

Cross-sectional geometry of the dentary in bats

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Abstract

Bats exhibit remarkable diversity in dietary habits, with species specializing on insects, fruit, nectar, vertebrates and blood. Studies of larger mammals have shown that structural differences in dentary cross-sectional properties exist among species with different diets. Unfortunately, few of these studies have considered the role of phylogeny in shaping these apparent form–function associations. Here we ask whether a relationship exists between diet and dentary structure in bats when phylogenetic history is factored into the analysis. To answer this question, we compared results from phylogenetic generalized least squares (PGLS) and traditional (nonphylogenetic) regression analyses of dentary cross-sectional shape in frugivorous, nectarivorous, and insectivorous bats (253 individuals representing 72 species). Cross-sectional moments of inertia of the dentary between M_1 and M_2 were computed from bone densitometry scans of skeletal specimens. Traditional regressions of cross-sectional parameters against dentary length detected significant departures from isometry among frugivores. In contrast, PGLS analyses indicated that cross-sectional variables for each dietary group scaled with isometry. Thus, the allometric patterns illuminated by traditional statistics are linked to the phylogenetic structure of the sample. Identical patterns of significant differences in slopes and intercepts between frugivores and nectarivores emerged from both traditional and PGLS analyses. As predicted, the cross-sectional shape of the dentary in frugivores is consistent with increased resistance to torsion and bending, while that of nectarivores suggested a less resistant dentary. Although traditional and PGLS analyses yielded some similar results, the phylogenetic structure of a sample can drive apparent patterns of scaling and should be considered in comparative functional analyses.

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Introduction

With 925 species or more (Simmons, 2001), Chiroptera is the second most specious order of mammals (Wilson and Reeder, 1993). The order is defined by the

synapomorphy of powered flight, with the modification of the forelimb and hand into a membranous wing. Nocturnality and flight enabled bats to expand into a wealth of ecological niches that were previously unexploited by mammals. In their subsequent adaptive radiation, bats exploded into an unparalleled range of dietary niches. Insectivory is the most common and probably the most primitive dietary specialization

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among bats, but frugivorous, nectarivorous, sanguivorous, and carnivorous clades have each arisen independently one or more times (Jones et al., 2002; Simmons and Geisler, 1998; Wetterer et al., 2000). This diversity in trophic adaptation, coupled with well-documented phylogenies for many families, makes bats an excellent group in which to study the evolution of functional aspects of craniofacial form.

The trophic diversity of bats is reflected in the structural diversity of the masticatory apparatus (e.g., Dumont, 1997; Freeman, 1981, 1988, 1995; Storch, 1968). Historically, the small size of most bats has limited most studies to traditional two- and three-dimensional morphometric techniques that elegantly illuminate large-scale patterns of variation but fall short of documenting details of dentary form. In contrast, studies of larger mammals have explored the use of cross-sectional imaging to evaluate the biomechanical properties of the dentary. This study takes advantage of recent technological innovations in small-scale densitometry to survey the cross-sectional geometry of the dentary and test specific functional hypotheses about feeding strategies in small mammals.

The relative strength of an elongate bone can be estimated from measures of the geometric distribution of cortical bone called “cross-sectional moments of inertia” (or “moments of area”, see Ferretti, 1995; Hibbeler, 1992; Turner and Burr, 2003). Interspecific differences in the magnitude and scaling of these parameters (or approximations thereof) are associated with differences in diet and, by extension, with variation in loading regimes encountered during biting and mastication (e.g., Biknevičius and Ruff, 1992; Bouvier, 1986a, b; Daegling, 1992; Ravosa, 1991, 1996).

We used bat species representing the three commonly recognized dietary categories of frugivory, nectarivory, and insectivory as a framework for exploring form–function relationships. The dentaries of these bats appear to be exposed routinely to different loading regimes. Behavioral analyses demonstrate that frugivorous bats often use feeding behaviors that may impose increased torsional stresses on the dentary, such as frequent unilateral biting and chewing for extended periods of time and during food preparation (Bonaccorso and Gush, 1987; Dumont, 1999, 2003; Dumont and O’Neal, 2004). In contrast, assessments of bite force in nectarivores suggests that their dentaries are relatively weak (Aguirre et al., 2002; Dumont and Herrel, 2003), probably in response to reduced emphasis on mastication and increased reliance on the tongue during feeding (Freeman, 1995; Nicolay and Dumont, 2000; Nicolay, 2001). Less is known about feeding mechanics in insectivorous bats, but observations of a few species suggest that they do not engage in the prolonged periods of unilateral loading that is characteristic of frugivores (Dumont, pers. obs.). However, there is no significant

difference in bite force production between the insectivorous and frugivorous bats that have been studied (Aguirre et al., 2002).

