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DIETARY HARDNESS, LOADING BEHAVIOR, AND THE EVOLUTION OF SKULL FORM IN BATS

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The morphology and biomechanics of the vertebrate skull reflect the physicalproperties of diet and behaviors used in food acquisition and processing. We use phyllostomid bats, the most diverse mammalian dietary radiation, to investigate if and how changes in dietary hardness and loading behaviors during feeding shaped the evolution of skull morphology and biomechanics. When selective regimes of food hardness are modeled, we found that species consuming harder foods have evolved skull shapes that allow for more efficient bite force production. These species have shorter skulls and a greater reliance on the temporalis muscle, both of which contribute to a higher mechanical advantage at an intermediate gape angle. The evolution of cranial morphology and biomechanics also appears to be related to loading behaviors. Evolutionary changes in skull shape and the relative role of the temporalis and masseter in generating bite force are correlated with changes in the use of torsional and bending loading behaviors. Functional equivalence appears to have evolved independently among three lineages of species that feed on liquids and are not obviously morphologically similar. These trends in cranial morphology and biomechanics provide insights into behavioral and ecological factors shaping the skull of a trophically diverse clade of mammals.

KEY WORDS: **Biomechanics, bite force, 3D bite force model, finite element analysis, frugivory, loading behavior, mechanical advantage, muscle moments, Phyllostomidae, strain.**

The vertebrate skull is a classic example of a complex anatomical system that is composed of numerous highly integrated units (Cheverud 1982; Klingenberg 2008). The morphology and function of the skull are presumed to be under strong selection and shaped by the physical properties of the diet and behaviors that improve food acquisition and processing. These selective pressures act on the performance of the cranial system as a whole and ultimately shape the morphology of its individual parts. For example, the ecological advantages of consuming hard mollusks have been linked to the evolution of high bite performance (bite force) in *Chamaeleolis* lizards (Herrel and Holanova 2008). High bite forces in these lizards are the result of tall heads with a pronounced temporal ridge and large jaw adductors, which are traits that reflect the biomechanics of the jaw system (Herrel and Holanova 2008). Thus, examining the mechanisms through which the morphology of cranial elements translates into function is a powerful approach to understanding how the vertebrate skull evolves. To date, few studies have been able to integrate the behavioral and ecological factors shaping the skull diversity across vertebrate lineages, but an extensive and continuously growing body of research has helped us elucidate skull biomechanics in a vast array of vertebrate species, from suction feeding in fish (reviewed in Westneat 2005) to biting in a wide array of vertebrates (e.g., Cleuren et al. 1995; Freeman and Lemen 2008; Curtis et al. 2010; Davis et al. 2010). These studies have set the stage for much-needed comparative approaches which, using recent

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developments in phylogenetic methods, could illuminate and confirm paradigms in the evolution of the skull's form and function.

The overarching goal of this study is to investigate the link among diet, feeding behavior and the diversity in vertebrate skull morphology and function. Among vertebrates, Neotropical leaf-nosed bats (family Phyllostomidae) offer a combination of features that makes them especially well suited for studying this topic. Phyllostomid species exhibit an outstanding dietary diversity that spans a wide variety of types of foods and physical properties, from liquids such as nectar and blood to very hard and resistant materials such as insect exoskeleton and vertebrate bone. The physical challenges posed by such different food types are matched by a remarkable range of derived morphological and functional cranial specializations, including long and narrow snouts in nectarivorous species and very short and broad skulls in species that eat very hard fruits (Fig. 1; Wetterer et al. 2000; Nogueira et al. 2009; Santana et al. 2010; Dumont et al. 2011). For example, species that eat increasingly harder foods (fruits, vertebrates) also tend to have large temporalis muscles that have a high mechanical advantage (MA), a trend that has also evolved in other mammals that consume resistant foods such as carnivores and ungulates (Smith and Savage 1959; Davis 1964; Perez-Barberia and Gordon 1999). In contrast, species that consume less-resistant foods, such as nectar and soft fruits, have relatively smaller temporalis muscles with lower MA (Santana et al. 2010).

The evolution of dietary specializations among phyllostomids is not only seen in gross differences in skull shape and cranial muscles; species also exhibit behavioral strategies to modulate bite force in response to the physical characteristics of foods (Dumont 1999, 2003; Santana and Dumont 2009). Matching predictions from simple lever models (Hylander 1975), bats increase their bite force by moving food items close to the jaw joint by biting with the molar teeth and often use this behavior when feeding on hard foods. In addition, the most morphologically derived frugivores use mostly the molar teeth on one side of the mouth (deep unilateral bites) when eating hard food items. These biting behaviors not only modulate bite force, but also impose different loads on the facial skeleton. Specifically, bilateral biting imposes symmetrical loads whereas unilateral biting imposes asymmetrical loads (see results below; Ross and Hylander 1996; Dumont et al. 2005; Chalk et al. 2011; Ross et al. 2011). These biting behaviors have been suggested to result in bending and torsion of the face (e.g., Ross and Hylander 1996; Ravosa et al. 2000), and the magnitude of their effects could be associated with the morphology of the facial skeleton.

Here, we explore four questions regarding the strength of association among diet, feeding behavior, and the diversity in skull morphology and function in phyllostomids. First, how have skull morphology and biomechanics evolved with diet? We expect the evolution of increasingly challenging diets to be associated with an elevated capacity to translate muscle force into bite force (MA) and, as shown previously (Santana et al. 2010), an increase in the importance of the temporalis in producing bite force. Second, do the biting behaviors used to eat challenging foods impose different types of loads on the facial skeleton? We predict that deep unilateral biting, the behavior predominantly used to consume hard foods, will cause torsion of the facial skeleton. Conversely, deep bilateral biting behaviors, which are normally used to eat softer foods, will bend the facial skeleton. Third, upon correcting for size differences, does the effect of loading regimes on the facial skeleton vary with cranial morphology? We predict that species with skull morphologies that have a higher MA (and thus relatively higher bite force) will exhibit relatively higher strain and more exaggerated twisting and bending than species with skull morphologies that have a lower MA. Finally, have cranial morphology and biomechanics evolved in tandem with the use of loading regimes characteristic of different species? Integrating the predictions above, we expect that increasing proportions of deep unilateral (torsional) biting will be associated with short faces, high MA, exaggerated bending and torsion of the skull coupled with relatively high strain magnitudes, and elevated MA for the temporalis.

