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Requirements for comparing the performance of finite element models of biological structures

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ABSTRACT

The widespread availability of three-dimensional imaging and computational power has fostered a rapid increase in the number of biologists using finite element analysis (FEA) to investigate the mechanical function of living and extinct organisms. The inevitable rise of studies that compare finite element models brings to the fore two critical questions about how such comparative analyses can and should be conducted: (1) what metrics are appropriate for assessing the performance of biological structures using finite element modeling? and, (2) how can performance be compared such that the effects of size and shape are disentangled? With respect to performance, we argue that energy efficiency is a reasonable optimality criterion for biological structures and we show that the total strain energy (a measure of work expended deforming a structure) is a robust metric for comparing the mechanical efficiency of structures modeled with finite elements. Results of finite element analyses can be interpreted with confidence when model input parameters (muscle forces, detailed material properties) and/or output parameters (reaction forces, strains) are well-documented by studies of living animals.

However, many researchers wish to compare species for which these input and validation data are difficult or impossible to acquire. In these cases, researchers can still compare the performance of structures that differ in shape if variation in size is controlled. We offer a theoretical framework and empirical data demonstrating that scaling finite element models to equal force: surface area ratios removes the effects of model size and provides a comparison of stress-strength performance based solely on shape.

Further, models scaled to have equal applied force:volume ratios provide the basis for strain energy comparison. Thus, although finite element analyses of biological structures should be validated experimentally whenever possible, this study demonstrates that the relative performance of un-validated models can be compared so long as they are scaled properly.

1. Introduction

Finite element analysis (FEA) is a computer-based technique used by engineers to predict the behavior (i.e. response) of engineered products and manufacturing processes to anticipated loading conditions, thereby enabling the design of these systems to be optimized digitally with minimum physical prototyping and testing (Zienkiewicz and Taylor, 2000). Biologists have only recently begun to harness the power of FEA to study the mechanical functions of organisms, but it has already led to new insights into the feeding mechanics of living and extinct vertebrates (Alexander, 2006; Barrett and Rayfield, 2006; McHenry et al., 2006; Thomassen et al., 2007), insect flight and mechanoreception (Combes and Daniel, 2003; Dechant et al., 2006; Wootton, 2003), and plant biomechanics (Fourcaud and Lac, 2003; Niklas, 1999). To date only a few studies have focused specifically on comparing models of different species (Dumont et al., 2005; Macho et al., 2005; McHenry et al., 2006; Wroe et al., 2007a), but interest in both inter- and intraspecific comparative analyses will increase as more finite element models are developed. The inevitable rise of studies that compare finite element models brings to the fore two critical questions about how such comparative analyses can and should be conducted: (1) what metrics are appropriate for assessing the performance of biological structures using finite element modeling? and, (2) how can performance be compared such that the effects of size and shape are disentangled?

The first question requires us to integrate concepts of "performance" derived from biology and engineering. The second question, disentangling size and shape, is ubiquitous in biology.

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Size has a profound impact on the biology of organisms, but it is often of interest to remove the effects of size and compare only shapes. This is particularly true in the field of functional morphology, where shape differences can signify fundamental shifts in how organisms accomplish mechanical tasks such as locomotion or feeding (Alexander, 2003; Koehl, 1996; Schmidt-Nielsen, 1984). Comparing the performance of shapes is particularly critical in finite element modeling studies because researchers often want to compare species that lack the *in vivo* experimental data needed to calibrate and validate FEA results. When such data are lacking it is impossible to know if a FEA returns accurate absolute values of stress, strain or reaction force. However, FEA can be used to compare some aspects of performance in two or more models *if* differences in size are controlled for. Because finite element models exist *in silico* they can be rescaled very easily. Thus they present a clear opportunity to investigate the importance of shape in mediating how structures perform under specified loading conditions.

In this paper, we present criteria for evaluating the mechanical performance of biological structures using FEA and demonstrate how linear, areal and volumetric approaches to scaling these structures affect mechanical performance measures that reflect strength and efficiency. The results are considered in the context of a practical discussion of the uses and limitations of finite element modeling in comparative biology. Not unexpectedly, the choice of an appropriate scaling method requires careful consideration of the data that are available to build and validate the finite element models and the biological questions being asked.

2. Methods and results

In contrast to kinematic analyses that describe rigid-body movements, FEA predicts deformations in systems that are constrained against rigid-body motion (Zienkiewicz and Taylor, 2000). In FEA the physical domain or shape of the system under study is approximated by a contiguous mesh of simple polyhedral shapes called ‘finite elements’, connected together at ‘nodes’, which are the vertices of the polyhedrons. The finite elements are assigned the appropriate material properties, the model is constrained against rigid-body motion, loads are applied, and the subsequent computer solution yields the complete response of the system in terms of its deformation, strains, and stresses at any location within the model.

