are both positive and negative represent morphological trade-offs characteristic of shape variation (Marcus, 1990; Klingenberg, 1996). Principal components were extracted from a covariance matrix describing the linear relationships among the seven log-transformed morphological variables. Only the first two principal components were retained for further analyses; in these particular analyses, these two components characterize the major axes of variation in size and shape, respectively, reflected in the morphological measurements (see Results). To further evaluate the validity of the size and shape axes, I compared the logarithm of body mass, PC-derived size and PC-derived shape of 201 bat species whose masses were found in

Jones *et al.* (2003). To facilitate comparisons between log-mass, size and shape distributions, variates were standardized by subtracting them from the mean and dividing by the standard deviation (Sokal and Rohlf, 1995).

Kolmogorov-Smirnov tests (Sokal and Rohlf, 1995) were used to assess deviations from log-normality for the log-mass, size and shape distributions as well as significant differences among these phenotypic attributes regarding moment statistics. I further evaluated differences by examining skewness and kurtosis separately. The 95% confidence intervals of those moments were generated from bootstrap analyses (Manly, 1986). For each iteration of a bootstrap analysis, I calculated the skewness and kurtosis of the bootstrapped sample. One thousand iterations for each distribution facilitate the determination of confidence intervals based on the same number of observations for each of the distributional statistics. Similar analyses were conducted to evaluate differences among functional groups with respect to their distribution on the log-mass, size and shape axes. Kolmogorov-Smirnov tests were used to assess pair-wise differences, whereas bootstrap analyses were used to assess differences based on the mean, variance, skewness and kurtosis of functional group distributions on log-mass, size and shape axes.

RESULTS

Principal components analysis

The first two principal components accounted for approximately 87% of the variation in the seven morphological characters among the 255 New World bat species. All seven morphological characters were positively and strongly correlated with PC1 (Fig. 1); this axis clearly reflects variation among species in size. The species with the smallest value on PC1 was *Rhogeessa mira* (a small aerial insectivore), whereas the species with the largest value was *Vampyrus spectrum* (the heaviest New World bat species). The strong relationship between size as measured by PC1 and body mass suggests the pervasiveness of this size axis (Fig. 2).

Variables exhibited both positive and negative, as well as moderate to weak, associations with PC2 (Fig. 1); this axis is one of variation in shape. Characters which measure relative length of the maxillary row of teeth and skull were positively correlated with PC2, whereas characters which measure the relative width of the tooth area and skull were negatively correlated with this axis. This axis reflects attributes of the geometry of the trophic apparatus, namely the tooth area used to process food and the associated cranial area that supports the musculature responsible for its movement and power. Moreover, this axis ranges from round crania at low values to oblong crania at high values. Accordingly, the species with the smallest score on this axis was *Centurio senex* (frugivore) and the species with the largest score on this axis was *Musonycteris harrisoni* (nectarivore). The shape axis, while of functional and ecological significance, represents an orthogonal measure of phenotypic variation that is independent not only of the size axis, but the log-mass of species as well (Fig. 2).

Phenotypic distributions

The distributions of log-mass and sizes (PC1) of all bats (Fig. 3) are unimodal, significantly right-skewed and consistent with many previously published body-size distributions (Gaston and Blackburn, 1999). The distribution of shapes (PC2) is also unimodal, significantly skewed and significantly leptokurtic (Fig. 3). Kolmogorov-Smirnov tests indicated that significant