Based on these behavioral and bite force data, we hypothesize that there are significant differences in the cross-sectional geometry of the dentary among frugivorous, insectivorous, and nectarivorous bats. We predict that frugivores possess strong dentaries that are especially resistant to torsion, while nectarivores are expected to have relatively smaller values in all measures of dentary strength. Insectivory is the presumed ancestral condition from which other dietary adaptations evolved (Hutcheon et al., 1998; Teeling et al., 2000; Wetterer et al., 2000). Therefore, we predict that estimates of dentary strength derived from assessments of cross-sectional geometry of insectivore dentaries are intermediate with respect to the two derived conditions.

The recognition that species are not independent but are linked by underlying phylogenetic structure is the cornerstone of modern comparative biology (e.g., Brooks and McLennan, 1991; Felsenstein, 1985; Harvey and Pagel, 1991; Martins, 2000). Therefore, we conducted our analyses using the phylogenetic generalized least squares (PGLS) approach (Martins, 2004; Martins and Hansen, 1997) to mediate the impact of phylogenetic structure on the data. We tested our predictions using least-squares bivariate and multivariate regression to evaluate the scaling of cross-sectional parameters and to compare slopes and intercepts among the three dietary categories. This phylogeny-controlled comparative approach is still relatively new to comparative morphology. Therefore, we compare the results of the PGLS analysis with results obtained using traditional (nonphylogenetic) statistical techniques to demonstrate the effect that phylogenetic control has on functional analysis.

Materials and methods

Comparative sample and morphometrics

We collected cross-sectional parameters reflecting dentary strength from 253 individuals representing 72 species and five families (Appendix A). Assignment of species to the dietary categories “frugivore” and “nectarivore” were based on dietary data reported in the literature (Ferrarezzi and Gimenez, 1996; Mickleburgh et al., 1992). Although macroglossines (Family Pteropodidae) sometimes consume fruit, we classified them as nectarivores because of their clear morphological and behavioral specializations for nectar feeding (Dumont, 1997; Freeman, 1995; Nicolay and Dumont, 2000). The category “insectivore” includes both insectivorous bats and a few species that also consume small

vertebrates. Our grouping of carnivores with insectivores is supported by the very limited differences in cranial shape between them (Freeman, 1984). Fig. 1 illustrates the phylogenetic relationships among the species within each dietary category.

As a proxy for overall size, we measured the length of the dentary from the condyle to the symphysis and parallel to the midline in all specimens. Dentary length is a local estimate of size that is commonly used in analyses of dentary form. This measurement reflects the role of the dentary as a lever. More global measures of size (e.g., skull length or body mass) are more likely to be influenced by factors that are less directly related to food acquisition and processing.

Cross-sectional imaging and analysis

Cross-sectional images of the dentary were generated using a Norland Scientific XCT Research M Bone Densitometer (pQCT) (Stratec/Norland, Pforzheim, Germany). For each specimen, the dentary was scanned between the first and second permanent lower molars, perpendicular to the long axis of the molar tooth row. Specimens were carefully aligned so that the occlusal plane of the molar teeth was horizontal. Each cross-sectional image (slice) represented an area that was 7 mm × 7 mm to facilitate comparison among images from individuals of different sizes. To obtain the best image, three slices from each specimen spaced 0.25 mm apart were taken, and the slice with the minimum amount of tooth (crown and root) and the best resolution of cortical bone was selected for further analysis.

The pQCT slices are composed of voxels that have a resolution (length and width) of 0.07 mm and a thickness of 0.55 mm (from which density of the area is determined). Converting the slice to a two-dimensional array (bitmap image) results in a plane of pixels with density values (Ferretti, 2000). We converted pQCT images to bitmap files and then edited the images using Adobe Photoshop® 4.0.1 (Adobe Systems, San Jose, CA) to manually erase any visible crowns and roots of teeth; so the final image contained only cortical bone (Fig. 2).