Methods

We collected cranial, behavioral, and performance data that allowed us to generate morphological and biomechanical variables, and investigate their relationship with diet and loading behaviors. Our analysis included morphological data collected from museum specimens, and behavioral and biomechanical data generated from free-ranging individuals and voucher specimens. The latter comprised 24 phyllostomid species that span all the major dietary specializations found within the family. These species were classified into dietary hardness categories that appear to be related to functional specializations of the phyllostomid skull (Fig. 1, Santana et al. 2010) and are based on previous dietary records (Howell and Burch 1973; Gardner 1977; Snow et al. 1980; Ferrarezi and Gimenez 1996; Aguirre et al. 2003; Giannini and Kalko 2004; Da Silva et al. 2008) and our own measurements of the hardness of prey items.

Biting Behavior

We collected data on feeding behavior on hard foods by recording bats in temporary captivity, using fruits for frugivores, insects for insectivores, and a combination of these for omnivores (Santana and Dumont 2009). Biting behaviors were classified following methods developed by Dumont (1999), which involve observing the biting movements employed by the bats and classifying each

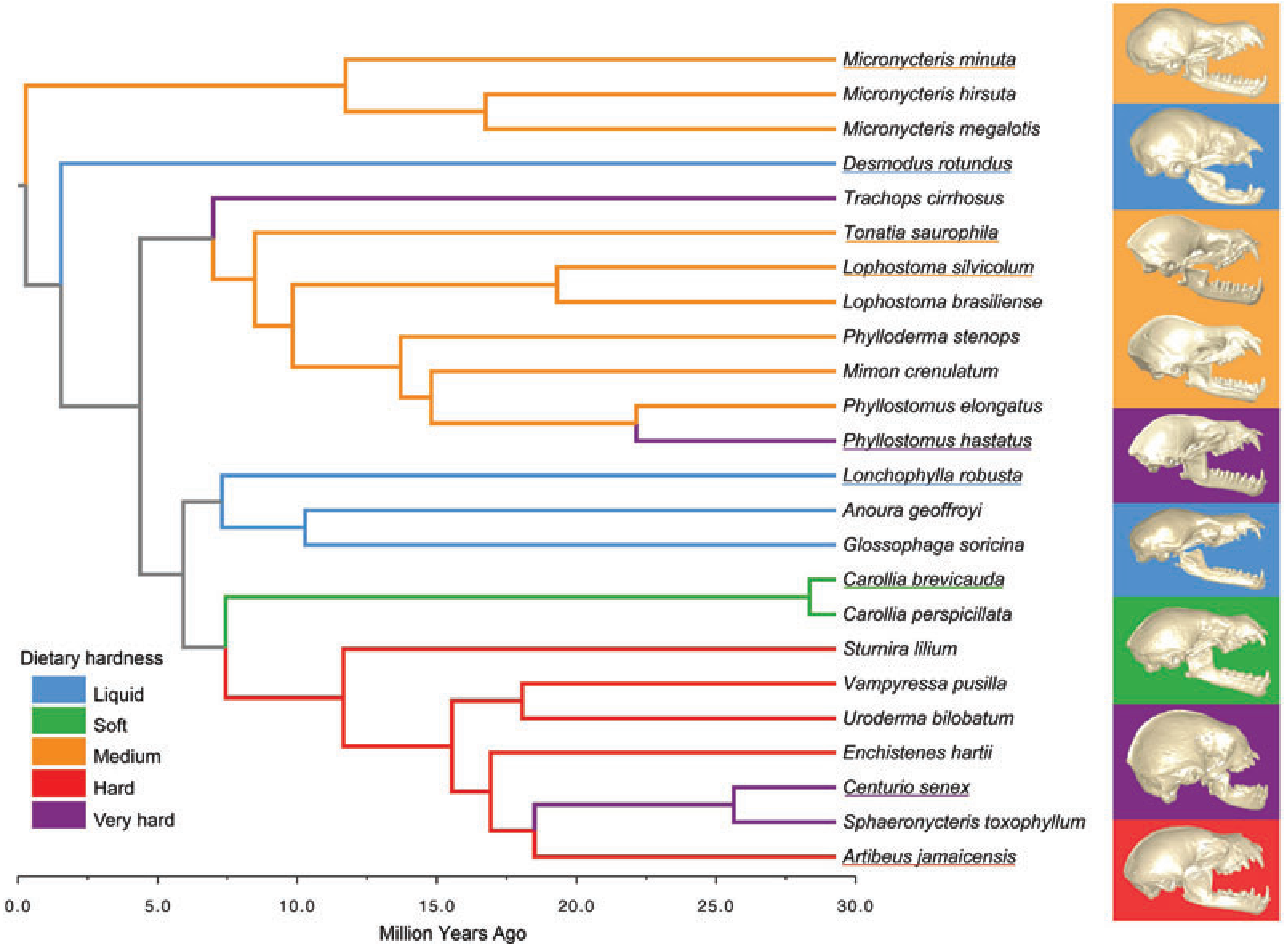

Figure 1. **Evolutionary relationship among the phyllostomid bats included in this study. Maximum likelihood reconstructions for the dietary hardness categories used in phylogenetic analyses are indicated, along with a sample of skulls illustrating morphological trends. Skulls shown are (from top to bottom): *Micronycteris hirsuta*, *Desmodus rotundus*, *Tonatia saurophila*, *Lophostoma silvicolum*, *Phyllostomus hastatus*, *Lonchophylla robusta*, *Carollia brevicauda*, *Centurio senex*, and *Artibeus jamaicensis*.**

bite used to remove a mouthful as either shallow bilateral, shallow unilateral, deep bilateral, or deep unilateral. We averaged the percentage of each bite type across bats of the same species. We only used the percentage of deep bilateral and deep unilateral bites in our analyses, as these are the bites most commonly used by all phyllostomids to consume food items (Dumont 1999; Santana and Dumont 2009).