Properly constructed finite element models yield solutions to the underlying continuum mechanics problem that approximate and converge to the theoretically exact solution. FEA is also versatile in that each of the many parts of a model (i.e. finite elements) may be assigned unique material properties, loads, and may have different shapes and sizes. This means that geometrically complex systems with complex loading conditions and even spatially dependent material properties can be modeled to any desired level of accuracy, limited only by computational resources and required modeling effort.

2.1. Performance concepts in comparative biology and engineering

Like many words in biology, “performance” has several specific meanings. The concept of organismal performance is rooted in the field of ecological morphology, where performance is a measurement of an organism’s ability to perform ecologically relevant tasks that impact fitness (Arnold, 1983; Lande and Arnold, 1983). Common examples of performance measures include sprint speed, a proxy for the ability to avoid predators, and bite force, a measure of potential dietary breadth based on food hardness. Performance data are typically correlated with fairly gross measures of morphological variation (e.g., relative head size or leg length) to document form–function associations. In contrast, finite element modeling offers biologists a tool for exploring the mechanical performance of specific structures. Here, concepts of performance can be borrowed from engineering, where structures are evaluated in terms of their strength and/or efficiency. Using these kinds of performance measures, finite element modeling can be used to explore the mechanistic links between morphology and performance that produce correlations we see in ecological studies. In this way FEA can help to elucidate the mechanisms that underlie ecologically relevant variation in organismal design.

Engineers use FEA to evaluate the performance of structures using measures of structural strength and shape optimality. With respect to strength, FEA of an automobile chassis subject to collision-type loads can accurately predict whether or not the chassis will be permanently bent, enabling engineers to optimize the design of the chassis for minimum weight and maximum structural reliability. The same kind of failure analysis can be applied to biological systems. In both cases, failure occurs when stress exceeds the maximum stress that a structure can withstand. Cortical bone, like most biological materials, is elastic and fails under a ductile model of fracture (Nalla et al., 2003). von Mises stress is a good predictor of failure under ductile fracture and is probably therefore an appropriate metric for comparing the relative strength of models of bones. Most comparative finite element analyses of bone are linear—they do not incorporate inelastic material behaviors. (Note, however, that recent biomedical work has employed complex nonlinear material models, such as the nonlinear Drucker–Prager model, for defining bone failure and material behavior beyond yielding (Bessho et al., 2007; Mercer et al., 2006)). In linear analyses it is not necessary to load finite element models to failure in order to visualize where failure will occur. When all other variables are held constant, changing the absolute magnitude of the applied loads does not change the predicted *relative* distribution of stress in a structure. Therefore, the potential for structural failure is always highest in the region of highest stress.

Structures can also fail through excessive deflection, even if no ductile yielding or brittle fracture has occurred. In this context, failure refers to a structure that is too flexible to perform a given task. For example, a limb bone must not deflect excessively, even elastically, if it is to support an animal’s weight. Excessive deflections occur when structures lack adequate stiffness. Failure by excessive deflection is directly proportional to the elastic compliance of a structure. Structures with higher stiffness (i.e. lower compliance) per unit weight are more optimal than structures with a lower stiffness (higher compliance) per unit weight. Fig. 1 illustrates linear force vs. deflection curves for two different systems to which the same force has been applied. Most simply, these systems could be uni-axial springs in which deflection corresponds to the displacement of the spring end due to an applied force and the slope of the load-deflection curve (k) is the stiffness of the spring. In a more complex analogy, each force-deflection curve could represent the effective stiffness characteristic of a different 3-D biological structure. In this case, force corresponds to the magnitude of total force applied to the system, the deflection is the deflection magnitude at any point of interest, and the slope is the effective stiffness of the structure. The deflection of the stiffer system is δ_1 and the deflection of the more compliant system is δ_2.

Whether modeling simple springs or complex geometries, the area under each load-deflection curve (A) is equal to the work done (W) by the force (F) in elastically deforming the structure; this work is stored in the structure as elastic strain energy. As is always the case in conservative elastic systems, the work done by the externally applied loads is identical to the system’s elastic

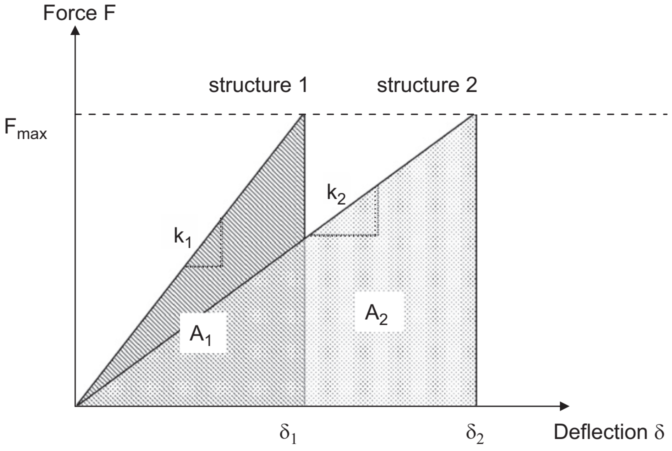

Fig. 1. Load-deflection curves representing two different linear elastic structures (structures 1 and 2). The area under each load-deflection curve (A) is equal to the work done (W) by the force (F) in elastically deforming the structure. The slope of each load-deflection curve (k) is the stiffness and δ is the deflection of each structure.