Cross-sectional parameters were calculated from edited images using Mathcad 2000 Professional® (MathSoft Inc., Cambridge, MA) (Nicolay, 2001). The first step in these calculations was to transform the edited pQCT image to a binary matrix (bone present or absent) from which biomechanical parameters were calculated. A threshold value was then used to define bone as present or not. The density value of each pixel was not included in the computations, and all pixels were assumed to have the same mechanical properties.

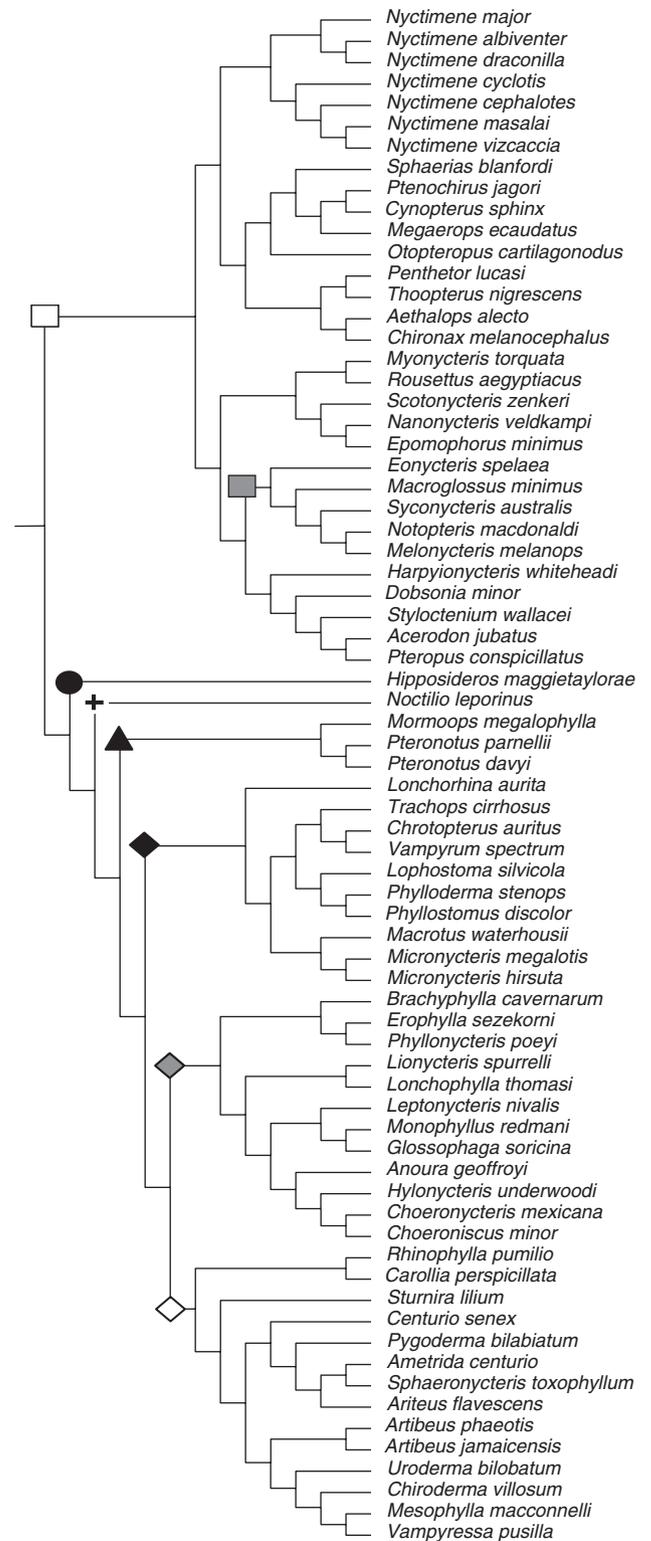


Fig. 1. Phylogenetic relationships among the frugivores, nectarivores, and insectivores used in this study. Each family is identified with a symbol: Pteropodidae (squares), Hipposideridae (circle), Mormoopidae (triangles), Noctilionidae (cross), and Phyllostomidae (diamonds). Dietary habits are illustrated by different symbol colors: frugivores (white), nectarivores (shaded), and insectivores (black). Branching sequence after Jones et al. (2005).