CRANIAL MORPHOLOGY

We used principal component (PC) scores derived from 10 linear measurements of 611 museum specimens belonging to 85 phyllostomid species (PC scores taken from Dumont et al. 2011). The linear measurements were adjusted for size using log geometric means (Jungers et al. 1995), and their variation summarized by applying a PC analysis to the correlation matrix with Varimax rotation. This produced statistically independent vectors that summarized morphological variation across phyllostomids. Out of these vectors, PC1 varied with qualitative dietary categories and was primarily associated with variation in skull length and robustness; low PC1 scores indicate short crania with elevated dentary condyles and low coronoid processes.

To generate data on the cranial muscles for the species under study (listed in Fig. 1), we collected voucher specimens from the individuals used in the feeding behavior experiments described above. We dissected all their major jaw-closing muscles (musculus masseter, m. temporalis, m. pterygoideus medius, m. pterygoideus lateralis), estimated the locations of their attachment regions, and measured their mass and fiber length. Muscle forces were calculated by multiplying each muscle's physiological cross-sectional areas (PCSA = muscle mass/(density × fiber length), Lieber 2002; density = 1.06 g/cm^3, Mendez and Keys 1960) by a muscle stress factor of 25 N/cm^2 (Herzog 1994). Note that the orientation and fiber lengths did not differ greatly across parts of the cranial muscles and pennation angles were not taken into account in these calculations as the muscles were not pennate (see also Herrel et al. 2008; Santana et al. 2010).

SKULL BIOMECHANICS: MA AND MUSCLE MOMENTS

We applied a three-dimensional (3D) lever model in Boneload version 6 (Davis et al. 2010) to simulate biting behaviors and estimate MA and the moments generated by the temporalis and masseter muscles (Santana et al. 2010). This modeling technique requires surface models of the skulls and information about the cranial muscles' attachments and forces. We used the skulls from voucher specimens to generate 3D sterolithography (stl) files from micro-Computer Tomography (CT) image stacks generated with a micro-CT scanner (Skyscan 1172 Microfocus X-radiographic Scanner, Skyscan, Belgium) and slice reconstruction software (NRecon version 1.5.1.4, MicroPhotonics Inc., Allentown, PA). The image stacks were imported into Mimics (version 12, Materialise, Belgium) and segmented to produce 3D sterolithography (stl) files. These raw stl files were then exported to Geomagic Studio (version 11, Geomagic Inc., Research Triangle Park, NC) and edited to remove small holes, spikes, and scanning artifacts. These surface models were also manipulated to open the jaw at a 30° gape angle. Assuming bilateral symmetry, we defined the areas of attachment on the right side of the skull and mandible for the jaw closing muscles (m. temporalis, m. masseter, m. pterygoideus medius, and m. pterygoideus lateralis), as well as the glenoid fossae. The 3D lever model applied a uniform pressure over each muscle attachment region on the skull. The pressure for each muscle was calculated as its total muscle force divided by the area of its attachment region and applied to the surface of each stl and directed toward the area centroid of its respective insertion region on the dentary (calculated using Area Centroids, Davis et al. 2010, freely available at http://www.biomesh.org/resources). Previous work demonstrated that this modeling method produces bite force estimates that are accurate predictors of in vivo bite force (Santana et al. 2010). For each individual, the moments about the temporomandibular joint (TMJ) axis were summed across all four major cranial muscles. This value was used to calculate the percentage of the moment about the TMJ axis generated by temporalis and masseter, the two largest jaw adductors. Finally, we calculated the MA for each species by dividing the predicted bite forces by the total calculated muscle forces (i.e., force out/force in). Moment percentages and MA were the biomechanical variables used in subsequent analyses.

BITING BEHAVIOR, TORSION, AND BENDING

We used finite element (FE) models to address the question of whether deep bilateral biting bends the facial skeleton and deep unilateral biting twists it and, if so, whether morphologies with different MA affect the magnitude of strain. Although the overall presence of bending and twisting moments could be calculated from much simpler models, we chose to use FE analysis because it provides a detailed visual summary of the location of strain vectors magnitudes. We constructed FE models of the crania of two bats, the lesser spear-nosed bat (*Phyllostomus elongatus*, specimen no. UMA5303; MA = 0.45) and the Jamaican fruit bat (*Artibeus jamaicensis*, specimen no. UMA2320; MA = 0.72). Methods for extracting and cleaning stl models were described above. These models were imported back into Mimics where we generated FE models using 10-noded tetrahedral elements (*P. elongatus* = 456,882 elements, *A. jamaicensis* = 491,547 elements). We did not segment teeth from the surrounding bone as our regions of interest were far from the dental alveolar region (Panagiotopoulou and Cobb 2011; Wood et al. 2011; but see Gröning et al. 2011). Following methods outlined in Dumont et al. (2005), we applied constraints to the tempormandibular joints and first molar teeth to mimic deep bilateral and unilateral biting. These constraints prevent the model from moving when forces are applied. We applied bilateral, symmetrical muscle forces to the models based on dissections and the relative contribution of the temporalis, masseter, and medial pterygoid muscles to the sum of their PCSA. This was done using the program Area Centroids and the Gradient Traction algorithm in Boneload version 6 (Grosse et al. 2007; Davis et al. 2010; both programs freely available at http://www.biomesh.org/resources). The application of symmetrical loads is supported by an electromyographic study of masticatory muscle function in another frugivorous bat (*Pteropus giganteus*) that also possesses a fused mandibular symphysis and uses similar food-processing strategies (De Gueldre and DeVree 1988; Dumont and O'Neal 2004). The models were assigned material properties drawn from the literature (Young's Modulus = 24.9 GPa, Poisson's ratio = 0.3; Erickson et al. 2002; Dumont et al. 2009) and subjected to linear static analyses. Following initial analyses, muscle forces for each model and loading condition were scaled isometrically to return average bite forces measured in the field from live *P. elongatus* and *A. jamaicensis* at a 30° gape angle. Force to surface area ratios was very similar between the two models, which largely removed the overall effects of differences in size from comparisons (Dumont et al. 2009).

