

Finite-Element Analysis of Biting Behavior and Bone Stress in the Facial Skeletons of Bats

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ABSTRACT

The wide range of dietary niches filled by modern mammals is reflected in morphological diversity of the feeding apparatus. Despite volumes of data on the biomechanics of feeding, the extent to which the shape of mammal skulls reflects stresses generated by feeding is still unknown. In addition to the feeding apparatus, the skull accommodates the structural needs of the sensory systems and brain. We turned to bats as a model system for separating optimization for masticatory loads from optimization for other functions. Because the energetic cost of flight increases with body mass, it is reasonable to suggest that bats have experienced selective pressure over evolutionary time to minimize mass. Therefore, the skulls of bats are likely to be optimized to meet functional demands. We investigate the hypothesis that there is a biomechanical link between biting style and craniofacial morphology by combining biting behavior and bite force data gathered in the field with finite-element (FE) analysis. Our FE experiments compared patterns of stress in the craniofacial skeletons within and between two species of bats (*Artibeus jamaicensis* and *Cynopterus brachyotis*) under routine and atypical loading conditions. For both species, routine loading produced low stresses in most of the skull. However, the skull of *Artibeus* was most resistant to loads applied via its typical biting style, suggesting a mechanical link between routine loading and skull form. The same was not true of *Cynopterus*, where factors other than feeding appear to have had a more significant impact on craniofacial morphology.

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Key words: biting behavior; bone stress; adaptation; finite-element analysis; Chiroptera

Mammal evolution is largely a story of the expansion of dietary niches from an insect-eating ancestor to include foods ranging from meat and bone to plankton. This diversity is clearly reflected in the morphology of the craniofacial skeleton. The association between skull structure and diet across distantly related mammals suggests that skull shape underwent selection over evolutionary time as new dietary niches were explored. Many excellent laboratory-based studies of feeding have provided a wealth of detailed information about the biomechanical behavior of bones and muscles under controlled experimental conditions. Building on this knowledge, morphologists are beginning to venture into the field to investigate how natural behaviors interact with morphology to define how animals function within their native environments. By

combining data gathered in the laboratory with behavior and performance data from the field, modern comparative

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TABLE 1. Proportions of biting styles used by *Artibeus jamaicensis* and *Cynopterus brachyotis* when feeding on soft and hard fruits*

	Unilateral canine	Bilateral canine	Unilateral molar	Bilateral molar	n
Hard fruit					
<i>Artibeus jamaicensis</i> ^a	0	9.3	80	10.7	3
<i>Cynopterus brachyotis</i>	7.98	39.33	7.15	45.58	3
Soft Fruit					
<i>Artibeus jamaicensis</i> ^a	29.1	39.7	19.1	11.3	3
<i>Cynopterus brachyotis</i>	0	61.67	2.76	35.56	4

*Mean percentages of biting styles and the number of individuals sampled (n) are reported. Each individual was represented by a series of at least 20 bites.

^aDumont (1999).

morphologists hope to discover the links between morphology and behavior and gain greater insight into the evolution of functional diversity.

One defining characteristic of mammals is the distinctive structure of their jaws and teeth. All mammals have a single paired lower jaw bone and most possess several types of complex teeth that occupy different functional regions of the mouth. In keeping with this complexity, field-based behavioral studies demonstrate that mammals use several different combinations of teeth when they bite food items (Van Valkenburgh, 1996; Dumont, 1999; Dumont and O'Neal, 2004). These biting styles can include teeth from one or both sides of the mouth and teeth from various locations along the tooth row. Importantly, each biting style loads the facial skeleton in a different way. Unilateral (one-sided) bites apply predominantly torsional loads, bilateral (two-sided) bites apply predominantly bending loads, and the location of a bite along the tooth row affects bite force (Dumont and Herrel, 2003). Field studies demonstrate that most species of carnivores and fruit bats studied thus far use characteristic biting styles that are statistically distinct even in the face of variation among individuals (Van Valkenburgh, 1996; Dumont, 1999; Dumont and O'Neal, 2004). In other words, the craniofacial skeletons of different species are often exposed to different loading regimes.

In this study, we addressed the hypothesis that there is a biomechanical link between biting style and craniofacial morphology by comparing patterns of stress in the craniofacial skeletons of two fruit bats (*Artibeus jamaicensis* and *Cynopterus brachyotis*) under normal and atypical loading regimes. Within each species, we compared stresses generated under the expected range of bite forces for each biting style (based on population statistics) as well as under a constant bite force. If craniofacial morphology is optimized for the most common biting styles, we predict that the skulls of these bats will be most resistant to loads applied through their preferred loading regime. We also compared the relative strength of *Artibeus* and *Cynopterus* under different loading conditions. This allowed us to investigate how these distantly related bats overcome the mechanical challenge of being small animals that eat hard fruits.

Evidence that morphology is optimized or tuned for preferred loading regimes would suggest that loads imposed by feeding played a role in the evolution of craniofacial morphology. Alternatively, the lack of an association between craniofacial morphology and biting behavior would support the contention that the craniofacial skele-

ton is not optimized solely for feeding (Hylander et al., 1991; Hylander and Johnson, 1997) and must be a compromise between conflicting functional demands.

To evaluate our hypothesis, we needed a method that would allow us to assess the impact of bite force over large regions of the skull and facial skeleton simultaneously. We also needed to be able to conduct experiments in which all loading variables could be manipulated very accurately. Traditional in vivo experimental methods, using strain gauges, for example, allow data to be collected from only a few small areas at a time and it is virtually impossible to control loading conditions precisely in live animals. Moreover, in very small animals such as bats, the surgical placement of strain gages likely would interfere with normal feeding. To overcome these limitations, we turned to finite-element analysis (FEA). FEA was developed to visualize and quantify stress and strain distributions across entire mechanical components due to known and controllable loading conditions (see Richmond et al., 2005, this issue). Because of these qualities, FEA was a good alternative to traditional in vivo experimental techniques.

MATERIALS AND METHODS

Comparative Sample and Experimental Design

Artibeus jamaicensis (family Phyllostomidae) and *Cynopterus brachyotis* (family Pteropodidae) represent independent lineages of fruit bat in the New and Old World tropics. We selected these species because of their convergence in ecological niche and body size. Although *Artibeus* and *Cynopterus* are relatively small, on average 42 and 44 g, respectively, both frequently include figs and other hard fruits in their diets (Fleming, 1988; Tan et al., 1998; Gianini and Kalko, 2004). They face similar mechanical challenges during feeding, but *Artibeus* and *Cynopterus* routinely employ significantly different biting styles (Table 1).