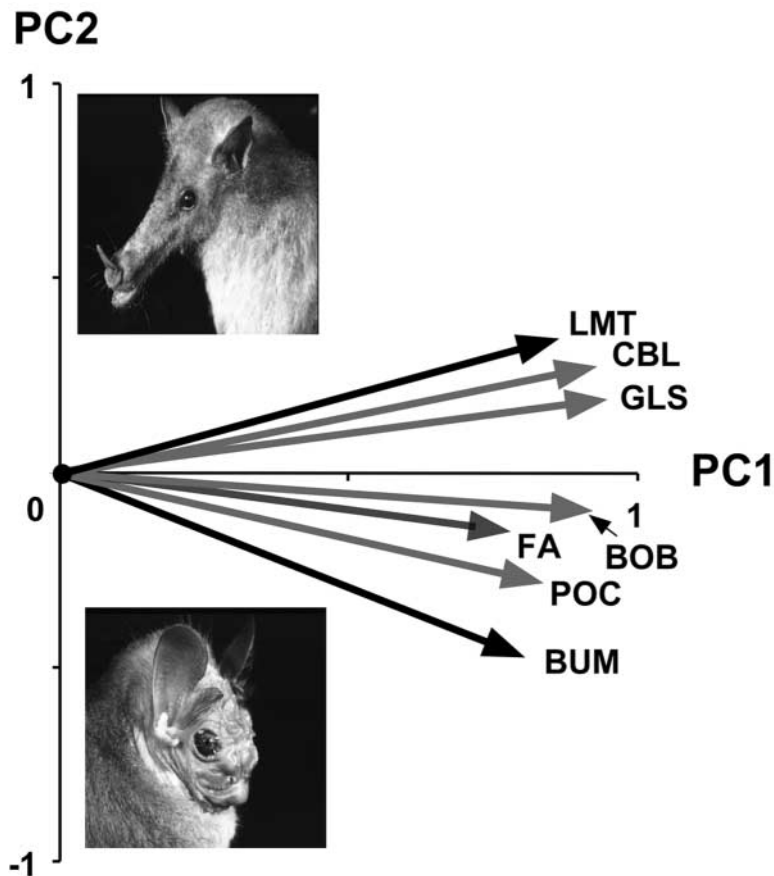


Fig. 1. Size and shape variation of New World bats. Star diagrams describing the simultaneous correlations (arrowhead) of each of the original morphometric characters with the first two principal components. Acronyms are as follow: BUM, breadth across upper molars; POC, width across post-orbital constriction; FA, length of forearm; BOB, breadth of braincase; GLS, greatest length of skull; CBL, condylobasal length; LMT, length of maxillary row of teeth. Solid black arrows correspond to dental characters, grey arrows correspond to cranial characters, and the black-hatched arrow corresponds to forearm length. Axes are of unit length and express the magnitude of correlation between a particular principal component and the variables. All variables were strongly and positively correlated with the first principal component; this axis is one of body size. The second principal component, however, exhibited both positive and negative correlations reflective of the morphological trade-offs indicative of shape variation and represents the principal shape axis characterizing New World bats. Photographs are of *Musonycteris harrisoni* (top) and *Centurio senex* (bottom) and represent the two extreme species on each end of the size axis (photographs kindly provided by Dr Marco Tschapka).

overall departures from log-normality existed only for the shape axis (log-mass, $Z = 0.697$, $P = 0.716$; size, $Z = 0.712$, $P = 0.691$; shape, $Z = 2.261$, $P < 0.001$). Significant overall pairwise differences exist between the size and shape distributions ($Z = 1.417$, $P = 0.036$) but not between log-mass and size ($Z = 0.399$, $P = 0.997$) or log-mass and shape ($Z = 1.288$, $P = 0.072$). The higher skew and significant leptokurtosis of the shape distribution likely contributes to this difference.