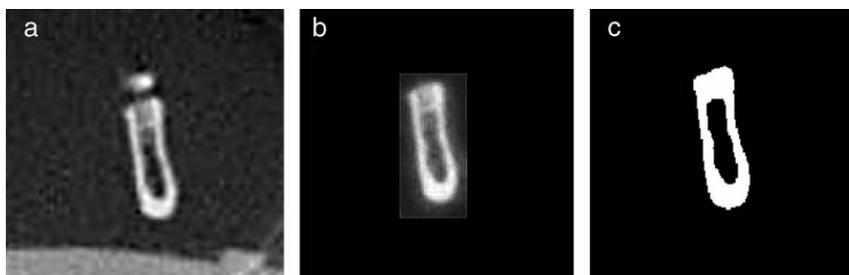


Fig. 2. CT section through the dentary of *Anoura geoffroyi* illustrating the stages of image processing and analysis. (a) Original pQCT scan in bitmap format. (b) Image “cleaned” in Photoshop[®] to isolate dentary. (c) Image filtered in MathCAD[®] to create a matrix of black (0) and white (1) pixels for analysis.

Cross-sectional moments of inertia (Ferretti, 1995) were calculated from the modified images.

Moments of inertia reflect the distribution of material about an axis of interest and are expressed in units of mm^4 (Hibbeler, 1992). Simply stated, the further any material is distributed from an axis of interest, the greater its resistance to bending and/or torsion will be. As in similar studies, we assumed that all cortical bones have equivalent intrinsic material properties, both within each slice and among different species. When the dentary is modeled as a beam, the maximum and minimum area moments of inertia (I_{\max} , I_{\min}) reflect the greatest and least resistance to bending of the section and the polar moment of inertia (J_0) indicates resistance to torsion about the centroid (axis of rotation) (An et al., 2000; Hibbeler, 1992).

The maximum and minimum area moments of inertia (I_{\max} , I_{\min}) and polar moment of inertia (J_0) were calculated from each cross-sectional image. Moments of inertia (I) were computed using summation algorithms following the general formula, $I = \sum(A_i d_i^2)$, where A_i is the area of each pixel and d_i is the distance of that pixel from the axis of interest (x , y , or z); in this case the centroid (center of mass) (Nicolay, 2001). This method calculates the cross-sectional properties exactly, regardless of the shape, based entirely on the distribution of material in the section. Fig. 3 presents scatter plots of the raw J_0 , I_{\max} , and I_{\min} data against dentary length.

Some bats exhibit sexual dimorphism in dentary size and shape (Nicolay, 2001). Therefore, we gave equal weight to dentary length and cross-sectional parameters derived from males and females when calculating species means. All values were transformed using natural logs (ln) prior to analysis to minimize the effects of variation in relative size and differences in scale.

Statistical analyses

Among available comparative methods, we selected PGLS because it incorporates flexible models of evolution that include stabilizing selection, employs an

iterative algorithm to assess the fit of a range of models using maximum likelihood statistics, and returns a “phylogeny-adjusted” data matrix that is suited to traditional statistical analyses (Martins and Hansen, 1997; Martins and Lamont, 1998; Martins et al., 2002). Unlike independent contrasts which return $n-1$ data points that represent internal nodes of a phylogeny (Felsenstein, 1985; Garland et al., 1992; Purvis and Rambaut, 1995), the adjusted data matrix derived from PGLS returns a value for each terminal taxon. We used COMPARE 4.6 (Martins, 2004) to carry out all PGLS analyses.

To investigate differences in scaling among the three dietary categories, we calculated separate PGLS and traditional regressions of J_0 , I_{\min} , and I_{\max} (dependent variables) against dentary length for frugivores, nectarivores, and insectivores (independent variables). *T*-tests were used to compare the regression coefficients for each dietary group to the expectation for isometry (slope (β) = 4.0) (Sokal and Rohlf, 1995). In addition, we conducted multiple regression analyses to generate interaction terms that provide a test for significant differences in slopes and intercepts between pairs of dietary groups.

The recently dated supertree of bat relationships which includes branch lengths (Jones et al., 2002, 2005) served as the phylogenetic framework for these analyses (Fig. 1). For each regression, the tree was pruned to include only the taxa of interest. Polytomies were treated as hard and resolved by adding extremely small branch lengths of 0.00000001 (Martins, 2004). All tree manipulations were performed using TreeEdit (Rambaut and Charleston, 2002).