If deep bilateral biting imposes a bending load, then the dorsal surface of the rostrum should experience compression whereas the ventral surface of the palate is subjected to tension. Conversely, if deep unilateral biting imposes a torsional load (in addition to bending), then both the dorsal surface of the rostrum and the ventral surface of the palate should show evidence of increase in shear. To test these predictions, we selected series of midline nodes on the dorsal surface of the rostrum and ventral surface of the palate (Fig. 2) and calculated the absolute value of the ratio $\varepsilon_{11}/\varepsilon_{33}$ (maximum principal strain/minimum principal strain; Tables S2 and S3) for each set of nodes under bilateral and unilateral loading for each species. If the strain ratio is zero, a state

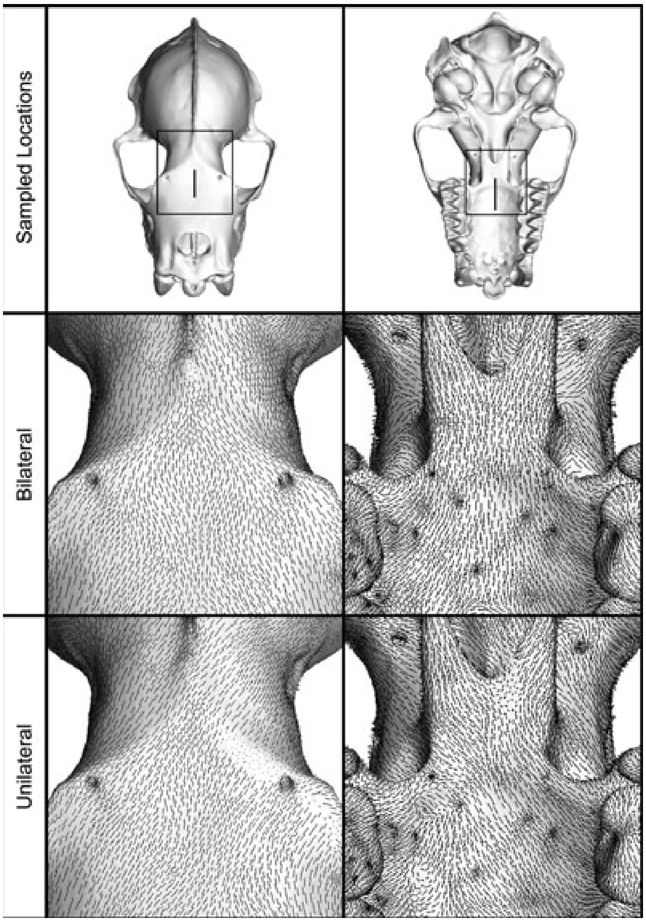

Figure 2. Sample locations (thin line) and strain vectors in a model of *Phyllostomus elongatus* in dorsal (left) and ventral (right) views. The model of *Artibeus jamaicensis* was sampled in the same locations. The middle panel illustrates strain vectors during bilateral molar loading, whereas bottom panel illustrates vectors during unilateral molar loading. Vectors on the dorsal surface (left) represent minimum principal strain and vectors on the palate (right) indicate the maximum principal strain. Note that the vectors are oriented anteroposteriorly during bilateral loading but shift to become more mediolateral during unilateral loading.

of uniaxial compression exists at this point. A strain ratio of 1 (with opposite signs of maximum and minimum principal strains) indicates a state of pure shear, and an infinite strain ratio indicates a state of uniaxial tension. In reality, complex geometries rarely exhibit states of pure uniaxial compression, pure uniaxial tension, or pure shear. Nevertheless, we can use the strain ratio to assess the degree to which the material is experiencing one of these three strain states. The closer the strain ratio is to 1, the more shear is occurring in the material. To investigate whether unilateral biting produced more shear than bilateral biting, we calculated the Euclidean distance of each sample of strain ratios from 1.0, smaller values indicated greater proximity to 1.0.

STATISTICAL ANALYSES

Comparative analyses were performed using a pruned version of Dumont et al.'s (2011) species-level phylogeny. This phylogeny is based on sequences of mitochondrial ribosomal, cytochrome b, partial mitochondrial cytochrome oxidase, and two partial nuclear recombination genes. We tested for adaptive evolution of skull biomechanics in relation to dietary hardness using three biomechanical variables: MA of the skull and proportions of the total moment by the two most important cranial muscles (temporalis and masseter). We compared the fit of evolutionary models that described dietary hardness, which included a Brownian motion (BM) model and four different Ornstein-Uhlenbeck (OU) models. This procedure allowed biomechanical variables to achieve different evolutionary optima according to dietary hardness. BM only had two parameters: the evolutionary rate, $\sigma2$, and root state of the trait, θ, which were obtained by fitting a BM model to the data using the "brown" function in the OUCH package for R (Butler and King 2004). The OU models added additional θ representing the optimal state for each diet regime modeled, and a parameter representing the strength of selection, α, which keeps values from straying too far from the optimum. We fit models with a single optimal biomechanical parameter for all bats (OU1), and separate optima for each dietary hardness category (OU2: liquid, soft, medium, hard, very hard; Table 1, bottom). If dietary hardness influences skull biomechanics, then we would expect OU2 to best fit our data. Conversely, if dietary hardness has no influence on skull biomechanics, BM or OU1 should provide better fits.