strain energy. Hence, for system 1, $W_1 = A_1 = F_{max}\delta_1/2$ and for system 2, $W_2 = A_2 = F_{max}\delta_2/2$. Accordingly, although the same force has been applied to each system, more work has been expended to deform the more compliant system (system 2), resulting in more elastically stored strain energy. For a simple spring system $F = k\delta$ and its strain energy is given by $k\delta^2/2$. For a finite element model the system's total strain energy U is computed by the formula:

$$U = \tfrac{1}{2}\{D\}^{\mathrm{T}}[K]\{D\} \tag{1}$$

where $\{D\}$[1] is the vector of nodal displacements and $[K]$ is the stiffness matrix of the finite element model (Cook et al., 2002). Most finite element codes will directly provide the model's total strain energy. If this information is not readily available, it can be computed from the work done by the applied loads W_{Loads} by summing up the work done by each externally applied nodal force $\vec{F}_i$:

$$U = W_{Loads} = \frac{1}{2}\sum_{i=1}^{N}\vec{F}_i \bullet \vec{D}_i \tag{2}$$

where N is the number of externally applied nodal loads, $\vec{D}_i$ is the resulting displacement vector of node i, and the symbol $\bullet$ denotes the vector dot product operator. When comparing finite element models of two different biological structures under a given applied load, the smaller the model's total strain energy, the less work that has been expended in deforming the structure and therefore the more efficient the structure is from a work perspective. It is worth noting that many shape optimization algorithms implemented in commercial finite element tools are based on this same concept. From an engineering perspective, optimal structures maximize static stiffness (or minimize compliance) for a given volume of material, thereby optimizing work efficiency (Bendsøe, 1989, 1995; Bendsøe and Kikuchi, 1988).

Using total strain energy as a performance variable assumes that structures that transmit forces as efficiently as possible (by maximizing the stiffness to weight ratio) are at an advantage from the perspective of energy savings and work efficiency. We suggest that the total-strain-energy performance measure works well for most mineralized tissues. It is important to point out, however, that a number of more compliant biological structures function by storing strain energy and then releasing it quickly. This is the fundamental principal underlying the function of the legs in small, jumping insects (reviewed in James et al., 2007), the tendons in the legs of vertebrates (e.g., Alexander, 2002; Biewener, 2006), the ballistic tongues of amphibians and chameleons (Deban et al., 2007; Lappin et al., 2006; Van Leeuwen et al., 2000), and the raptorial appendages of mantis shrimp (Patek et al., 2007). These flexible, compliant structures accumulate strain energy by applying relatively small forces over long distances and then releasing them quickly to generate relatively large forces that act over short distances. For these specialized systems, the ability to *maximize* total strain energy per volume of material (i.e. volumetric average strain energy density) may be a good performance measure. In this paper, however, we explicitly focus on systems that seek to minimize this measure of work.

2.2. *Scaling finite element models*

When comparing finite element models, performance measures based on structural strength require that force per unit area be held constant, while strain energy performance requires identical loads and volumes. Physical material testing has shown that failure by ductile yielding of a material is closely correlated with von Mises stress, while failure by brittle fracture is closely correlated with maximum principal stress (Juvinall and Marshek, 2005). Even for the complex nonlinear Drucker–Prager material failure model which employs both hydrostatic stresses and deviatoric stresses to define the yield criteria, failure is directly related to the stress tensor. Thus, in all three cases, and indeed in the vast majority of material failure theories including fatigue models for cyclic loading, stress governs failure, and stress is directly proportional to force and inversely proportional to area. Therefore, in order to scale a model and preserve its stress-limited strength-to-weight ratio, the load applied to the scaled model must be adjusted such that the original value of force per unit surface area is preserved. On the other hand, strain energy is proportional to the square of the load and to volume. Therefore, in order to compare total strain energy between two models, the total applied loads and volumes of the models must be identical.

Given these performance criteria, we offer fundamental scaling guidelines for linear finite element models that enable comparisons of both stress-based performance and work efficiency. When comparing the impact of shape on the strength performance of finite element models of biological structures, one can remove the effects of size by scaling the applied loads to maintain a constant value of force per unit surface area.