Results

Traditional multiple regressions yielded a wide range of slopes and intercepts for the three dietary groups (Table 1). Frugivores exhibited significantly negative allometry ($\beta < 4.0$) for all cross-sectional parameters;

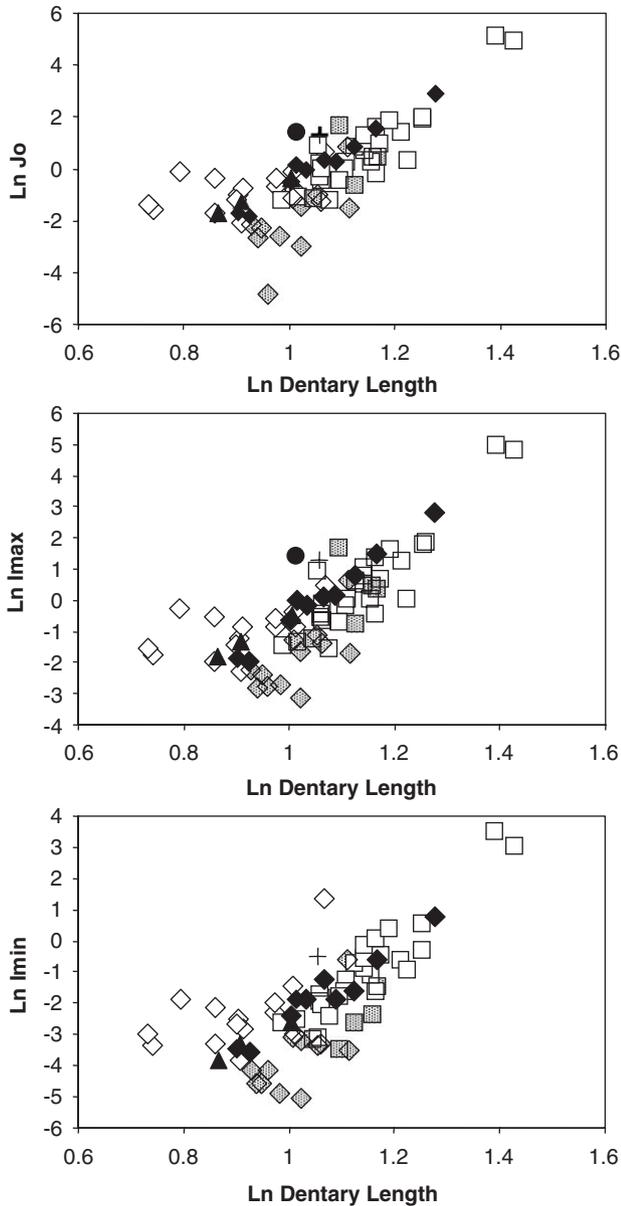


Fig. 3. Scatter plots of $\ln J_0$, $\ln I_{\max}$ and $\ln I_{\min}$ against \ln dentary length. Each family is identified with a symbol: Pteropodidae (square), Hipposideridae (circle), Mormoopidae (triangle), Noctilionidae (cross), and Phyllostomidae (diamond). Dietary habits are illustrated by different symbol colors: frugivores (white), nectarivores (shaded), and insectivores (black).

insectivores and nectarivores scaled with isometry. In contrast, the range of slope and intercept values determined by PGLS regressions was much narrower and all slopes scaled with isometry.

Within both traditional and PGLS regressions, nectarivores consistently exhibited the highest slopes and lowest intercepts, while frugivores tended to exhibit the lowest slopes and highest intercepts. Using both traditional and PGLS and multiple regressions, signifi-

cant differences were found only between frugivore and nectarivore intercepts for J_0 and frugivore and nectarivore slopes and intercepts for I_{\max} (Table 2). With the exception of J_0 among nectarivores, PGLS regressions earned a higher maximum likelihood score than the corresponding traditional regressions (Table 3).

Discussion

Previous allometric studies of mammals with diverse diets, notably carnivorans and primates, have illustrated differences in the scaling of cross-sectional dentary shape between groups of species with different diets (Biknevicius and Ruff, 1992; Daegling, 1992; Ravosa, 1991, 1996). Our analysis of bat dentaries yielded different results. After incorporating the phylogenetic structure of the data, we found that bats representing different dietary categories exhibit the same, isometric scaling of cross-sectional parameters against dentary length. There are two possible explanations for this result that are not necessarily mutually exclusive.