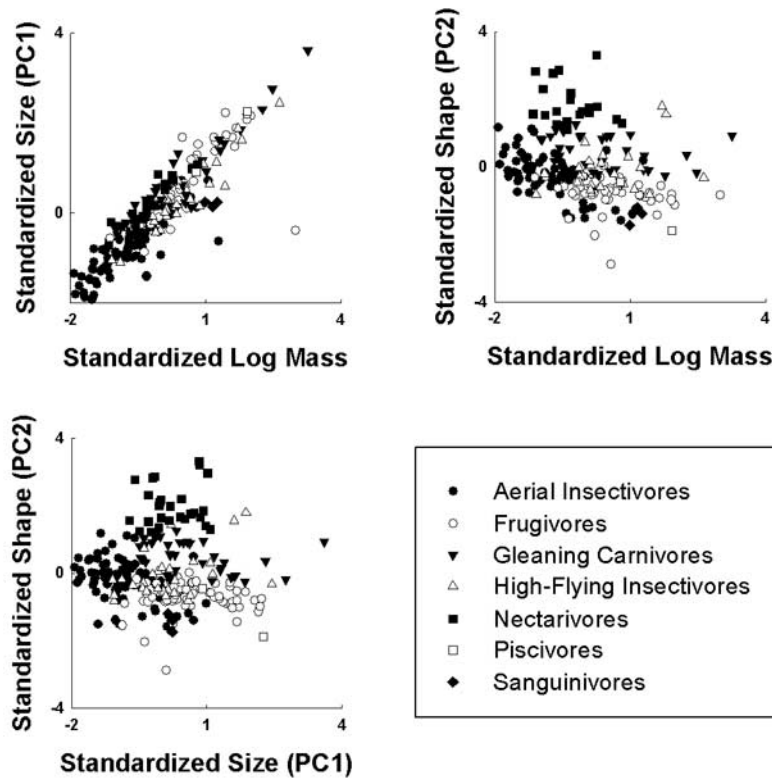


Fig. 2. Relationships between size, shape and mass of 201 bat species included in the analyses.

In general, log-mass and size distributions of each of the functional groups presented a number of similarities (Fig. 4). The majority of these distributions were modal, right skewed and exhibited no significant kurtosis (Fig. 5). Pair-wise K-S tests indicated highly significant differences between aerial insectivores and all other functional groups on both the log-mass and the size axes (Table 1). Bootstrap analyses indicated that the greatest difference among functional groups involved the mean, whereby aerial insectivores were significantly smaller than all other functional groups. Nectarivores exhibited the lowest variance in log-mass and size. Frugivores and high-flying insectivores exhibited no significant skew, whereas aerial insectivores and gleaning insectivores/carnivores were significantly right skewed. Nectarivores were significantly right skewed on the size axis but exhibited normal skew on the log-mass axis. Finally, functional groups exhibited normal values of kurtosis except for the aerial insectivores, which were leptokurtic on the size axis, and high-flying insectivores and nectarivores, which were platykurtic on the log-mass axis.

Shape distributions for functional groups were typically modal and exhibited normal kurtosis, but exhibited variable right, left and normal skew. Differences among functional groups on the shape axis were highly significant (Table 1). With the exception of aerial insectivores and high-flying insectivores, the functional groups were all different regarding the mean of their distributions on the shape axis. No significant differences were observed