Artibeus exhibits a significant difference in biting style when eating soft and hard fruits (Dumont, 1999) and responds to the mechanical challenge of breaking apart hard fruit by switching to unilateral molar bites. While higher forces are produced during unilateral molar biting (Table 2), this loading regime primarily twists the facial skeleton dorsally on the working side. In contrast to *Artibeus*, there is no statistical difference in the combination of biting styles used by *Cynopterus* during soft- and hard-fruit feeding. *Cynopterus* consistently emphasizes bilateral biting, which applies primarily bending loads to the rostrum.

TABLE 2. Means and standard deviations of bite forces (in Newtons) during unilateral canine, bilateral canine, and unilateral molar biting for *Artibeus jamaicensis* and *Cynopterus brachyotis**

	Unilateral canine	n	Bilateral canine	n	Unilateral molar	n
<i>Artibeus jamaicensis</i>	9.49 ± 2.74	10	18.8 ± 5.56	19	22.5 ± 10.95	24
<i>Cynopterus brachyotis</i>	11.5 ± 1.19	10	11.4 ± 3.17	5	14.0 ± 2.23	10

*Data from Dumont and Herrel (2003) and Aguirre et al. (2002).

Based on these biting behavior data, we conducted finite-element (FE) experiments to investigate the hypothesis that the skulls of *Artibeus* and *Cynopterus* are more resistant to loads imposed by their typical biting behaviors than by loads imposed by atypical biting behaviors. First, we modeled the effects of each species' typical biting behavior during hard-fruit feeding by loading each model iteratively until known average bite forces were generated. Second, we use the same procedure to model atypical biting behaviors in each species. Third, we compared the response of each model to atypical and typical loading by applying the same bite force at each of the two bite points. This allowed us specifically to assess the role of craniofacial structure in dissipating loads applied at different locations. Finally, to assess the effects of geometry and loading condition on patterns of stress transmission, each model was loaded with a bite force of 22.5 N (the average bite force for *Artibeus* in unilateral molar biting) under each loading regime. Overall, these experiments provided two independent tests of the association between biting behavior and stress in the craniofacial skeleton: one in *Artibeus* and another in *Cynopterus*.

In contrast to engineered products, it is important to consider the impact of individual variation when modeling organisms. Although our models were constructed and loaded with data from full-grown adult bats, it is possible that the specimens we modeled did not represent average morphologies or produce average bite forces. Ideally, one would assess individual variation by constructing models from a series of individuals with known bite forces. Because that is not feasible given current modeling techniques, we addressed the issue of variation more simply by applying bite forces to our models at magnitudes ranging from the mean to the mean plus two standard deviations.

FE Modeling

The first step in a successful FEA is to generate a sufficiently accurate geometric model of the structure of interest. For engineered structures, this is often a straightforward process in which structures are built by developing a parametrically controlled model (i.e., inputting structures with predefined sizes and shapes). The highly irregular shape of biological structures and the frequent need to build models from imported data greatly complicates the process of generating FE models.

To build FE models of the skulls of *Artibeus* and *Cynopterus*, we acquired 3D stereolithography (STL)-formatted surfaces representing the geometry of each skull from the University of Texas High-Resolution Computed Tomography Facility at Austin, Texas. These files were generated from stacks of 2D micro-CT scans with a spatial resolution of 0.019 mm.

The STL format consists of a tessellated surface mesh composed of three-noded triangular elements. These tri-

angles may be considered first-order representations of real-world geometries in that while element vertices reside on true surfaces, the STL surfaces are planar interpolations between vertices. As with any similar representation of second- or higher-order real-world surfaces, as the quantity of elements and vertices increase, their overall geometric precision increases. This is particularly important in the case of structures with complex and organic geometries, where accurate geometric representation must be weighed against the information-handling capability of computer hardware.

The initial STL surfaces contained approximately 500,000 triangular elements, which were too large to superimpose directly into an FE model. Even if there were fewer elements, the quality of the elements and mesh were unsuitable for FE modeling because of unevenly skewed internal angles and location mismatch of adjacent nodes. In addition, numerous geometric errors existed in the initial STL surface representation due to spurious pixels captured by the pixel thresholding method, inadvertently omitted pixels in desired regions, and fine-grain geometries in certain sections of the skulls. Comparative size differentials and geometric complexity led to further difficulties in generating a representative model.

Based on our experience in modeling, we took these factors into consideration while refining the STL model using Raindrop's Geomagic Studio, a rapid prototyping software tool. For example, we decided that the thinness, complex geometry, and load-bearing capacity of nasal conchae provided justification for simplifying this region. We also corrected artificial holes, surface irregularities, and extraneous geometry that resulted from the digital reconstruction process. Fortunately, the skulls of these adult bats did not have visible sutures and could be modeled accurately as a continuous bony structure that varies in thickness. Once the overall surface geometry of each skull was resolved to represent a fully enclosed, "water-tight" volume, a new STL surface mesh was generated and exported.

The next step in the process was to import the water-tight STL surface mesh into an FEA tool. For our FE meshing and analysis, we employed Strand7 (G+D Computing, Sydney, Australia). Within Strand7, we were able to use the STL surface representation as a geometric basis for automatically generating an FE mesh of three-noded triangular plate elements. The main differences between this mesh and the imported STL surface representation were significantly less distortion (i.e., improved triangular shapes) and the use of adaptive element sizes (i.e., smaller elements in areas of complex geometry and larger elements in areas of less geometric complexity) (Fig. 1).

Once the FEA tool automatically generated a plate element surface mesh, interactive editing of the mesh was required to resolve a handful of meshing errors, such as