First, it is possible that the mechanical demands associated with different diets in bats are not sufficient to impose selective pressure on the scaling of dentary structure. This seems unlikely because bats with different diets produce different bite forces (Aguirre, 2002; Dumont and Herrel, 2003) and consume food items of quite different physical properties (Aguirre et al., 2003). Species belonging to different dietary classes can be easily recognized by the morphology of their teeth, jaws, skulls, and tongues, which appear to have undergone selection for the demands of specific diets. It seems unlikely that dentary cross-sectional parameters would remain unaffected in light of otherwise global morphological changes in the feeding apparatus.

Second, it is possible that there is too much variance within each of our dietary categories for significant trends to appear. Not only are the diets of bats very diverse, but the dietary habits of individual species are often quite broad and flexible. Although species can be assigned easily to dietary categories based on both morphology and the food resources most frequently consumed, many (and perhaps most) species of bats classified as frugivores or nectarivores are moderately to highly omnivorous. Assigning a species to a dietary category does not mean that it never consumes other kinds of foods, and secondary resources are especially important to some species. Individual species of frugivores are known to include a range of resources in the diet, shift diets seasonally, and vary slightly in diet along geographic gradients (see review in Dumont, 2003). Moreover, frugivores may tend to feed on fruits of different hardness (Dumont, 1999; Dumont and O'Neal, 2004), insectivores may tend to feed on prey

Table 1. Regression coefficients (β), intercepts (a), their standard errors (SEb and SEa) for traditional and PGLS analyses of J_0 , I_{\max} , and I_{\min} against dentary length for each dietary group

	Traditional		PGLS	
	$\beta \pm \text{SEb}$	$a \pm \text{SEa}$	$\beta \pm \text{SEb}$	$a \pm \text{SEa}$
J_0				
Frugivores	2.74 \pm 0.26*	-8.43 \pm 0.77	3.53 \pm 0.31	-10.29 \pm 0.98
Insectivores	4.03 \pm 0.52	-11.20 \pm 1.47	4.12 \pm 0.39	-11.02 \pm 1.20
Nectarivores	5.15 \pm 1.75	-15.61 \pm 5.00	4.47 \pm 1.97	-13.72 \pm 5.63
I_{\max}				
Frugivores	2.96 \pm 0.27*	-8.64 \pm 0.81	3.54 \pm 0.33	-10.56 \pm 1.02
Insectivores	4.06 \pm 0.54	-11.43 \pm 1.53	4.21 \pm 0.38	-11.29 \pm 1.24
Nectarivores	5.04 \pm 1.03	-15.55 \pm 2.93	4.71 \pm 0.91	-14.51 \pm 2.65
I_{\min}				
Frugivores	2.97 \pm 0.30*	-10.09 \pm 0.89	3.75 \pm 0.37	-12.60 \pm 1.13
Insectivores	3.82 \pm 0.42	-12.71 \pm 1.17	3.76 \pm 0.41	-12.47 \pm 1.15
Nectarivores	4.12 \pm 0.90	-15.12 \pm 2.57	4.47 \pm 0.78	-16.06 \pm 2.29

Slopes that differ significantly from the hypothesis of isometry ($\beta = 4.0$) are marked with an asterisk.

with different mechanical properties (Freeman, 1981), and nectarivores may tend to utilize flowers that differ in morphology in ways that affect feeding (von Helversen, 1993; Winter and Von Helversen, 2003). It is possible that the traditional dietary categories we used were too broad to capture meaningful patterns of morphological diversity associated with diet.

A brief review of Table 1 suggests that if we had relied on traditional, nonphylogenetic techniques, significant allometric differences among the dietary groups would have emerged. We would have concluded that frugivores exhibited significant negative allometry ($\beta < 4.0$) in all cross-sectional parameters. In contrast, the results of PGLS regressions failed to reject the null hypothesis of isometric scaling within the three dietary categories. The discrepancy between the traditional and PGLS analyses highlights the overriding influence of phylogeny on

dentary cross-sectional measurements. More importantly, it illustrates that failure to account for phylogenetic structure in a comparative functional analysis can produce inaccurate results and lead to erroneous interpretations.