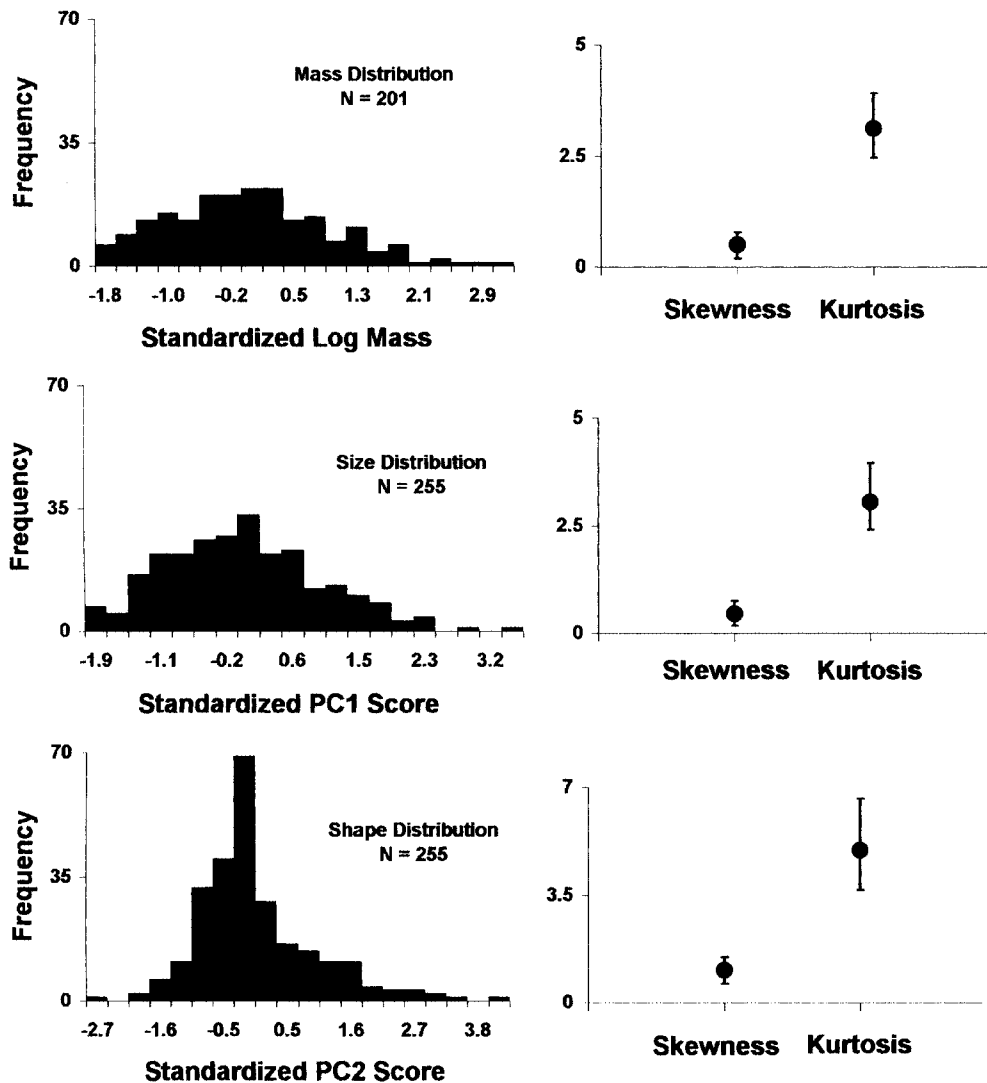


Fig. 3. Size and shape distributions for all bats occurring in the continental New World (left column). Bootstrapped confidence intervals for degrees of skewness and kurtosis of size and shape distributions (right column).

regarding variance. Frugivores exhibited left skew, aerial insectivores and gleaning carnivores/insectivores normal skew, and high-flying insectivores and nectarivores right skew. Only gleaning carnivores/insectivores were leptokurtic.

DISCUSSION

Body size is a phenotypic characteristic that is reflected not only in the mass of organisms, but also in the allometric relationships that integrate diverse morphological features. To this