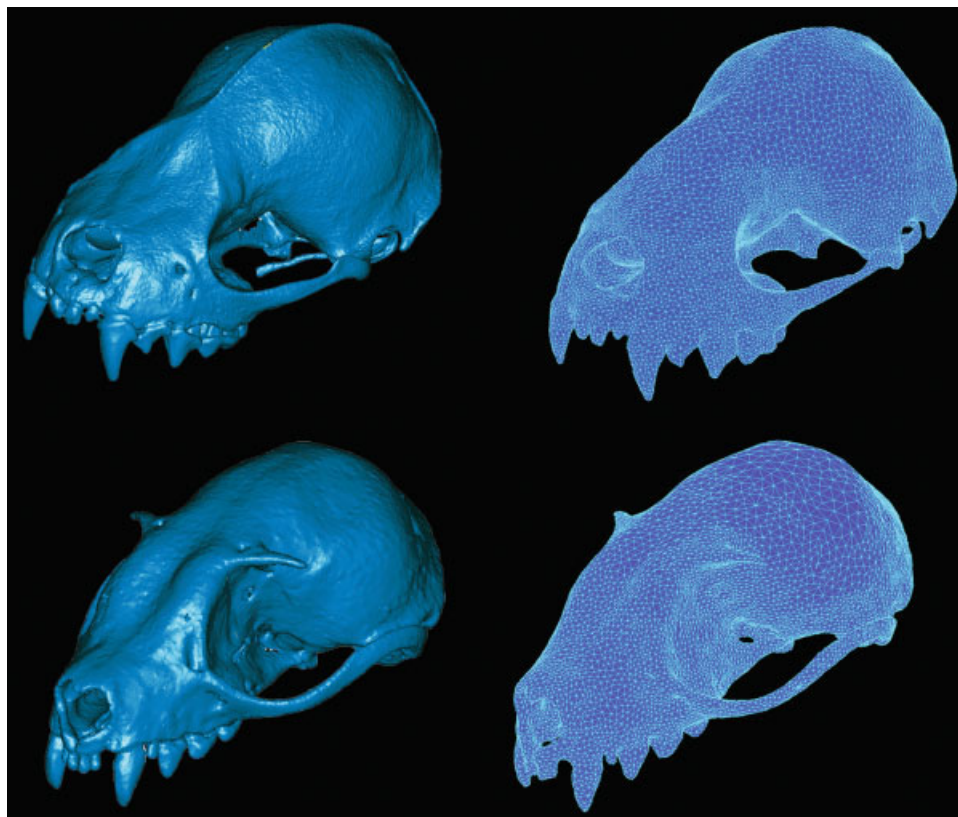


Fig. 1. Comparison between STL surface representations and 10-noded finite-element models for *Artibeus jamaicensis* (top) and *Cynopterus brachyotis* (bottom). STL representations are on the left and finite-element models on the right.

the existence of free (i.e., unattached) plate element edges. Using the refined plate element surface mesh, the Strand7 automatic tetrahedral mesher created a volumetric mesh of 10-noded tetrahedrals. At the end of this step, all plate elements were removed from the FE model, leaving only a volumetric mesh that defined the geometry of the skull (Fig. 1). The completed *Artibeus* model contained 251,968 10-noded tetrahedral elements, 399,806 nodes, and approximately 1.2 million degrees of freedom. Due to improved grading of the mesh, the *Cynopterus* model had fewer elements (138,037), nodes (235,097), and degrees of freedom (approximately 700,000). Overall, very little detail was lost between the initial STL files and the 10-noded tetrahedral models.

Ten-noded tetrahedrals are quadratic elements in which the displacement field may vary quadratically over each element volume, and thus the stress and strain may vary linearly over each element volume. In contrast, four-noded tetrahedrals are linear elements, admitting a linear displacement field and constant stress and strain fields over each element volume. Thus, for a given element size, 10-noded tetrahedral elements are more accurate for modeling complex stress and strain distributions compared to 4-noded tetrahedral elements. Of course, four-noded elements require less computational resources. Sufficiently refined models, however, should converge to identical results for both 4- and 10-noded meshes. We compared analyses using 4- and 10-noded tetrahedral versions of our bat

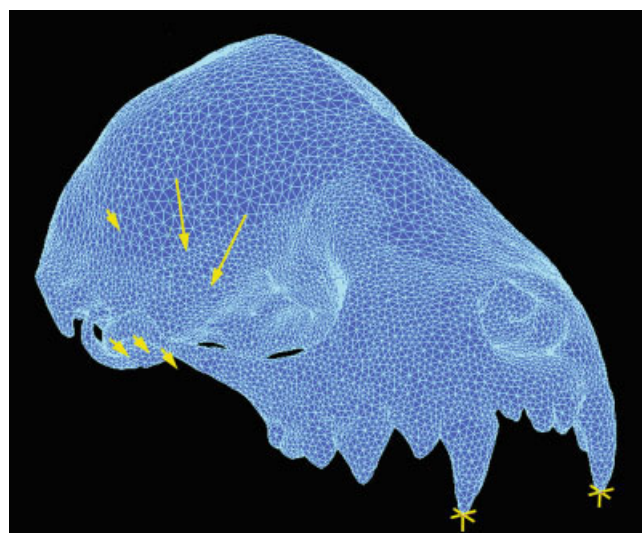


Fig. 2. Finite-element model of *Artibeus jamaicensis* illustrating the applied muscle forces (arrows) and kinematic constraints (crosses) for the bilateral canine load case. In addition to the constraints at the canine tips, a single node in the center of each temporomandibular joint (not visible from this perspective) was constrained in the x-, y-, and z-planes. Note that the same muscle forces illustrated here were also applied to the other side of the skull.

models and found that mean stress values were within 10%. This difference is minimal and indicates that both of our models are robust. Ultimately, we elected to use the 10-noded models because of their increased accuracy.

Material Properties, Constraints, and Loading Conditions

The second requirement for successful FE analyses is a realistic estimate of the material properties of the structure being modeled. Perhaps not surprisingly, there are no data summarizing Young's modulus or Poisson's ratio for the very thin and highly curved bones of bat skulls. However, comparative studies of the stiffness and yield strength of cortical bone suggest that material properties are relatively constant over a wide taxonomic range (Erickson et al., 2002). Based on these comparative data, we assigned our models average values of Young's modulus ($E = 2 \times 10^{10}$ Pa) and Poisson's ratio ($\nu = 0.3$) based on mammalian bone.

Many studies have documented that bone is anisotropic and that its material properties vary regionally (Turner and Burr, 2003). However, for modeling simplicity and due to the lack of reference data, we assumed in this analysis that the bone of bat skulls is homogeneous and isotropic. We suspect that regional variation in material properties may be less of an issue for bat skulls than for the skulls of larger mammals because bat skulls are almost completely composed of exceptionally thin cortical bone. The facial skeletons of larger mammals contain significantly more cancellous bone and cortical bone of varying thickness. On the other hand, because all bone investigated thus far is anisotropic, we also suspect that the same is true of the bone of bat skulls. Because we assume that bat skull bone is homogeneous and isotropic, the absolute stress values obtained from our analyses must be interpreted cautiously. However, it is important to emphasize that assuming the material properties of *Artibeus* and *Cynopterus* skulls are similar, we can compare the relative magnitude and distribution of stress in the two species with a great deal of confidence.

The third requirement for successful FE modeling is to apply realistic forces and constraints to the model. We modeled the forces exerted on the skull by the masseter and temporalis muscles by applying loads to three nodes representing the region of each muscle attachment (Fig. 2). The load vectors applied to nodes approximated the direction of muscle fibers and the proportion of total force generated by masseter and temporalis was based on muscle mass data from closely related species (*Artibeus lituratus* and *Nyctimene robinsoni*) (Storch, 1968). We modeled the relative contribution of temporalis:masseter to jaw adduction as 80:20 in *Artibeus* and 56:44 in *Cynopterus*. The pterygoid muscles are very small in both species; we did not model their forces.