Although traditional and PGLS regressions revealed different patterns of scaling, both types of analyses illuminated differences between frugivorous and nectarivorous species that support our predictions regarding the structure and, by implication, the strength of their dentaries. Compared to frugivores, nectarivores exhibited significantly lower intercepts for J_0 and I_{\max} . Purely on the basis of jaw structure, this implies that the dentaries of nectar-feeding bats are weaker in both torsion and bending. This result fits well with the observation that nectarivores produce lower bite force values than frugivores or insectivores (Aguirre et al.,

Table 2. Comparisons among slopes and intercepts derived from traditional and PGLS regressions of frugivores, insectivores and nectarivores for the variables J_0 , I_{\max} , and I_{\min}

	Traditional			PGLS		
	J_0	I_{\max}	I_{\min}	J_0	I_{\max}	I_{\min}
Frugivores vs. insectivores						
Slopes	0.24	0.13	0.21	0.27	0.16	0.38
Intercepts	0.28	0.18	0.25	0.23	0.21	0.35
Frugivores vs. nectarivores						
Slopes	0.06	0.03	0.23	0.09	0.04	0.37
Intercepts	0.03	0.01	0.07	0.05	0.02	0.16
Insectivores vs nectarivores						
Slopes	0.42	0.4	0.79	0.46	0.3	0.85
Intercepts	0.26	0.2	0.45	0.2	0.19	0.53

Values are exact probabilities that the slopes or intercepts are significantly different. Probabilities ≤ 0.05 are in bold.

Table 3. Comparison of likelihood scores for traditional and PGLS regressions

	Traditional	PGLS	
	Log <i>L</i>	Log <i>L</i>	α
Frugivores			
<i>J</i> ₀	−7.53	−2.81	3.77
<i>I</i> _{max}	−8.64	−4.54	3.68
<i>I</i> _{min}	−12.88	−9.37	4.06
Insectivores			
<i>J</i> ₀	1.19	4.33	0.50
<i>I</i> _{max}	0.64	4.72	0.50
<i>I</i> _{min}	4.32	4.70	0.93
Nectarivores			
<i>J</i> ₀	−14.69	−16.85	15.5
<i>I</i> _{max}	−5.61	−3.28	3.28
<i>I</i> _{min}	−3.40	−0.77	3.30

Selection coefficients (α) are given for PGLS regressions. Selection coefficients for traditional regressions are uniformly large (<15.5; Martins, 2004).

2002; Dumont and Herrel, 2003). Conversely, the cross-sectional shape of the dentary among frugivores suggests that it is significantly stronger under both loading regimes. The bite forces produced by frugivores and insectivores are quite similar (Aguirre et al., 2002) but many frugivores also engage in long periods of chewing, which applies a cyclic unilateral load to the dentary (Bonaccorso and Gush, 1987; Dumont, 2003; Dumont and O'Neal, 2004). This behavior may be reflected in the cross-sectional parameters of the dentary. Although regression statistics for nectarivores and frugivores did not differ significantly from those of insectivores, it is noteworthy that the slopes and intercepts for the insectivores were, as predicted, intermediate between them.

The accuracy of this or any phylogeny-adjusted analysis depends on the accuracy of the underlying phylogeny. Using a consensus-based supertree employed a summary of the available phylogenetic analyses and, to the extent possible, offered a conservative hypothesis of the “true” phylogeny. It is worth reiterating that analyses using phylogenetic corrections to assess form–function relationships are also limited by the accuracy of functional categories (e.g., diet), variance within those categories, and the number of species that can ultimately be included in the analysis.

The range of resources upon which an organism can potentially feed is limited by its anatomy and physiology. An animal must be able to capture, process, ingest, and digest a food item – many potential food items are simply too big, too hard, too small, or too toxic to be viable resources. These constraints arise from the fact that anatomy and physiology are inter-related and, to a

large extent, determined by phylogenetic history. Therefore, we cannot expect that dietary adaptations can truly vary independently from phylogeny. By incorporating phylogenetic techniques into our analysis, it became clear that at least some of the apparent functional variation in our sample could be traced to the underlying phylogenetic structure of the data.

Finally, it is noteworthy that none of the PGLS regressions yield a selection coefficient consistent with the Brownian motion model of evolution assumed by independent contrasts ($\alpha = 0$). Evolutionary models that incorporated some degree of stabilizing selection ($\alpha > 0$) were the best fit to the data in all cases. These results underscore that selecting an appropriate evolutionary model hinges on the structure of the sample and highlights the utility of flexible analysis tools. We strongly urge other morphologists to make use of PGLS and other comparative techniques as they can offer a novel, and perhaps more accurate, perspective on form–function relationships and the evolution of morphological systems.