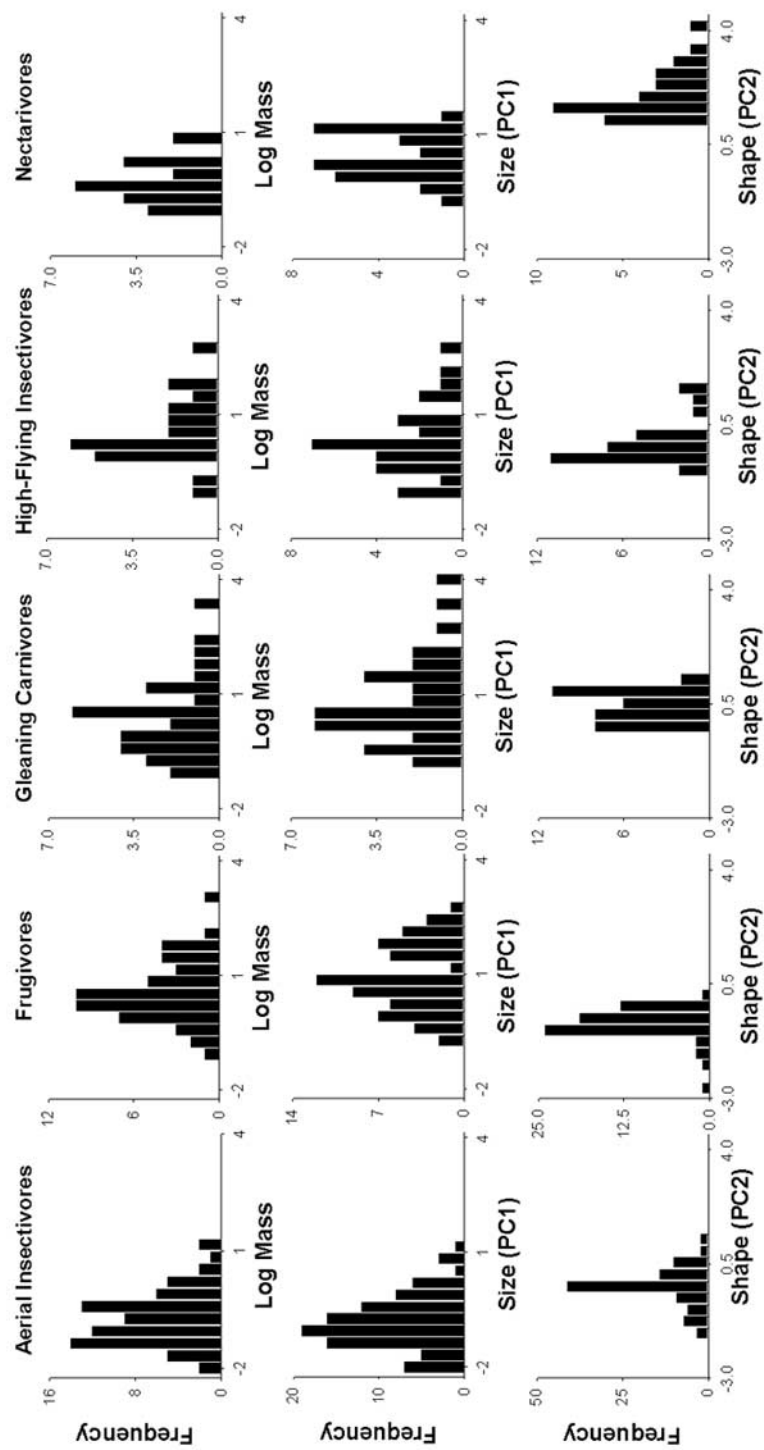


Fig. 4. Size and shape distributions for New World bat functional groups.