We followed the methods outlined by Strait et al. (2002, 2005, this issue) for applying constraints to the model. To model reaction forces at the temporomandibular joint (TMJ), a single node at each TMJ was constrained against displacement. This effectively created an axis of rotation for the skull due to the application of the muscle forces. To prevent this rigid body motion and induce elastic deformation in the skull due to biting forces, nodes on the tips of the appropriate teeth were constrained against displacement (i.e., displacements in the x-, y-, and z-planes were set equal to 0). For bilateral canine biting, a single

node on the tip of each of the canine was fully constrained. For unilateral canine biting and unilateral molar biting, a single node on the tip of the appropriate tooth was fully constrained. Note that the displacement constraints we imposed at the bite point(s) and at the TMJs prevented all possible modes of rigid body motion, including rotations about any axis. It should be emphasized that solid elements, such as the linear or quadratic tetrahedrals, do not have rotational degrees of freedom. Hence, to prevent rigid body rotation in an FE model composed of solid elements, sufficient displacement constraints must be imposed at nodes to prevent rigid body rotation about any axis. This requires careful attention to the kinematics of the system in order to specify constraints sufficient to prevent rigid body motion while not overconstraining the system. Too many constraints may produce unrealistic stresses and strains due to Poisson's effect.

Each analysis of a biting behavior was completed in two steps. Initially, an arbitrary total amount of muscle force, F_T , was divided between the masseter and temporalis muscles based on muscle mass proportions. All muscles were assumed to act simultaneously and all dynamic or transient effects were neglected. Once the analysis problem was solved, the reaction forces at the constrained tooth (or teeth for the bilateral canine case) necessary for system static equilibrium were determined. This reaction force, F_R^n , was then compared to experimental in vivo bite force measured for the bat species, F_{exp} . Since the computed reaction force is in direct proportion to the total applied muscle load, the required total amount of muscle force, $(F_T)_{new}$, necessary to yield the experimentally measured bite force is given simply by

$$(F_T)_{new} = \left(\frac{F_{exp}}{F_R^n} \right) F_T$$

In the second step of the analysis, the computed total amount of muscle force, $(F_T)_{new}$, was distributed among the masseter and temporalis muscles based on muscle mass portions. The solution of this second analysis problem yielded the deformation of the bat skull, strains, and stresses for a particular feeding behavior that resulted in reaction force(s) at the constrained tooth (teeth) that identically matched voluntary bite force values collected in the field (Table 2) (Aguirre et al., 2002; Dumont and Herrel, 2003). Essentially, known bite forces values were used to calculate the muscle forces required to maintain static equilibrium in the analysis.

It is important to note that our bite force measurement technique provided a bite force that was essentially normal (perpendicular) to the palate of the bat. Therefore, in the above equation, the reaction force, F_R^n , was obtained by taking the projection of the total reaction force vector at the tooth node (or nodes) in the direction normal to the palate, i.e., the dot product between the nodal reaction force vector and the unit normal to the palate, $\hat{n}$:

$$F_R^n = |\vec{F}_R \cdot \hat{n}|$$

The unit normal to the palate, $\hat{n}$, was computed using the coordinates of finite-element nodes residing on the palate and vector algebra.

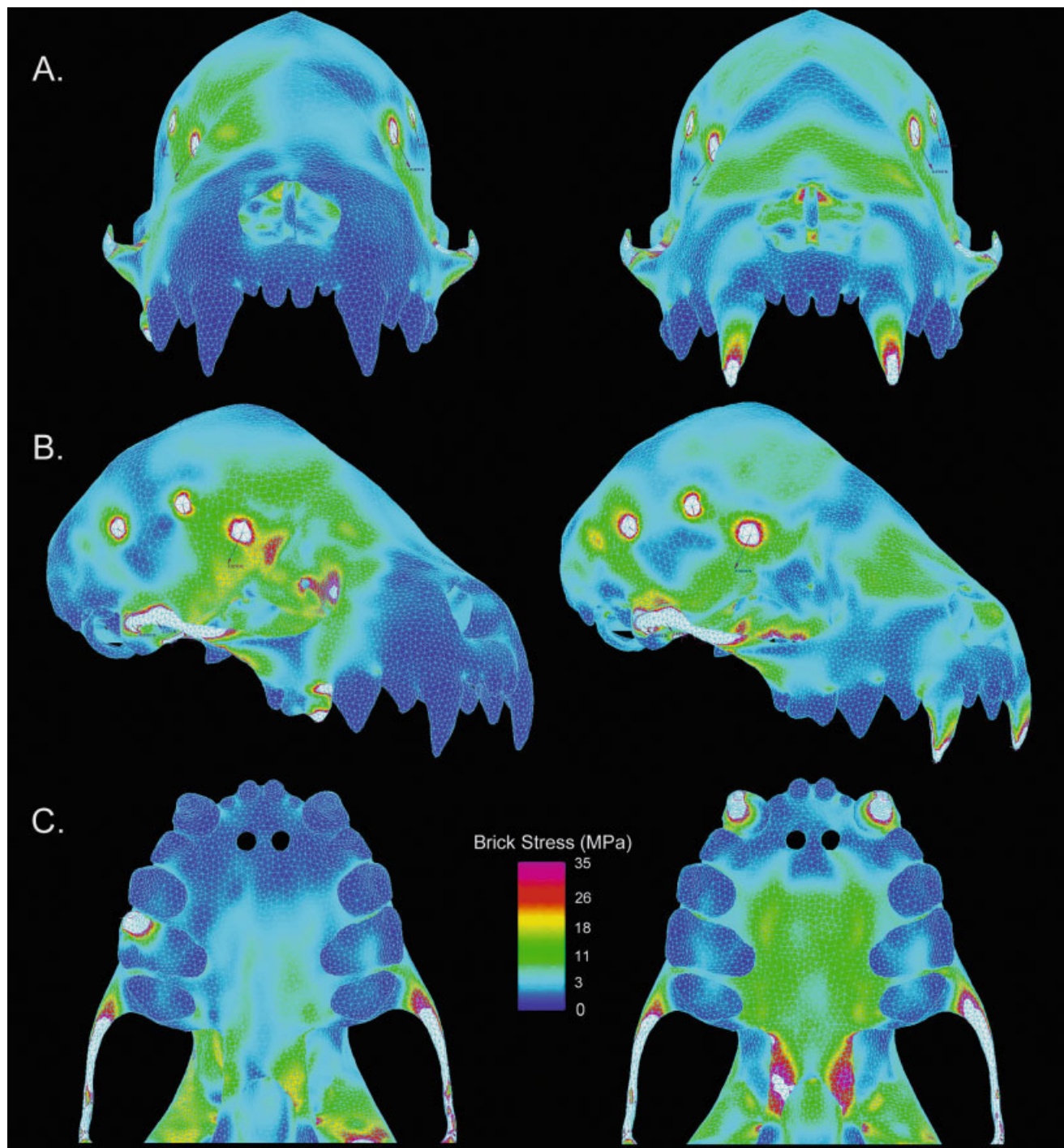


Fig. 3. Von Mises stress during unilateral molar biting (right) and bilateral canine biting (left) in *Artibeus jamaicensis*. Views of the craniofacial skeleton include frontal view (A), three-quarters lateral view of the right side (B), and the palate (C).