Acknowledgments

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Appendix A

Cross-sectional images were collected from specimens housed at the American Museum of Natural History, the National Museum of Natural History, and the Carnegie Museum of Natural History.

Frugivores: Family Phyllostomidae, *Ametrida centurio* (1f, 1m), *Ariteus flavescens* (2f, 2m), *Artibeus jamaicensis* (4f, 5m), *Artibeus phaeotis* (5f, 6m), *Carollia perspicillata* (5f, 5m), *Centurio senex* (4f, 2m), *Chiroderma villosum* (1f, 1m), *Mesophylla macconnelli* (1f, 1m), *Pygoderma bilabiatum* (1f, 1m), *Rhinophylla pumilio* (2f, 2m), *Sphaeronycteris toxophyllum* (1f, 1m), *Sturnira lilium* (3f, 3m), *Uroderma bilobatum* (1f, 1m), *Vampyressa pusilla* (1f, 1m), *Vampyrodes caraccioli* (1f, 1m), Family Pteropodidae, *Acerodon jubatus* (1f, 1m), *Aethalops alecto* (1f, 1m), *Chironax melanocephalus* (2f), *Cynopterus sphinx* (1f, 1m), *Dobsonia minor* (2f, 1m),

Epomophorus minimus (1f, 1m), *Haplonycteris fischeri* (1f, 1m), *Harpionycteris whiteheadi* (1f, 1m), *Megaerops ecaudatus* (1f, 1m), *Myonycteris torquata* (1f, 1m), *Nanonycteris veldkampii* (1f, 1m), *Nyctimene albiventer* (1f, 1m), *Nyctimene cephalotes* (1f, 1m), *Nyctimene cyclotis* (1f), *Nyctimene draconilla* (1f, 1m), *Nyctimene major* (2 sex unknown), *Nyctimene masalai* (1f, 1m), *Nyctimene vizcaccia* (1m), *Otopteropus cartilagonodus* (1f, 1m), *Penthetor lucasi* (1m), *Ptenochirus jagori* (1f, 1m), *Pteropus conspicillatus* (1f, 3m), *Rousettus aegyptiacus* (1f, 1m), *Scotonycteris zenkeri* (1f, 1m), *Sphaeris blanfordi* (1f, 1m), *Styloctenium wallacei* (1f), *Syconycteris australis* (1f), *Thoopterus nigrescens* (1f, 1m).

Nectarivores: Family Phyllostomidae, *Anoura geoffroyi* (5f, 5m), *Brachyphylla cavernarum* (2f, 2m), *Choeroniscus minor* (3f, 2m), *Choeronycteris mexicana* (5f, 5m), *Erophylla sezekorni* (1f, 1m), *Glossophaga soricina* (5f, 4m), *Hylonycteris underwoodi* (3f, 1m), *Leptonycteris nivalis* (6f, 6m), *Lionycteris spurrelli* (2f, 1m), *Lonchophylla thomasi* (2f, 3m), *Monophyllus redmani* (3f, 4m), *Phyllonycteris poeyi* (1f, 1m), Family Pteropodidae, *Eonycteris spelaea* (1f, 1m), *Macroglossus minimus* (1f, 1m), *Notopteris macdonadli* (2f) *Melonycteris melanops* (1f, 1m).

Insectivores: Family Phyllostomidae, *Chrotopterus auritus* (1f, 1m), *Lonchorhina aurita* (2f, 1m), *Lophostoma sylvicola* (1f, 1m), *Macrotus waterhousii* (2f, 2m), *Micronycteris hirsuta* (1f, 3m), *Micronycteris megalotis* (1f, 1m), *Phylloderma stenops* (2f) *Phyllostomus discolor* (5f, 5m), *Trachops cirrhosis* (1f, 1m), *Vampyrus spectrum* (1f, 1m), Family Hipposideridae, *Hipposideros maggietylori* (1f, 1m), Family Mormoopidae, *Mormoops megalophylla* (1f, 1m), *Pteronotus parnellii* (4f, 2m), *Pteronotus davyi* (1f, 1m), Family Noctilionidae, *Noctilio leporinus* (2f, 2m).

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