We subsequently fit two additional models to account for more specific evolutionary hypotheses. OU3 condensed medium and soft diets into one category, accounting for the possibility that only liquid, hard and very hard diets required adaptations to optimal skull function. OU4 condensed medium and soft, and hard and very hard diets, accounting for the possibility that only liquid diets did not require biomechanical adaptations toward high bite force. We fit all models to the Dumont at al. (2011) consensus tree using OUCH 2.6–1 in R version 2.11.1 (Butler and King 2004). We assigned dietary hardness states to internal branches using maximum likelihood estimates of ancestral states computed using functions in the APE package for R (Paradis et al. 2006). The state with the highest marginal likelihood was assigned in each case. Where two or more states had equal marginal likelihoods, we selected a state at random. We compared model fit using average scores for Akaike's Information Criterion corrected for finite sample sizes (AICc), and considered three units as the cutoff for significant differences among models. AICc provides a measure of the relative goodness of fit of a statistical model while taking into account the number of parameters in the model and small sample sizes.

We investigated whether cranial morphology and biomechanics have evolved in tandem with the use of particular loading

Table 1. Parameters from Brownian motion (BM) and Ornstein-Uhlenbeck (OU) models fit to biomechanical variables, σ^2: rate of evolution, α: selection strength, AICc: Akaike's Information Criterion corrected for small sample sizes, ΔAICc: change in AICc from the lowest value across models. Bold font indicates the scores for the best models. Refer to text for further information about the parameters.

Model	σ^2	α	AICc	ΔAICc
Mechanical advantage (force out/force in)				
BM	0.0808		1.9231	15.7349
OU1	7.5429	145.0372	1.5207	8.8655
OU2	0.4065	7.2271	−0.8778	6.467
OU3	0.5025	8.8260	−4.1212	3.2236
OU4	0.5032	8.8373	**−7.3448**	–
Moment by temporalis muscle				
BM	0.0051		−63.1717	1.0456
OU1	0.0188	4.8797	−61.4297	2.7876
OU2	0.0176	4.1344	**−64.2173**	–
OU3	0.0191	3.3647	−60.1272	4.0901
OU4	0.0167	2.6545	−60.3651	3.8522
Moment by masseter muscle				
BM	0.0017		−91.2705	5.2146
OU1	0.0033	3.0950	−92.6002	3.8849
OU2	0.0037	3.1199	−94.2694	2.2157
OU3	0.0044	3.5212	**−96.4851**	–
OU4	0.0032	1.2381	−86.3256	10.1595

OU1 = liquid, soft, medium, hard, very hard.
OU2 = liquid, (soft+medium), hard, very hard.
OU3 = liquid, (soft+medium), (hard+very hard).
OU4 = liquid, (soft+medium+hard+very hard).

behaviors, and specifically if the evolution of shorter faces and a larger moment generated by the temporalis was associated with the use of torsional loads while feeding on hard foods. We ran phylogenetic generalized least square (PGLS) regressions with loading behavior (percentage of bending or torsional loads while feeding in hard foods) as the response variable and PC1 scores, the proportion of the moment about the TMJ axis by the masseter and temporalis as the predictor variables.

Results

HOW HAVE SKULL MORPHOLOGY AND BIOMECHANICS EVOLVED WITH DIET?

Our results indicate that more efficient bite force production evolved in species consuming food items that are solid and harder. Based on AICc score differences, a two-optima model was the best fit to the evolution of skull MA, although a three-optima model was not less likely (Table 1). The optima for MA doubled from liquid to solid diets (θ_{liquid}: 0.3259, $\theta_{\mathrm{soft+medium+hard+veryhard}}$: 0.6606) in that model, and in the three-optima model, optima MA increased with dietary hardness (θ_{liquid}: 0.3259, $\theta_{\mathrm{soft+medium}}$: 0.6582, $\theta_{\mathrm{hard+veryhard}}$: 0.6634).

The temporalis evolved as the predominant muscle in selective regimes of increasing dietary hardness. Several models were the best fit for the evolution of the moments generated by the major cranial muscles. A four optima model was the best fit for the temporalis moment, although it was not significantly different from the five optima model and BM. Optima for the temporalis moment was highest for very hard diets ($\theta_{\mathrm{veryhard}}$: 0.8342), followed by hard diets (θ_{hard}: 0.7335), and lowest for soft diets ($\theta_{\mathrm{soft+medium}}$: 0.7289). Conversely, optima for the masseter moment was lowest for hard diets ($\theta_{\mathrm{hard+veryhard}}$: 0.0947) and highest for soft diets ($\theta_{\mathrm{soft+medium}}$: 0.1581). Liquid diets had an intermediate optima for both cranial muscles (θ_{liquid}, temporalis: 0.7334, masseter: 0.1066).

DO DIFFERENT BITING BEHAVIORS IMPOSE DIFFERENT TYPES OF LOADS ON THE FACIAL SKELETON?

We found strong evidence of bending deformation during deep bilateral biting in both species, as indicated by dominant principal compressive strains (strain ratios < 1.0) in the rostrum and dominant tensile strains (strain ratios > 1.0) in the palate (Table 2). Directions of the compressive principal strain in the rostrum and tensile principal strain in the palate were also well aligned in the rostro-caudal direction during bilateral loading in both species, providing further evidence of bending deformation (Fig. 2). Conversely, under unilateral biting, there is evidence of torsional deformation in both species, but especially in *A. jamaicensis*. There is still primarily compression in the rostrum and primarily tension in the palate, but a trend toward torsion is illustrated by average strain ratios that are closer to 1.0 (pure shear). The comparison of Euclidean distances from 1.0 for the strain values makes this result even clearer (Table 2).

DOES THE EFFECT OF LOADING REGIMES ON THE FACIAL SKELETON VARY WITH CRANIAL MORPHOLOGY?