Assessing Stress

Any discussion of stress and strain must address the nature of stress and strain as second-order tensors. Consider three mutually orthogonal planes at a material point with each unit outward normal to the plane aligned with

a coordinate axis of a Cartesian x-y-z coordinate system. In a general state of stress, there are six components of stress (and strain) that act on these planes: three components normal to these planes (σ_x , σ_y , and σ_z) and three tangential or shear components (τ_{xy} , τ_{xz} , and τ_{yz}). How-

ever, at any material point, there is a rotation of this coordinate system and its associated orthogonal planes that will maximize the normal component of stress while at the same time eliminate all the shear stress components acting on the newly oriented planes. This is called the principal state of stress with the coordinate axis defining this orientation of planes designated as 1, 2, and 3. The normal stress components acting on the planes defined by the 1, 2, and 3 directions are called principal stresses and are designated as σ_1 , σ_2 , and σ_3 .

Bone, like most biological materials, is elastic and fails under a ductile model of fracture (Nalla et al., 2003). Therefore, we chose to report a type of stress, the Von Mises stress, which is a good predictor of failure under ductile fracture. The failure of ductile materials most often occurs due to distortion. The Von Mises stress (σ_v) is a scalar function of the principal stresses σ_1 , σ_2 , and σ_3 that directly measures how the state of stress at any point distorts the material:

$$\sigma_v = \left[\frac{1}{2} ((\sigma_1 - \sigma_2)^2 + (\sigma_1 - \sigma_3)^2 + (\sigma_2 - \sigma_3)^2) \right]^{\frac{1}{2}}$$

In fact, the square of the Von Mises stress is directly proportional to the strain energy of distortion. Further, the difference between any two principal stresses is equal to twice the maximum shear stress that acts on a plane parallel to the other principal stress. Hence, the Von Mises stress is related to the maximum shear stresses found on three orthogonal planes. Ductile failure is predicted when the Von Mises stress reaches the yield strength of the material.

For each species and loading condition, we plotted the volume of the skull that was stressed at values ranging from 0 to an upper limit imposed by singularities in the experimental results. This range included stress data for 98–99% of model volume for both models and loading conditions. Using this range, we also calculated mean stress (adjusted for volume differences among individual finite elements). We estimated the upper limit of stress conservatively as the minimum stress value at which the singularities caused by point loads on the zygomatic arch coalesced. These singularities are certainly artifacts of modeling muscle forces with point loads. Unfortunately, they make it impossible to identify the highest stresses produced in the models with any degree of certainty. However, maximum stress may be of more biological importance than mean stress since it reflects the occasional, perhaps dangerously high load that an animal may encounter. In order to compare maximum stresses between loading conditions and models, we focused on maximum stress values in the palate, a region that was not affected by our use of point loads and in which we could easily identify local stress maxima.

RESULTS

Biting in *Artibeus jamaicensis*

Artibeus focuses on unilateral molar biting during hard-fruit feeding and uses bilateral canine biting much less frequently (Table 1). There are significant differences in the patterns of stress under these two loading conditions (Fig. 3). The superior surface of the rostrum experiences the highest stress during bilateral canine loading (Fig.

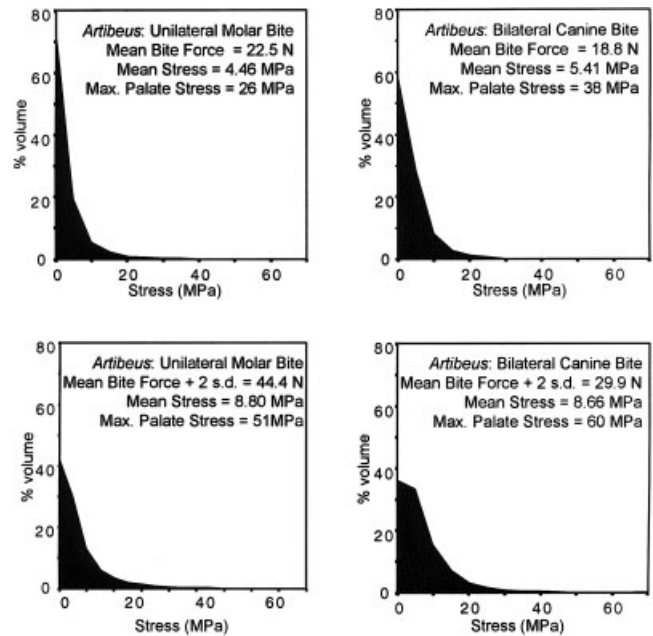


Fig. 4. The volume of the skull stressed (% volume) plotted against stress during biting (stress, in MPa) in *Artibeus jamaicensis*. Graphs illustrate stress under mean bite forces (top) and bite forces that are two standard deviations above the mean (bottom). Unilateral molar bites are on the left and bilateral canine bites on the right; 98–99% of total skull volume is plotted on each graph.

3A). Likewise, the medial surface of the orbit, infratemporal fossa, and rostrum experience the highest strains during unilateral molar loading (Fig. 3B). The most dramatic differences between loading regimes are seen in the palate (Fig. 3C). Stress is widely distributed through the palate and is concentrated in the pterygoid plates during bilateral canine biting. In contrast, unilateral molar biting produces much lower and more localized stresses. These observations are supported by quantitative differences between the two loading regimes (Fig. 4).

At average bite forces, both mean stress and maximum stress in the palate are lowest during unilateral molar loading, despite the fact that bite force is higher. The discrepancy between unilateral and bilateral loading is much larger when bite forces were increased by two standard deviations. Bite force is 67% higher in unilateral molar biting, but maximum stress in the palate is lower and mean stress is very similar to the values generated under bilateral canine biting. At two standard deviations above mean bite force, maximum stress in the palate reaches 51 and 60 MPa in unilateral molar and bilateral canine loading, respectively. To evaluate the relative strength of the *Artibeus* model in unilateral molar and bilateral canine loading, a bite force of 22.5 N was applied to both loading conditions (Fig. 5). Mean stress was 45% greater and maximum stress in the palate was 58% greater under bilateral canine loading.