We recommend that the models be scaled to the same surface area and the same total load be applied to each one. Then any differences in the stress and strain fields between the two models are entirely due to differences in shape, and contour plots of stress and strain can be compared. If on the other hand rescaling the models and/or loads to yield identical force:surface area ratio (or force:volume ratio, see below) is difficult or time consuming, one can still make comparisons by appropriately scaling the results. Suppose we have two finite element models A and B of different shapes that have been loaded with total force values F_A and F_B and analyzed. We now wish to compare the performance of the two models but they have different volumes (V_A and V_B) and different surface areas (SA_A and SA_B). For strength comparison the models should have the same applied force per surface area. To match force:surface area ratios, one can scale the force applied to model B, creating a new model, called B', to match the force:surface area ratio of model A. Thus,

$$F'_B = \left(\frac{SA_B}{SA_A}\right)F_A \tag{3}$$

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[1] $\{D\}^{\mathrm{T}}$ in Eq. (1) denotes the transpose of the vector of nodal displacements.

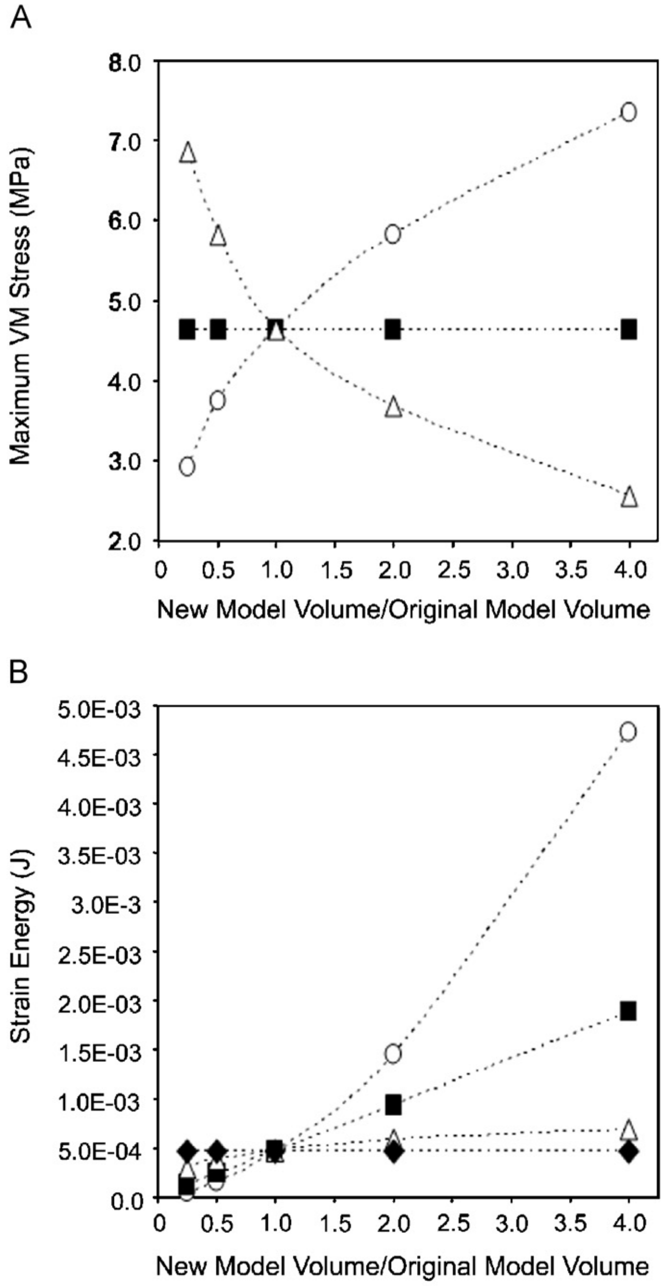

Fig. 2. The scaling of von Mises stress (A) and strain energy (B) in a single finite element model at 0.25 ×, 0.5 ×, 1 ×, 2 × and 4 × original volume with applied forces scaling with linear dimensions (triangles), area (squares), model volume (circles), and the sixth root of volume (diamonds).

where F'_B is the force applied to model B. Because stress and strain are linearly proportional to the applied force, model B' does not have to be analyzed. Instead, one can multiply the stress and/or strain metric (i.e., maximum von Mises stress, maximium principal strain, etc.) obtained from model B due to load F_B by the ratio of (F'_B/F_B) and then compare this result to the stress and/or strain metric obtained from model A. For example, if the metric is maximum principal stress $\sigma_{1\,\max}$ then

$$(\sigma_{1\,\max})_{B'} = \left(\frac{SA_B}{SA_A}\right)\left(\frac{F_A}{F_B}\right)(\sigma_{1\,\max})_B \tag{4}$$

This value can be compared to the maximum principal stress obtained from model A. Similarly, for strain energy comparison the models should have the same force per volume ratio. Strain energy is directly proportional to the load squared and inversely proportional to the cube root of volume. Therefore, to compare the strain energy in model A, the strain energy computed in model B can be scaled according to the formula

$$U_{B'} = \left(\frac{V_B}{V_A}\right)^{1/3}\left(\frac{F_A}{F_B}\right)^2 U_B \tag{5}$$

This value of strain energy can then be compared to the value obtained for model A.