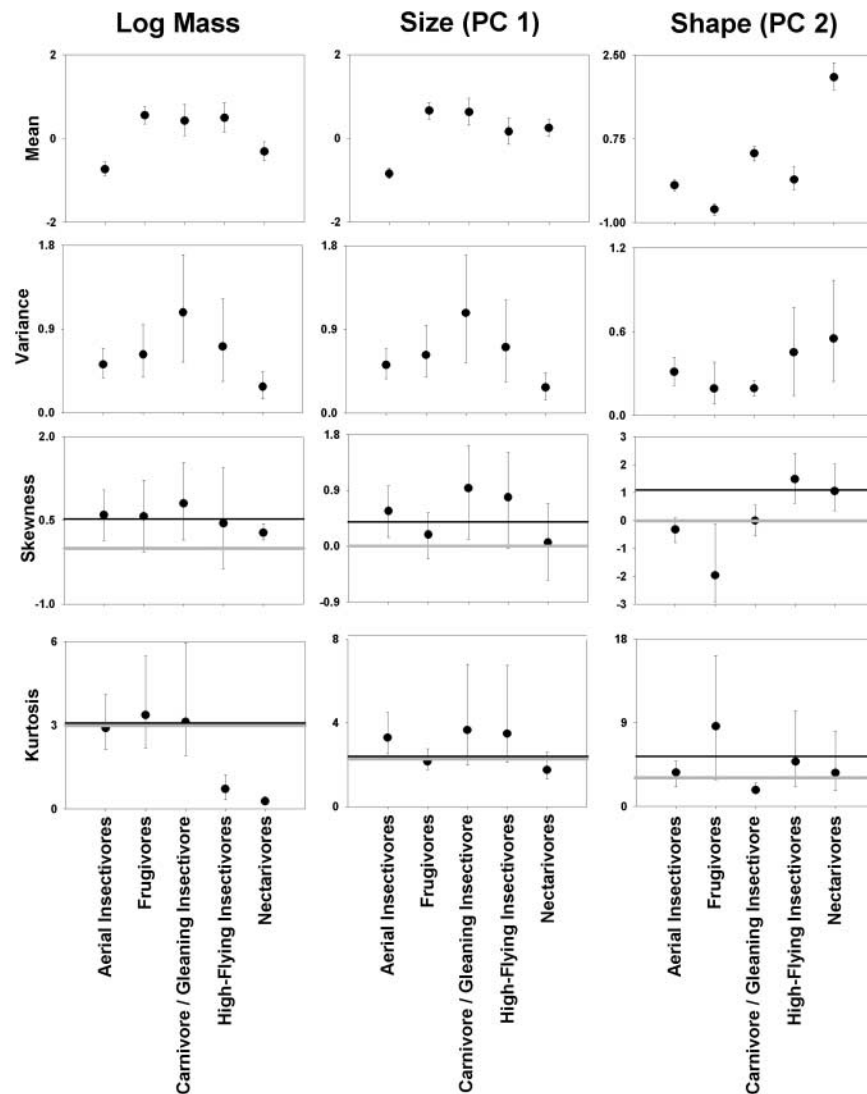


Fig. 5. Means and 95% confidence intervals for distributional characteristics for each functional group on the mass (left column), size (middle column) and shape (right column) axes. In figures involving skewness and kurtosis, horizontal black bars represent expectations from a normal distribution, whereas horizontal grey bars represent the observed value for the distribution involving all bats.

end, multivariate methods provide an ideal framework from which to evaluate macroecological patterns of body size. A limitation to these particular analyses is that they focus primarily on only a single trophic structure, the skull. Thus, the measures used and the composite variable 'size' that emerges from these analyses pertain directly only to the size of the skull and only indirectly to overall size. Nonetheless, as demonstrated by these analyses, variation in composite measures of body size is directly comparable to body size estimated

Table 1. Kolmogorov-Smirnov tests evaluating significant pair-wise differences between phenotypic distributions for each trophic group

	AEINS	FRUGI	GLEAN	HIFLY	NECTA
Size and shape distributions					
AEINS	—	4.510***	3.452***	2.844***	3.419***
FRUGI	3.367***	—	0.632	1.600	1.485
GLEAN	2.714***	4.367***	—	1.173	1.252
HIFLY	0.946	2.098***	2.244***	—	0.788
NECTA	4.608***	4.456***	3.869***	3.414***	—
Mass distributions					
AEINS	—	3.686***	2.244***	2.925***	1.531***
FRUGI	—	—	0.971	0.733	2.074
GLEAN	—	—	—	0.889	1.540
HIFLY	—	—	—	—	1.763
NECTA	—	—	—	—	—

Note: The upper matrix describes results for size and shape distribution, whereas the lower matrix describes log-mass distributions. The upper triangle of the upper matrix corresponds to comparisons based on the size distribution, whereas the lower triangle corresponds to comparisons based on the shape distribution. Values correspond to the Kolmogorov-Smirnov test statistic, while asterisks indicate significance after a Bonferroni sequential adjustment (Rice, 1989). AEINS = aerial insectivores, FRUGI = frugivores, GLEAN = gleaning carnivores; HIFLY = high-flying insectivores, NECTA = nectarivores.

by log-mass. Indeed, body size should be thought of as a latent variable that reflects the size of all structures, from particular differentiated cells, to organs and organ systems, to the entire body. From this perspective, even mass is an indirect measure of size, possibly no more indirect than a derived variable constructed from the combination of a number of morphological features.

Multivariate methods have the added advantage of facilitating the quantification of other, independent components of phenotypic variation, in particular shape variation. The shape component emerging from these analyses does not represent a random weighting of morphological characteristics that have no ecological meaning. Rather, it is an ecomorphological axis describing the functional morphology of bats. When the size and shape axes are considered jointly, they provide consistent discrimination among functional groups (Stevens and Willig, 1999) (see also Fig. 2). Nonetheless, there is some variation in other relevant trophic structures that likely is not reflected in variation of the skull. For example, much work has attempted to understand the functional morphology and ecological consequences of variation in shapes of bat wings. Bat wings have evolved to provide maximum efficiency in flight under a large number of circumstances, many related to diet and foraging behaviour (Norberg and Rayner, 1987). As with the skull, the coordinated evolution of wing morphology has led to distinct functional groups of bats (in many cases different from the functional groups based on broad dietary categories) that underscore the importance of this trophic structure (Kalko, 1998). Indeed, similar analyses of size and shape distributions of other relevant trophic structures would provide insight into the generalities of the distributional characteristics of size and shape variation.