Of the two species compared, *A. jamaicensis* has a much higher MA (0.72) than *P. elongatus* (0.42; Table S1). Under both deep unilateral and deep bilateral biting, bending and twisting strains, respectively, are much higher in *P. elongatus* than in *A. jamaicensis*. Under unilateral biting, the average maximum tensile strain (ε_{11}) in the palate of *P. elongatus* is 1.42 E-04 MPa and for *A. jamaicensis* it is 6.76E-05 MPa. Similar results hold for minimum principal compressive strain ($\varepsilon_{33,}$ *P. elongatus*: −9. 40 E-05 MPa, *A. jamaicensis*; −4.58 E-05 MPA) and for bilateral biting (Tables S1 and S2).

Table 2. Strain ratios for each of the 10 points measured in the rostrum and palate (from Fig. 2, listed in aterioposterior direction) during finite element simulations of deep bilateral and deep unilateral biting in *Artibeus jamaicensis* and *Phyllostomus elongatus.* Strain ratio means and Euclidean distances (E.D.) to 1 are highlighted in bold. Strain ratios closer to 1 (i.e., lower E.D.) indicate more shear in the skull.

	Rostrum		Palate	
Artibeus jamaicensis	Deep bilateral	Deep unilateral	Deep bilateral	Deep unilateral
1	0.56	0.48	1.42	0.96
2	0.53	0.58	2.53	1.51
3	0.79	0.61	2.20	1.35
4	0.74	0.58	2.22	1.48
5	0.61	0.65	1.66	1.08
6	0.48	0.69	1.45	1.77
7	0.38	0.66	1.41	1.33
8	0.33	0.69	1.27	1.65
9	0.57	0.84	1.26	1.80
10	0.85	0.98	1.39	1.60
Mean strain ratio	**0.58**	**0.68**	**1.68**	**1.45**
E.D. to 1	**1.41**	**1.11**	**2.55**	**1.66**
Phyllostomus elongatus				
1	0.70	0.82	2.88	2.38
2	0.68	0.73	2.37	2.71
3	0.71	0.77	2.43	3.01
4	0.67	0.70	2.92	2.89
5	0.53	0.58	2.87	2.72
6	0.35	0.42	3.06	1.88
7	0.33	0.32	1.85	1.48
8	0.36	0.34	0.83	0.84
9	0.35	0.33	0.77	0.75
10	0.33	0.32	0.89	0.70
Mean strain ratio	**0.50**	**0.53**	**2.09**	**1.94**
E.D. to 1	**1.67**	**1.60**	**4.44**	**4.07**

HAVE CRANIAL MORPHOLOGY AND BIOMECHANICS EVOLVED WITH LOADING REGIMES?

The best multiple regression (PGLS) models predicting loading behavior were those including the cranial shape variable (PC1) and the proportions of the moment about the TMJ produced by the temporalis and the masseter muscles (Table 3, Fig. 3). Species that engage more in torsional loading behaviors tend to have shorter and more robust skulls (low PC1) and a higher proportion of the moment produced by the temporalis muscle than the masseter muscle (slopes: PC1: −15.31, temporalis: 204.48, masseter: −42.10). Conversely, species that engage more in bending loading behaviors tend to have longer skulls (high PC1) and a higher proportion of the moment produced by the masseter (slopes: PC1: 19.26, temporalis: −79.26, masseter: 258.99).

Table 3. AICc scores for phylogenetic generalized least squares regression models of loading behaviors (deep unilateral and bilateral) on skull shape and biomechanical variables. Bold font indicates the scores for the best models.

Model	AICc
Deep bilateral	
PC1	150.3068
Temporalis	143.4124
Masseter	143.3984
PC1+temporalis	136.6957
PC1+masseter	136.5004
Temporalis+masseter	131.6617
PC1+temporalis+masseter	**125.0161**
Deep unilateral	
PC1	147.3366
Temporalis	145.6345
Masseter	144.2266
PC1+temporalis	137.9702
PC1+masseter	136.5217
Temporalis+masseter	133.4351
PC1+temporalis+masseter	**125.7748**

Discussion

DIETARY HARDNESS AND THE EVOLUTION OF SKULL BIOMECHANICS

The importance of diet in shaping mammalian skull morphology and biomechanics is a paradigm inboth evolutionary biology and functional morphology, yet testing evolutionary hypotheses about this relationship still represents a challenge. Taking advantage of the outstanding dietary diversity found in phyllostomids bats, we present evidence that connects diet with the evolution of skull morphology and 3D biomechanics. Supporting our hypothesis, the simulation of selective regimes of dietary hardness reveals a trend toward the evolution of higher capacity to translate muscle force into bite force (MA) as diets become more physically challenging. Increases in MA can be achieved by changes in muscle and skull architecture, including increases in muscle physiological cross-section (PCSA, which in turn is a function of muscle mass, fiber length, and pennation angle; Lieber 2002), and changes in the skull lever system that maximize the muscles' moment arms and reduce the out lever (Greaves 2000).

Tests of evolutionary models regarding individual components of the feeding apparatus further allowed us to explore the potential mechanisms underlying the evolution of skull biomechanics in relation to dietary hardness. Mirroring the results for MA, the evolution of the temporalis and masseter muscles fit models of selective regimes based on dietary hardness. As indicated by a higher evolutionary optimum, the temporalis becomes increasingly important in bite force production in durophagous species.