Biting in *Cynopterus brachyotis*

Cynopterus frequently uses bilateral canine biting during feeding; unilateral molar biting is rare. Contour plots

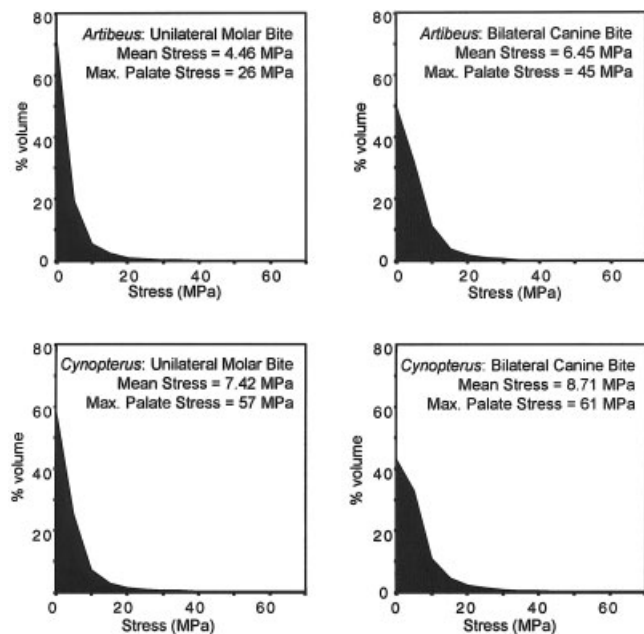


Fig. 5. The volume of the skull stressed (% volume) plotted against stress during biting (stress, in MPa) in *Artibeus jamaicensis* (top) and *Cynopterus brachyotis* (bottom) at a bite force of 22.5 N. Unilateral molar bites are on the left and bilateral canine bites on the right.

illustrate that the distribution and intensity of stress differed subtly between the two loading conditions (Fig. 6). During bilateral canine biting, stress in the palate was more evenly distributed and lower than during unilateral molar loading. Bilateral canine biting also resulted in lower and less extensive stress along the inferior margin of the orbit. More minor differences between the effects of the two biting styles can be logically traced to the loading conditions, namely, higher stresses occurred above the molar tooth during unilateral molar loading and along the superior surface of the rostrum in bilateral canine loading. The apparent similarities between the two loading regimes were supported by quantitative data (Fig. 7).

At average bite forces, unilateral molar loading resulted in slightly higher mean stress as well as 16% greater maximum stress in the palate. When bite force was increased by two standard deviations, mean stress values remained within 10% of one another and maximum stress in the palate was nearly identical under the two loading conditions (49 and 48 MPa). To compare the strength of the *Cynopterus* model under the two loading conditions, a bite force of 22.5 N was applied under both unilateral molar and bilateral canine biting (Fig. 5). Mean stress was 15% greater under bilateral canine loading but the maximum stress in the palate was again nearly identical between the two cases.

Biting in *Artibeus jamaicensis* vs. *Cynopterus brachyotis*

Given an equal bite force of 22.5 N, the *Artibeus* model encountered lower mean stress and lower maximum stress in the palate than did the *Cynopterus* model (Fig. 5). The difference between the two species was greatest

during unilateral molar biting, where average stresses in *Cynopterus* were 66% higher than in *Artibeus* and maximum stress in the palate of *Cynopterus* was more than twice that seen in *Artibeus*.

DISCUSSION

Our initial prediction was that the skulls of these bats are most resistant to loads applied through their preferred loading regime. We tested this prediction in two ways. By investigating mean and maximum stresses under a predicted range of normal bite forces, we modeled how the skulls transmit loads under an expected range of loading conditions associated with feeding. Under these conditions, our prediction was largely supported by maximum palate stress data. At average bite forces, maximum stress in the palate was highest under the atypical loading condition in both species (i.e., bilateral canine loading in *Artibeus* and unilateral molar loading in *Cynopterus*). This relationship held for *Artibeus* when bite forces were increased by two standard deviations. In contrast, maximum stress in the palate of *Cynopterus* was essentially equal under the higher loads. Mean stress appears to be less informative in that it varied little between loading regimes except in *Artibeus*, where mean stress was much higher during bilateral canine with average bite forces. Perhaps it is not surprising that mean stress is less informative than maximum stress values as infrequent large loads are more likely to result in structural failure than average loads (Alexander, 1997).

On a purely structural level, we also evaluated the ability of each model to resist loads during unilateral molar and bilateral canine biting by applying the same force (22.5 N) through both loading conditions. At the same bite force, a stronger structure will be less stressed. In other words, a much higher load would be required to stress that structure to its ultimate yield point. *Artibeus* was strongest against unilateral molar loading as evidenced by the lower mean and maximum palate stresses. This is reflected in living animals, where unilateral molar bite forces are larger and more variable than bilateral canine bite forces. *Cynopterus* was also stronger in unilateral canine biting but, in contrast to *Artibeus*, the difference between the two loading regimes was extremely small. Again, this is reflected in the behavior of living animals in which the forces generated in unilateral molar and bilateral canine biting are very similar. As in *Artibeus*, bite force in *Cynopterus* is most variable under the preferred, in this case bilateral canine, biting style.

These data help to explain why *Artibeus* focuses on unilateral molar bites when it is confronted with a hard food item. The skull of *Artibeus* is strongest against unilateral molar loading and therefore, *Artibeus* can generate the largest bite forces during unilateral molar biting. It is less clear why *Cynopterus* emphasizes bilateral canine biting. One possibility is that it is associated with the morphology of its teeth. Although *Cynopterus* can generate slightly higher (by 0.8 N) bite forces during forceful unilateral molar biting, its canine teeth are much sharper than its molars (data not shown). Therefore, the canines may be more effective at concentrating available forces on small areas of contact with food items and thereby initiate cracks (Lucas, 1979; Lucas and Luke, 1984; Evans and Sanson, 1998). Whether the combination of bite force and sharp teeth renders bilateral canine biting in *Cynopterus*