Functional scaling

Strong functional scaling in terms of log-mass, size and shape are indicated by the non-random positions of functional groups on these three axes as well as deviations of functional groups from the distributions for all bats. Significantly different means and variances smaller than that for the distribution of all bats indicate the unique positions of each functional group on both axes. Perhaps the most striking patterns involve the positions of aerial insectivores on the size axis and nectarivores and frugivores on the shape axis. These differences reflect phenotypic attributes important to the trophic success of species. Aerial insectivores are constrained to small sizes because of the trade-off between flight performance and echolocation sound-wave length, both of which scale with body size (Barclay and Brigham, 1991; Jones and Rydell, 2003; Simmons and Conway, 2003). The extreme values of frugivores and nectarivores on the shape axis are undoubtedly related to the resources that they consume. Nonetheless, functional scaling appears to operate differently from spatial scaling (*sensu* Brown and Nicolletto, 1991). While decreases in skew associated with functional scaling are similar to those involving spatial scaling, distributions do not become uniform but remain strongly modal. The modal nature of functional group distributions suggests that groups have unique phenotypic optima on each axis. Moreover, the significant skew of most functional groups on each axis suggests unique directions of evolutionary potential. This is especially true for frugivores and nectarivores in terms of shape. These two groups represent the two extremes of this axis. Moreover, their direction of skew is towards the particular end of the shape axis on which they reside. Thus, frugivores appear to have a hard bound on oblong shape and a softer bound on round shape, whereas nectarivores have a hard bound on round shape and a softer bound on oblong shape. Moreover, frugivores likely have greater evolutionary potential towards round crania than oblong crania, whereas nectarivores demonstrate the opposite potential.

Unimodality of phenotypic distributions

Because size and shape distributions represent two independent estimates of phenotypic variation, their comparison can identify important generalizations describing the distribution of species in nature. For example, all three distributions for all bats were unimodal and skewed but varied in terms of kurtosis. These three characteristics provide different but important indications about the diversity of phenotypes. Unimodality is likely a general characteristic of phenotypic distributions that reflects continuous variation of traits affected by the controls of epistasis and co-adapted gene complexes (Hartl, 1988). Moreover, the peak of these unimodal distributions could identify the 'ideal' state for a group of organisms under consideration (Brown, 1995). Accordingly, the ideal state for New World bats on log-mass, size and shape axes is one that represents intermediate size and an intermediate degree of specialization of their trophic apparatus. Thus, although more extreme morphologies such as exceptionally oblong or exceptionally round crania have undoubtedly allowed some taxa to invade novel adaptive zones (Freeman, 2000), radiations such as these have not come to represent an important drive in the phenotypic evolution of New World bats.

Kurtosis

The kurtosis of a distribution can be interpreted as describing the degree of variation relative to the fill of that distribution. In other words, a leptokurtic distribution has

relatively more observations towards the centre of the distribution and a platykurtic distribution has relatively more observations situated in the tails (Sokal and Rohlf, 1995). Platykurtic distributions may be reflective of mechanisms that encourage the diversification of taxa, such as divergent evolution, competitive interactions and spatial heterogeneity. In contrast, leptokurtic distributions may be reflective of mechanisms such as convergent evolution, constraint or spatial homogeneity. Of the distributions examined for all bats, only the shape distribution was leptokurtic (e.g. neither the log-mass nor the size distribution deviated from normality based on degree of kurtosis), indicating that cranial shapes were less variable relative to the fill of the distribution than expected from a normal distribution and this could reflect the constrained way that shape changes can evolve. Whereas changes in size simply can occur through changes in the timing of ontogenetic events, changes in shape require the decomposition and subsequent re-association of character correlations (Cheverud, 1982; Atchley *et al.*, 1992). Thus, mechanical constraints and developmental epistasis may limit diversification along the shape axis and render other forms of phenotypic variation more labile than shape variation.