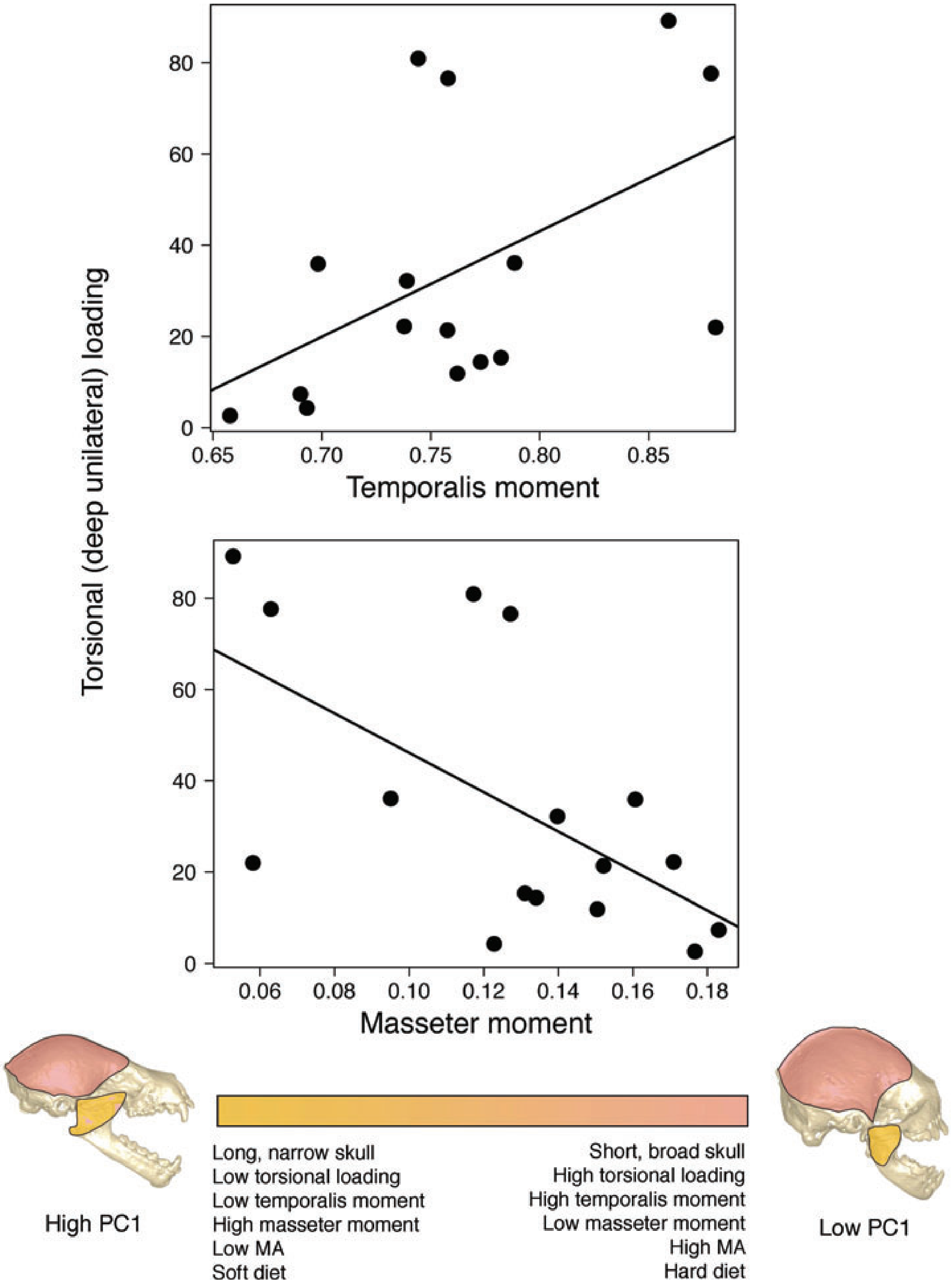

Figure 3. Regression plots of loading behavior on the best predictor variables (from Table 1). General trends in the data are illustrated in the figure below. Regression parameters are provided in the text.

This group is composed of species that specialize on either hard fruits or hard insects and vertebrates. Consuming these hard foods requires the production of high bite forces at large gape angles, because of the positive scaling of food hardness with prey size (Aguirre et al. 2003; Dumont 2003; Freeman and Lemen 2007). Large gape angles can cause stretching of the fibers within cranial muscles, especially the masseter (Herring and Herring 1974) rendering this muscle less effective for generating bite forces. A higher allocation of muscle force to the temporalis at the expense of the masseter is a potential evolutionary solution to eating large and hard foods. This pattern is common to other mammals that require high bite forces at large gape angles (e.g., carnivores, Greaves 1985; Slater et al. 2009).

Conversely, as diets become less physically challenging, we found increases in evolutionary optima for the role of the masseter in generating bite force. In other groups of mammals such as ungulates and primates, emphasis on the masseter has evolved in association with prolonged mastication, which requires high bite forces at low gapes (e.g., herbivores). However, the category of soft diets in our dataset is comprised mainly by insectivorous and omnivorous species that chew their prey for relatively short periods of time, when compared to mammalian herbivores (Santana et al. 2011). We propose two potential scenarios that may explain this result. First, crushing insect prey requires high bite forces at relatively low gapes, and experimental evidence suggests that chewing insects for longer periods results in a higher degree of prey breakdown and thus higher potential for nutrient availability (Santana et al. 2011). Therefore, an elevated importance of the masseter could be related to benefits related to longer chewing of insect prey. Second, the masseter could gain some importance at the expense of the temporalis due to changes in skull shape that affect attachment area of the temporalis, and relaxed selection on the role of this muscle. Despite the association between a large masseter and soft foods, the temporalis still constitutes the largest muscle in species that feed on soft foods.

The feeding apparatus can exhibit functional equivalence because it is an anatomical system that is composed by many parts (Alfaro et al. 2005; Wainwright et al. 2005). The skull, cranial muscles, and teeth are examples of parts that perform specific functions, and modification of any of these components can result in a diversity of morphological solutions to the same functional requirements imposed by diet. Within phyllostomids, liquid feeding seems to constitute an example of functional equivalence. In both the two- and three-optima OU models, bats with a liquid diet have the lowest optimum for MA. This is not surprising given the minimal bite force requirements posed by liquid diets (vampire bats have very sharp incisors that allow them to easily cut through their prey's skin; Greenhall 1972). Still, this trend is particularly striking given that this dietary group is composed of three clades in which liquid feeding has evolved independently and on fluids from very different sources (Desmodontinae: vampire bats; Lonchophyllinae and Glossophaginae: nectarivorous bats; Datzmann et al. 2010). Furthermore, functional convergence in these groups has been achieved through skull morphologies that are not obviously similar to one another (e.g., see *Lonchophylla robusta* and *Desmodus rotundus* in Fig. 1).