To illustrate this scaling rule, we took a recently published finite element model of a bat skull (Grosse et al., 2007) and rescaled it to 0.25 ×, 0.5 ×, 1 ×, 2 × and 4 × its original volume. We then completed finite element analyses of each rescaled model in which the ratio of applied loads to linear distances, model area and model volume were held constant. Fig. 2A illustrates that values of von Mises stress total remain constant across finite element models only when the ratio of applied load relative to model area is constant. (Note that in this special case of resizing a single model, $[\text{volume}]^{2/3}$ or $[\text{length}]^2$ can be substituted for area: see below.) Scaling loads in direct proportion to either total volume of the model or a linear measurement will lead to artificially elevated or depressed stress values. Fig. 2B shows that strain energy increases linearly when the force:area ratio is preserved, reflecting the fact that the stress and strain state (and therefore strain energy density) is preserved. On the other hand, strain energy is constant when force is scaled in proportion to the sixth root of the volume ratio. These results, as well as a simple mechanics example provided in Appendix A, validate our isometric dimensional scaling axiom. In Appendix A we also illustrate why forces scaled according to volume ratio to the 1/6th power preserves the total strain energy.

2.3. *Case study: a comparative finite element analysis*

Researchers often wish to use FEA to compare some aspect of performance in species for which there are no experimental data to use as input parameters or calibration points. In these cases it is difficult to know whether an analysis provides accurate predictions of absolute values of stress, strain or reaction force. However, it is still possible to directly compare the impact of variation in shape on the relative performance of the models if one first controls for variation in size. To illustrate this shape-based comparison, we took previously published models of two bat skulls, *Cynopterus brachyotis* and *Artibeus jamaicensis* (Dumont et al., 2005; Grosse et al., 2007) and scaled them to the same surface area. [In this case 189.4 mm^2 but the choice of surface area is arbitrary and does not affect the comparison made here]. We then applied the same total muscle force (100 N) to each model using BoneLoad, a computer program we developed to automatically distribute and apply muscle forces across curved bone surfaces (Grosse et al., 2007).

Although we chose to rescale the models to the same surface area and apply the same forces, it not necessary to rescale models at all so long as the forces applied to each model result in identical force:area ratios. It is important to emphasize that $(\text{volume})^{2/3}$ and $(\text{length})^2$ cannot be substituted for area when comparing models that differ in shape. Models with different shapes do not necessarily have the same surface area to volume ratios. For example, at the same surface area, the volume of the *Artibeus* skull is 471.6 mm^3 while that of the *Cynopterus* skull is 433.7 mm^3. This problem is equally complicated for linear dimensions. Given the identical surface area, the distance between the tips of the canines is 5.9 mm *Artibeus* and 4.4 mm in *Cynopterus*. Rescaling these models to the same bicanine breadth would result in very different surface areas and therefore inherently biased