Patterns of skewness

The magnitude and direction of skewness likely indicates directional bias in phenotypic attributes. If one side of a phenotypic distribution was absolutely bounded, for instance by mechanical or physiological constraints, or if diversification proceeded more expediently on one side of a distribution than the other, skewness would result. All three distributions likely have a hard boundary on one end and a relatively soft one on the other. For size, organisms are probably more constrained by the physiological and thermoregulatory difficulties of small size [i.e. reflecting barrier (Kozłowski and Gawelczyk, 2002)]; however, the large end of the size spectrum may be relatively soft and reflect constraint due only to the stochasticity of the direction and rate of evolutionary change. Such a process describes the evolution of body size for terrestrial mammals during the Cenozoic (Alroy, 1998). In fact, mammalian body sizes retained a constant minimum mass while exhibiting a consistent expansion of the upper size limit repeated in different lineages through the Cenozoic.

The left side of the shape axis may also identify a relatively harder bound on phenotypic evolution than the right side. The direction of skew of New World bats towards oblong crania likely reflects relatively more potential to evolve oblong crania than round ones. This is because evolution may be bounded on one end of the shape axis by perfect roundness. Much more evolutionary potential for bats may exist for elongation than for the relative widening of the rostrum such that species diversify more rapidly in the direction of relatively longer than wider morphologies. Thus, species such as *Centurio senex* may reflect the extreme morphological limits to cranial roundness exhibited by New World bats. Nonetheless, the extent to which crania are oblong may have much more evolutionary potential and this may be reflected in the longer tail on the right side of the shape distribution.

Brown (1995) has suggested that the direction of skewness can be used to identify the direction of greatest evolutionary potential. Moreover, Kozłowski and Gawelczyk (2002) have suggested that size-biased speciation and extinction probabilities together with anagenetic processes enhance the skewness of size distributions. This is consistent with the observations of Alroy (1998) that the form of the size distribution, in particular skewness, for terrestrial mammals is the product of dual point attractors. A globally stable equilibrium driven by mechanical and thermodynamic constraints on small-sized organisms causes an

invariant small-size limit. Meanwhile, on the other side of the size spectrum a second locally stable equilibrium defines the upper bound. Because the globally stable equilibrium is more invariant than the locally stable equilibrium, the distribution is right skewed. That distributions have relatively harder bounds on one end than another may not be unique to size distributions or even phenotypic distributions that characterize morphological variation, but may be a general characteristic of many distributions that characterize ecological and evolutionary characteristics of large groups of taxa. For example, the typical left skew of geographic range-size distributions could be due to an absolute bound on the upper limit to range size imposed by the size of land or water masses, whereas the bounds to small size may be softer and controlled by differential extinction probabilities which in and of themselves may have the potential to evolve. Similarly, abundance distributions may be absolutely bounded by zero, or a minimum viable population size on one end of the abundance spectrum and less strongly bounded by the potential of population growth and variation in carrying capacities on the other end. Although the type of constraints affecting particular distributions may be unique, they may in general set the absolute bounds on phenotypic distributions and their differential strength may determine a general pattern of skewness that prevails across most reported distributions.

Similarities between distributions of size and shape as well as those of range size and abundance suggest universal macroecological patterns common to all forms of phenotypic variation. For example, unimodality and significant degrees of skewness common to phenotypic distributions likely result from the limited ways that species evolve and ultimately diversify through space and time. Just like similarities among distributions characterizing a single phenotypic trait such as body size suggest the action of universal structuring mechanisms on that particular trait across a diversity of taxa, similarities among distributions describing different aspects of the phenotype suggest universal ways that phenotypic variation is distributed in nature. Distinguishing between universalities in variation of a particular phenotypic trait examined across a number of taxa and universalities in the distributional characteristics of a number of different traits will enhance our understanding of macroecological patterns, and likely suggest fruitful avenues from which to pursue their mechanistic bases.

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