Functional characterizations of ecological differences have proven useful in understanding the link between ecology and morphology (Losos 1992; Herrel et al. 2002; Huber et al. 2005; Herrel and Holanova 2008). At the level of gross skull biomechanics in a family-level clade, a few rather intuitively defined dietary hardness categories were sufficient to shed light on the evolution of the feeding system in phyllostomids. Although these categories are useful in characterizing evolutionary trends in skull biomechanics, they may not be informative for studies of more detailed interactions (e.g., between teeth and food), or convergences in diet among widely separated phylogenetic groups (e.g., carnivorans and bats). As the field of evolutionary comparative biomechanics expands, an integration of ecological data and behavioral observations will be necessary to determine which functional categories and potential selective regimes are relevant for the questions under study. Overall, our results corroborate that most of the variation observed in phyllostomid skull form and biomechanics is underlined by broad changes in dietary hardness.

THE INTERPLAY AMONG BEHAVIOR, SKULL MORPHOLOGY AND FUNCTION

Our FE analyses indicate that (1) the skulls of phyllostomids are subjected to bending loads during deep bilateral biting, and to both bending and torsional loads during deep unilateral biting behaviors (see also Ross and Hylander 1996), and (2) contrary to our expectations, the magnitude of the strain created by these loads decreases in cranial morphologies that have a higher MA. Both average maximum and minimum principal strains in the rostrum and palate of *P. elongatus* (MA $= 0.45$) are much higher than those of *A. jamaicensis* (MA $= 0.72$). Higher bite forces due to higher MA would result in higher stresses and strains in the rostrum and palate of models loaded with a similar ratio of force/surface area, but the short, broad skulls of *A. jamaicensis* seem not only to improve its bite force, but also its structural strength to these loads.

Across all phyllostomids studied, specializations for either torsional or bending loads during feeding are strongly associated with the evolution of skull morphology and biomechanics. Species that engage more in loading behaviors that introduce shear stresses due to torsion tend to have shorter rostra, overall more robust skulls and higher proportion of the jaw moment produced by the temporalis muscle (Fig. 3). For a fixed gape angle, the evolution of shorter skulls is predicted to increase bite force output by reducing the out lever and increasing the temporalis moment arm (Greaves 2000). Interestingly, these short-faced bats further increase their bite forces through unilateral (torsional) loading behaviors (as demonstrated by behavioral observations and in vivo bite force measurements; Dumont 1999; Santana and Dumont 2009). It remains to be tested whether or how the evolution of robust skulls and the temporalis as the dominant muscle have an effect in reducing the torsional strains produced during unilateral biting in these short-faced species.

Some behavioral traits, such as behavioral plasticity, are expected to slow morphological specialization and broaden resource use (West-Eberhard 1989). Although some durophagous phyllostomids are highly plastic for loading behaviors in response to food types (Dumont 1999; Santana and Dumont 2009), this plasticity did not preclude specializations in skull biomechanics. Seasonal variation in food availability and competition with bats and other mammals might be responsible for maintaining selection on morphological and biomechanical traits that grant access to hard foods. For example, *A. jamaicensis* consumes soft fruits throughout the year, but eats large quantities of hard figs when these are available (Handley and Gardner 1991). Fig trees fruit abundantly but asynchronously and with marked seasonal peaks (Handley and Leigh 1991). When *A. jamaicensis* eats hard figs, it uses torsional loadings predominantly, but it is able to dramatically switch to bilateral biting when confronted with softer foods (Dumont 1999; Santana and Dumont 2009). Nevertheless, *A. jamaicensis* has a relatively high temporalis moment and a robust skull shape (Fig. 1, bottom) that seem to improve strength during torsional loads (Dumont et al. 2005).

Like many other tropical mammals, phyllostomids can experience strong competition for resources within the species-rich communities that they are part of (Bonaccorso et al. 2007; Rex et al. 2010). If the combined evolution of morphological, behavioral, and biomechanical traits described here opens the access to otherwise unavailable resources (e.g., hard foods), species are likely to expand their niche space and experience a reduction in interspecific competition (ecological character displacement; Dayan and Simberloff 2005). As resource competition and ecological character displacement are thought to play a major role in driving evolutionary diversification, the evolutionary strategies described here contribute to understanding the potential mechanisms underlying phyllostomid diversification.

Conclusion

This study illustrates the association among diet, loading behaviors, and the integrated evolution of morphological and biomechanical traits of the mammalian feeding apparatus. As predicted by behavioral drive models of evolution, diet and loading behaviors are not only closely associated with the evolution of cranial morphology and function, but can also be linked through models that simulate selective regimes. The indication that selection has acted on skull function and has caused changes on its morphology opens the door for future studies that investigate which aspects of skull function are detected by selection and how selection may act upon them.

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Supporting Information

The following supporting information is available for this article:

Table S1. Raw data used in our analyses: dietary hardness categories, PC scores for cranial morphology, mechanical advantage (MA) values, percentages of the jaw moment for the two major cranial muscles, and percentages of the two most used loading behaviors when feeding on hard foods.

Table S2. Maximum tensile and minimum compressive principal strains (ε_{11} and ε_{33}, in MPa), and strain ratios across 10 nodes located in the rostrum and palate of *Artibeus jamaicensis* and *Phyllostomus elongatus* during bilateral molar (deep) biting simulations.

Table S3. Maximum tensile and minimum compressive principal strains (ε_{11} and ε_{33}, in MPa), and strain ratios across 10 nodes located in the rostrum and palate of *Artibeus jamaicensis* and *Phyllostomus elongatus* during unilateral molar (deep) biting simulations.

Supporting Information may be found in the online version of this article.