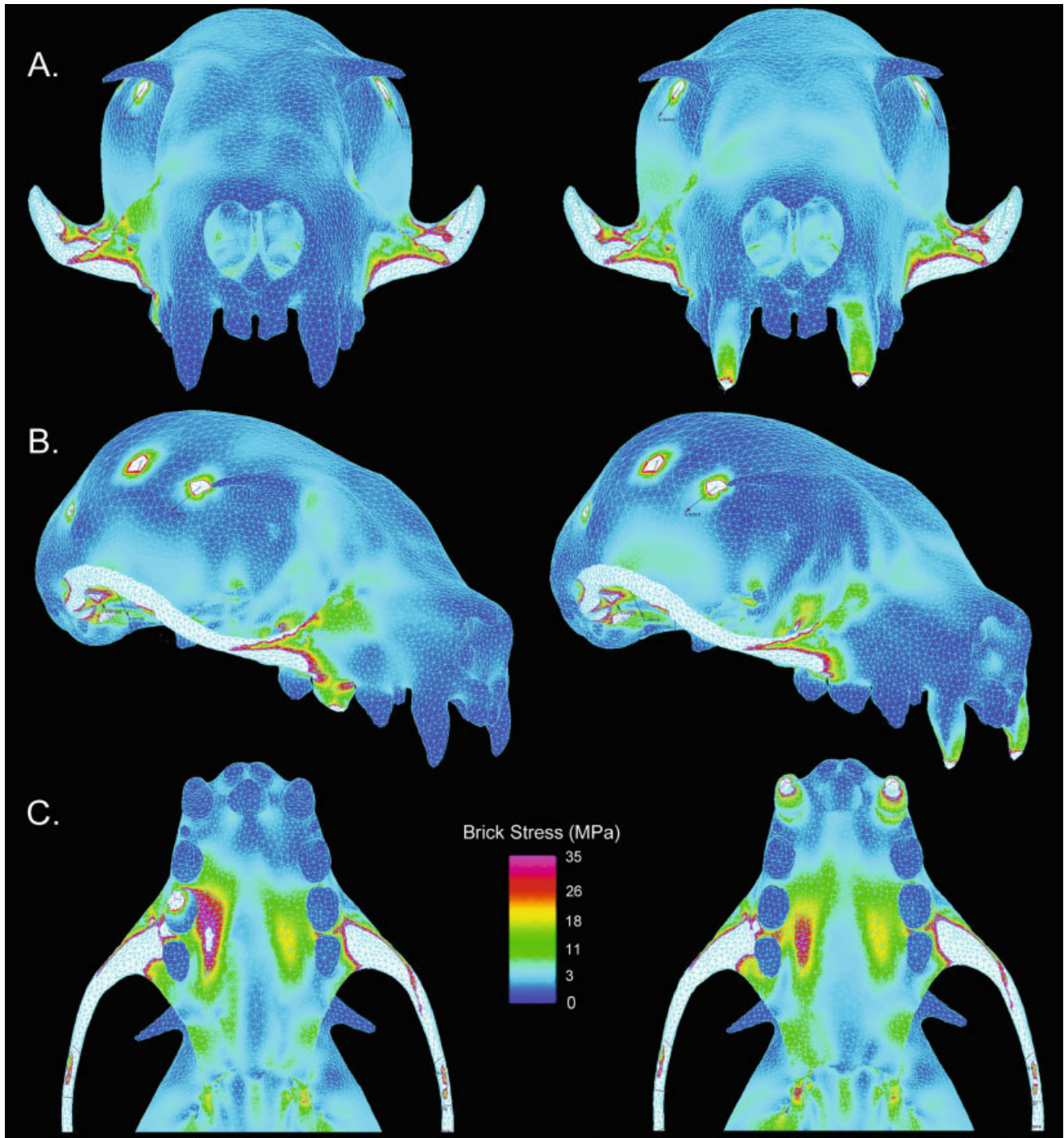


Fig. 6. Von Mises stress during unilateral molar biting (right) and bilateral canine biting (left) in *Cynopterus brachyotis*. Views of the craniofacial skeleton include frontal view (A), three-quarters lateral view of the right side (B), and the palate (C).

more effective in breaking apart hard food items than unilateral molar biting is an interesting prospect that will require further experimentation.

To take our comparisons further, we removed the effect of bite force and focused on the consequences that bone geometry and patterns of muscle loading could have on differences between *Artibeus* and *Cynopterus* (Fig. 7). The

skull of *Artibeus* is much stronger than the skull of *Cynopterus* under both biting styles and dramatically stronger in unilateral molar biting. *Cynopterus*, on the other hand, consistently experiences higher stresses and is more evenly stressed than *Artibeus*.

Differences in geometry probably account for the fact that stress in the facial skeleton of *Artibeus* is frequently

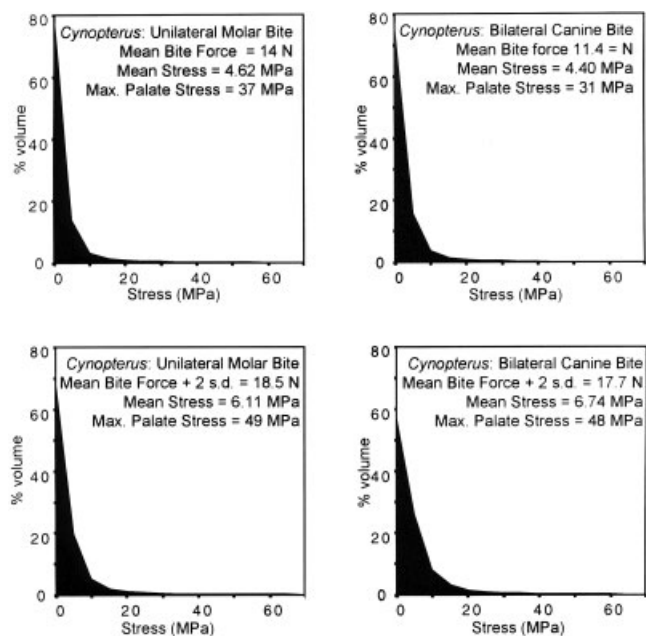


Fig. 7. The volume of the skull stressed (% volume) plotted against stress during biting (stress, in MPa) in *Cynopterus brachyotis*. Graphs illustrate stress under mean bite forces (top) and bite forces that are two standard deviations above the mean (bottom). Unilateral molar bites are on the left and bilateral canine bites on the right; 98–99% of total skull volume is plotted on each graph.

transmitted through the anterior portion of the rostrum, while stress in *Cynopterus* is transmitted more posteriorly through the maxilla near the root of the zygomatic arch. The shorter, more rounded palate and a sloped rostrum of *Artibeus* may provide a better pathway for stress transmission than the longer and more squared rostrum of *Cynopterus*. Likewise, the wider and more substantial zygomatic arches of *Cynopterus*, in combination with a longer palate, may provide the predominant load transmission pathway.