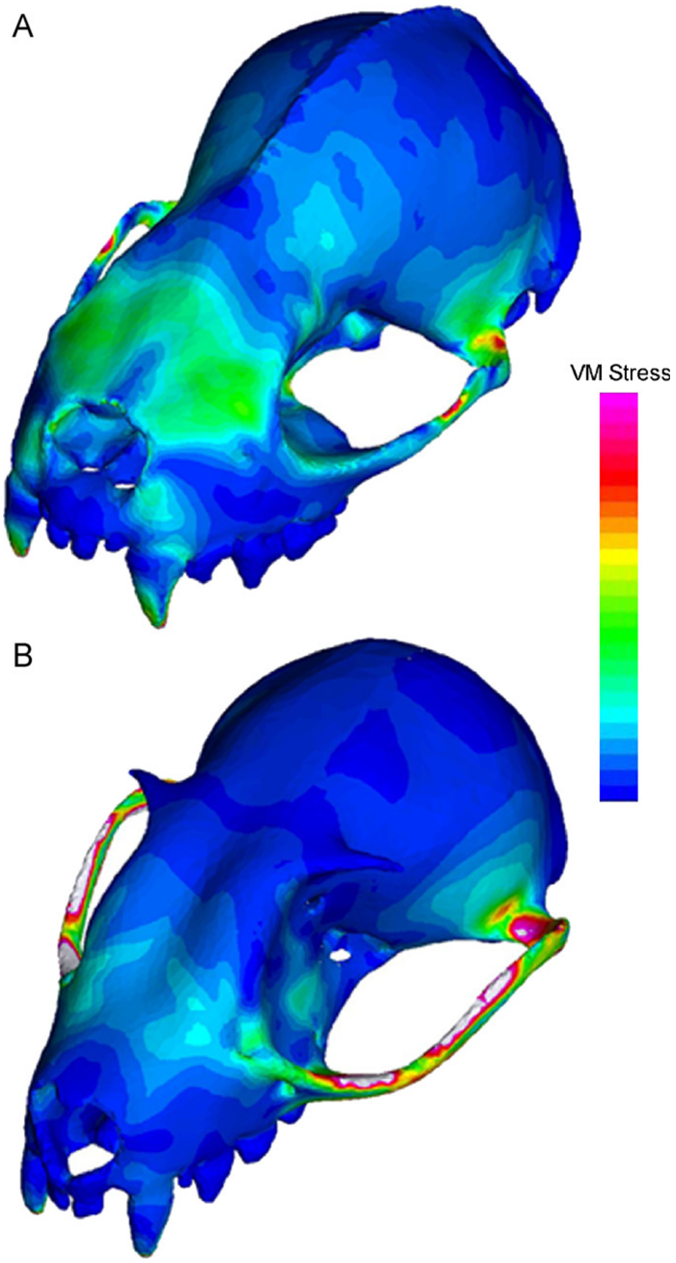

Fig. 3. The distribution of von Mises stress in finite element models of the skulls of *Artibeus jamaicensis* (top) and *Cynopterus brachyotis* (bottom). Models are scaled to the same surface area (189.4 mm^2) and loaded with the same total muscle force (100 N). Warm colors indicate high stress and cool colors indicate regions of low stress. Areas shown in white exceed the stress scale.

comparisons of von Mises stress. Moreover, while bicanine breadth is homologous, it has been molded by separate evolutionary trajectories and masks broader shape differences between the two species. This is not to say that a researcher cannot re-size models to comparable volumes or linear dimensions as personal preference dictates. In these cases, however, it is imperative to use identical ratios of force to surface area if the goal is to compare model performance in terms of strength. This can be achieved simply by applying different forces to the two models to maintain equal force:area ratios.

For our *Artibeus* and *Cynopterus* models the proportion of the total force assigned to the temporalis, masseter and pterygoid muscles was based on the relative muscle mass of the three muscles (which are known and differ between the two species) and both models were assigned average material properties for cortical bone (Young's modulus $= 2 \times 10^4$ MPa, Poisson's ratio $= 0.3$ (Dumont et al., 2005)). The models were constrained from rigid-body motion in a way that mimicked bilateral canine biting. A single node in each glenoid fossa was constrained to establish an axis of rotation through the temporomandibular joints and a single node at the tip of each canine was constrained to generate a bite reaction force.

Fig. 3 illustrates that despite the general similarities in skull form, the distribution and magnitude of von Mises stress differ between the two models.

Stress is spread widely across the rostrum of the *Artibeus* model while stress is concentrated in the zygomatic arches of *Cynopterus*. Fig. 3 also illustrates that maximum von Mises stress is highest in the *Cynopterus* model, indicating that it is the weaker of the two structures under this specific loading condition. Under higher loads *Cynopterus* would fail first and failure would begin along the zygomatic arches. In terms of work, the total strain energy is lower for *Artibeus* than for *Cynopterus* (6.37×10^{-4} versus 8.06×10^{-4} J), indicating that it is more efficient, stiffer structure that undergoes less deformation. From a structural perspective, the shape of the *Artibeus* skull is superior to the shape of the *Cynopterus* skull under this loading condition (i.e., *Cynopterus* may in fact perform better that *Artibeus* under a different loading condition). *Artibeus*' superior performance in terms of work efficiency is expressed visually by differences in the magnitude of von Mises stress and quantitatively by its total strain energy value being 21% lower than that of *Cynopterus* for the same force:volume ratio.

In practice, many finite element analyses of biological systems contain artificially high stresses and strains at specific points due to kinematic constraints, point loads, or even sharp corners. These artificially high stresses are due to the fact that the theory of elasticity admits stress and strain singularities due to these idealizations, and the finite element solution approximates the exact solution admitted by the theory of elasticity. A singularity is a point at which stress or strain is infinite. Such singularities are indicative of the fact that these modeling idealizations are physically impossible (i.e., a point load is an artificial construct). In accordance with Saint Venant's principle, these modeling artifacts are highly localized and do not impact stress values in other regions of the model (Cook and Young, 1985). However, they do make it difficult to extract accurate values of maximum von Mises stress values from the analysis. In contrast, although strain energy is theoretically infinite at points that admit a stress or strain singularity, the strain energy contained in a finite volume of material encompassing such points is finite. Thus, strain energy is not sensitive to the presence of idealized kinematic constraints, point loads, etc. Therefore it is a more reliable and informative metric of overall model performance with respect to work efficiency.

When interpreting the results of this or any other finite element analyses of complex biological systems, it is critical to acknowledge that the model is unlikely to include all of the variables that affect the system. Our models, for example, do not include the effects of passive or active soft tissues and variations in material properties that may alter stress pathways or mitigate stress concentrations. These kinds of effects are neglected largely because, at present, they are not fully understood. Fortunately, experimental biomechanical studies are making significant progress toward quantifying these variables. For the present, an inherent assumption of this (and most other) comparative finite element analyses of skeletal systems is that the effects of soft tissues and variations in material properties are comparable across the species being compared.