In addition to skull geometry, the ratio of temporalis to masseter muscles may have had a significant impact on the patterns of stress generated within the two models. In our model, jaw adduction in *Artibeus* is dominated by the temporalis muscle (80% of total force), which focused high forces on the lateral wall of the skull in both loading conditions. In contrast, we assigned the masseter muscle in *Cynopterus* two times more force than in *Artibeus* (44% vs. 20% of total force). The larger masseter loads may be responsible for the high stresses seen in the zygomatic arches of *Cynopterus* under both loading regimes. In both species, focal areas of extremely high stress occurred where the point loads representing muscles were applied, and these modeling artifacts were excluded from quantitative analyses. It is important to point out, however, that areas of high stress away from the load application points were not affected by this idealization due to Saint-Venant's principle (Cook and Young, 1985). Therefore, most of the stress in the two models is unaffected by the point load artifacts. Another aspect of muscle biology that may have impact the stress distributions we saw was our assumption that the jaw adductors fire simultaneously and

contribute in accordance with (an estimate of) their relative strength. Teasing apart the roles of bone geometry, relative muscle size, and muscle firing sequences on patterns of stress could provide insights into the kinds of evolutionary changes that are most likely to affect skull function.

From an evolutionary perspective, one of the most intriguing questions to arise from this study is why *Artibeus* and *Cynopterus* represent such different solutions to the challenge of being a small mammal that eats hard foods. Both species are short-faced members of their respective lineages and they are approximately the same size. Despite these convergences in ecology, skull shape, and body size, their skulls appear to dissipate bite forces in very different ways. *Artibeus* exhibits a greater than expected difference in strength between unilateral molar and bilateral canine biting. Given the relatively long palate of *Cynopterus*, the strength of the two biting behaviors is more equal than would be expected. In addition, the skull of *Artibeus* is stronger than the skull of *Cynopterus* despite the fact that the two species are similar in size. Without a broader comparative sample, it is impossible to determine whether one or both species is specialized (*Artibeus* for strong unilateral molar biting, *Cynopterus* for strong bilateral canine biting) or whether each one simply epitomizes the typical condition of most bats within its respective clade.

Although we have established that *Artibeus* and *Cynopterus* are very different, an interesting similarity between them is the concentration of stresses/strains on the palate and pterygoid plates. Theoretical analyses of craniofacial biomechanics have suggested that both regions transmit masticatory stress (Cartmill, 1977; Thomason and Russell, 1986; Covey and Greaves, 1994). The palate and pterygoid plates demonstrate a good example of the utility of FE analysis. Models of palate and pterygoid plate function have not been verified in vivo in small mammals because the placement of strain gages is both technically difficult and likely to interfere with normal feeding behaviors. In this case, FE analyses offered a glimpse of the stress states of regions that are otherwise difficult to access and suggests that in vivo investigations of the palate may yield interesting results. Whether these results are accurate depends, of course, on the quality of our FE models, the authenticity of our loading conditions, and our assumptions about the physical properties of bat skull bone.

Given the current lack of data on the physical properties of bat skull bone, it is impossible to determine the effect of the stresses generated under our predicted range of bite force values. Stresses could be either approaching the ultimate strength of the bone, just high enough to stimulate bone remodeling (and thus avoid fatigue fracture), or so low as to have no impact on bone remodeling and maintenance. Behavioral studies do illustrate that these bats engage in long periods of biting and chewing and suggest that repetitive loading may be an issue for these animals (Dumont, 1999; unpublished data from this study). It is also interesting to note that if our stress values are reasonably accurate, then the palate approaches the ultimate strength of cortical bone in shear with a safety factor of approximately 2.8 during strong biting. In the case of *Artibeus* during bilateral canine biting, the safety factor may drop to 2.3. [These estimates assume an ultimate stress in shear for bone of 70 MPa

(Nordin and Frankel, 2001), which translates into 140 MPa on the Von Mises stress scale.] While these are tantalizing observations, both experimental strain data and bone material properties data are absolutely essential before safety factors in bat skulls can be investigated rigorously.

These data do, however, demonstrate that the bat skull does not constitute what engineers term a fully stressed design. Man-made products that are optimized to bear routine loads while being as lightweight as possible experience high uniform stresses under normal loading conditions. These finite-element analyses of bats are in agreement with experimental studies of other mammals that demonstrate strong strain gradients in the facial skeleton (Ravosa et al., 2000; Herring et al., 2001; Ross, 2001). These data add further support to the conclusion that the skulls of mammals are not optimized solely for feeding (Hylander et al., 1991; Hylander and Johnson, 1997), but must represent a compromise between competing functional demands. Nevertheless, it also appears that feeding behavior (i.e., loading regime) is strongly associated with craniofacial form.

The only way to validate FE models is to compare the results to in vivo/in vitro analyses of bone strain. To date, there are no data on bone strain in the skulls of bats. However, two lines of evidence suggest that our analyses were meaningful. First, both models responded to loading conditions in ways that could be predicted from in vivo studies. Predominantly bending loads (bilateral canine biting) resulted in more or less symmetrical stresses on the superior surface of the rostrum and on the palate. In contrast, predominantly torsional loads (unilateral molar biting) produced more asymmetrical stresses on the rostrum and palate that are topographically consistent with in vivo assessments of shear. Second, our microstrain values were in a range that is reasonable based on in vivo analyses of strain in the facial skeletons of other mammals. Again, the accuracy of absolute stress values generated by our analyses is unknown because they have not been validated through in vivo experimentation. However, our models were geometrically accurate and, assuming that our loading conditions, material properties assignments, and constraints were reasonable approximations of reality, the patterns of stress distribution in *Artibeus* and *Cynopterus* are comparable. The differences between these patterns appear to highlight fundamental functional differences between the skulls of the two species.

In sum, this study demonstrates a clear association between feeding ecology, biting behavior, and craniofacial form in *Artibeus jamaicensis*. Hard fruits are bitten primarily with unilateral molar bites, where the highest bite forces are produced by virtue of the great strength of the skull against loading regime. The relationship among feeding ecology, biting behavior, and craniofacial form is not so clear in *Cynopterus brachyotis*, although its skull is stronger than expected under its preferred bilateral canine loading regime. Whether this approximates equality in bite force and skull strength under unilateral molar and bilateral canine biting represents a derived condition must await data from a broad range of pteropodid species. While this analysis affirms the conclusion that craniofacial form is surely a result of many competing functional demands, it does illustrates

a clear association between stresses generated during feeding and the resistance of the skull to those stresses. If bite force is a performance variable that ultimately impacts fitness, then it is entirely possible that selection for increased bite force could drive evolutionary changes in craniofacial morphology and/or feeding behavior.

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