In addition to strength- and work-based measures of performance that are relevant to any model, we can also ask questions about the *relative* performance of the *Artibeus* and *Cynopterus* models that are particular to feeding systems. Specifically, we can compare whether bite performance varies between the models scaled for stress comparisons by summing the node reaction forces at the canine constraints to get an estimate of bite force. It is essential to point out that this does *not* provide accurate estimates of absolute bite force. Rather, it speaks to the efficiency of force transfer from the chewing muscles to the bite points. At the same surface area and under the same loading conditions, bite reaction force is relatively higher in *A. jamaicensis* (20.4 N) than in *C. brachyotis* (11.3 N). One can directly compare these bite force values *only if* the applied force to surface area ratio is constant *and* the models have the same surface area. If the force to surface area ratio is the same but the surface areas of the models differ, the larger model will always return higher bite reaction forces. In these cases, therefore, one must compare the *ratio* of muscle force to bite force.

3. Discussion

A fundamental question arising from this study is whether the strength- and work-based performance measures we describe are biologically meaningful. The utility of ecomorphological measures of performance lies in their link to fitness via selection; individuals that perform better (bite harder, run faster, etc.), have more offspring. Engineering-based measures of performance are valuable to the extent that they evaluate the efficacy of the mechanisms that drive ecomorphological correlations. Of the two performance criteria we propose, total strain energy is a direct measure of the energy expended to deform a structure with a given volume. The second law of thermodynamics dictates that some of the elastic strain energy stored in a structure when it is loaded will be lost upon unloading. Therefore, structures that are more efficient in terms of work (i.e., they store less strain energy) will lose less energy per unit volume than structures that are less efficient.

Energy is a fundamental currency for all organisms and it is reasonable to hypothesize that selection for energy efficiency is common in many systems. The extent to which selection for energy efficiency tunes the evolution of biomechanical systems is debated. On one hand evolutionary processes have given rise to an amazing diversity of locomotor and feeding systems. The presence of functional tradeoffs and energy-saving mechanisms in these systems provides at least corroborating evidence that selection for energy efficiency exists. On the other hand, experimental studies indicate that some bones exhibit strong strain gradients and are not fully stressed during routine (or even extreme) loading, suggesting that they are not optimally designed for strength (e.g., Ross and Metzger, 2004). Although this raises the possibility that selection for mechanical efficiency has not shaped these structures, it is also likely that they perform competing functions which would be compromised if mechanical efficiency were the sole selective force. In this light, selection for mechanical efficiency is one of many processes guiding the evolution of organismal design. FEA allows investigators to evaluate the performance (i.e. strength and energy efficiency) of structures that exhibit subtle variations in shape. It is the responsibility of biologists who use FEA to determine whether differences in performance are meaningful with respect to ecologically, and thus evolutionarily, relevant variation in function.

The ability to compare model performance while controlling size and loading parameters is a significant strength of FEA. By altering a single variable while holding the others constant, researchers can use FEA to evaluate individually the influence of the magnitude and vectors of applied forces, shape, and size on model performance (Grosse et al., 2007; Strait et al., 2007; Tanner et al., 2008). Although not the focus of this paper, FEA also enables researchers to isolate and observe the effect of varying material properties on model performance (e.g., Strait et al., 2005; Wroe et al., 2007b). This level of experimental control is only available when working with models; living organisms are simply not as easily manipulated.

Despite the power of FEA as a modeling tool, only in the best of circumstances can one compare the performance of models that differ in size and shape. In order for this kind of comparison to return meaningful results, a researcher must have a great deal of confidence in the input variables. For analyses of feeding mechanics, this means that bite force, muscle forces and/or bone strain must be available in the form of *in vivo* experimental data. It is inherently appealing to report bite force values derived from FEA because bite force is commonly used as a measure of organismal performance. However, it is critical to acknowledge that predictions of bite force that are not validated with *in vivo* experimental data return estimates that are unquestionably hypothetical and, in the case of fossil organisms, un-testable.

On the other hand, this study illustrates that comparing the *relative* performance of finite element models does not necessarily require bone strain or bite force data if the models are properly scaled. In order to compare only the effects of model shape on structural strength, size must be controlled either by scaling models to the same surface area and applying the same muscle forces or, alternatively, by keeping models at their normal sizes and simply applying the same ratio of force to surface area. The *relative* performance of the models with respect to strength (von Mises or maximum principal stress) is identical in either case. Similarly, to remove the effects of size and compare the work efficiency of two models, the ratio of force to volume must be held constant.

As the popularity of FEA continues to rise among biologists, it is important to remain circumspect about what it can and cannot do. Most importantly, FEA is a modeling technique. At best, results can only be of as high a quality as the structures, material properties and loading conditions that are entered into the analysis. We are strong advocates of building and loading finite element models using data that are carefully collected in laboratory and/or field settings. At this point in time, it is not entirely clear how robust finite element models are in the face of altering input parameters. However, several studies show that patterns of stress distribution and strain magnitudes predicted by FEA are more sensitive to variation in model shape than to variation in material properties and muscle loading (e.g., Ross et al., 2005; Strait et al., 2005). These results are consistent with the concept of the sensitivity of stress and strain to geometry. For example, for a homogeneous cylinder under torsion, maximum shear stress and strain are inversely proportional to d^3, where d is the diameter of the cylinder. However, maximum shear stress is independent of its shear modulus G and maximum shear strain is inversely proportional to G. Therefore, changes in d have a larger effect on stresses and strains than do changes in G.

Comparative biologists are now beginning to validate their finite element models experimentally (Kupczik et al., 2007; Ross et al., 2005), something that engineers have been doing for a very long time, and we applaud and encourage that effort. In the meantime, this study demonstrates that it is still possible to compare the relative strength and work performance of models that are not experimentally validated so long as those comparisons are done correctly.

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Appendix A

In this appendix we show with simple mechanics the relationships between strain, stress, total strain energy, and volumetric average strain energy density with respect to isometric scaling of a model. Consider a simple round bar under uni-axial loading as shown in Fig. A1.

The subscript 0 indicates unscaled dimensional and load values. The bar is under a state of uni-axial stress and strain with strain, stress, total strain energy, and volumetric average strain energy density given by

$$\varepsilon_0 = \frac{P_0}{EA_0} = \frac{P_0}{E\pi R_0^2}$$

$$\sigma_0 = \frac{P_0}{A_0} = \frac{P_0}{\pi R_0^2}$$

$$U_0 = \frac{P_0^2 L_0}{2E\pi R_0^2}$$

$$(u_{ave})_0 = \frac{P_0^2}{2E\pi^2 R_0^4}$$

We now wish to scale this model isometrically and examine how these quantities are affected. Let the dimensional scale factor be a constant C, so that for the scaled model $L = CL_0$ and $R = CR_0$. Note that C is also given by $(V/V_0)^{1/3}$. For the scaled model one has

$$\varepsilon = \frac{P}{E\pi R^2} = \frac{P}{E\pi C^2 R_0^2}$$

$$\sigma = \frac{P}{\pi C^2 R_0^2}$$

$$U = \frac{P^2 L}{2E\pi R^2} = \frac{P^2 C L_0}{2E\pi C^2 R_0^2} = \frac{P^2 L_0}{2E\pi C R_0^2}$$

$$u_{ave} = \frac{P^2}{2E\pi^2 R^4} = \frac{P^2}{2E\pi^2 C^4 R_0^4}$$

Note stress, strain, strain energy, and strain energy density are inversely proportional to the dimensional scaling factor C, raised to the various powers as shown in the equations above. Thus, if the force is unchanged, increasing the size of a model isometrically will decrease its stress and strain by the volume ratio to the $\frac{2}{3}$ power, decrease its total strain energy by the cube root of the volume ratio, and decrease its strain energy density by the volume ratio to the $\frac{4}{3}$ power.

If we let $P = C^2\, P_0$, the state of strain, stress, and volumetric strain energy density in the scaled model will be exactly equal to that of the unscaled model, and total strain energy will change linearly with respect to volume:

$$\varepsilon = \frac{C^2 P_0}{E\pi C^2 R_0^2} = \frac{P_0}{E\pi R_0^2} = \varepsilon_0$$

$$\sigma = \frac{C^2 P_0}{\pi C^2 R_0^2} = \frac{P_0}{\pi R_0^2} = \sigma_0$$

$$U = \frac{(C^2 P_0)^2 L_0}{2E\pi C R_0^2} = \frac{C^3 P_0 L_0}{2E\pi R_0^2} = C^3 U_0 = (V/V_0) U_0$$

$$u_{ave} = \frac{(C^2 P_0)^2}{2E\pi^2 C^4 R_0^4} = \frac{P_0^2}{2E\pi^2 R_0^4} = (u_{ave})_0$$

Since surface area of the scaled model will be equal to C^2 times the surface area of the unscaled model, this confirms our scaling axiom that maintaining the same ratio of force to surface area when scaling models will preserve stress and strain states. Finally, let us determine the force scaling rule needed such that the total strain energy is preserved for models that are isometrically scaled. This condition requires that

$$U_0 = \frac{P_0^2 L_0}{2E\pi R_0^2} = U = \frac{P^2 L_0}{2E\pi C R_0^2}$$

which yields

$$P = \sqrt{C} P_0 = (V/V_0)^{1/6} P_0.$$

Note that these results can be shown to be true for a beam under bending and a bar under torsion, and we have shown it be true numerically with a complex structure under a non-uniform 3-D state of stress and strain.

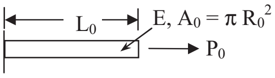

Fig. A1. Round bar of length L_0, radius R_0, cross-sectional area A_0, Young's modulus E, fixed at left end and loaded at right end with load P_0.

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