

Feeding mechanisms in bats: variation within the constraints of flight

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Synopsis By any standard, bats are a successful group of mammals and the evolution of flight and echolocation were certainly key innovations behind their success. That is only part of the story, however. Bats have diversified into trophic niches that range from insectivory to feeding on blood, fruit, or nectar. While flight places fundamental constraints on the shape of the postcranial skeleton, skull shape in bats is remarkably diverse. Morphological studies of individual families and sympatric assemblages demonstrate that variation in skull shape is clearly associated with trophic specialization. Field experiments demonstrate that species-specific biting behaviors during feeding are common and analyses indicate that the evolution of cranial morphology and feeding behavior are correlated. Modeling experiments further suggest that feeding (loading) behaviors and skull shape are functionally linked. If the skulls of bats are under selective pressure for minimal mass because of the energetic demands of flight, then they may be more “optimized” to meet mechanical demands than are the skulls of other mammals. This would make bats a unique model system for studying the evolution of diversity in skull shape and its functional implications for the evolution of feeding strategies in mammals.

Introduction

A great deal is known about the function of the feeding apparatus of fishes, amphibians, and snakes and the role that functional transitions have played in their evolution (this volume). There is significant morphological and functional diversity within these groups, and many different species from each one have been studied. We know far less about the diversity of function in the feeding apparatus of mammals. In large part this is because research on mammalian feeding has focused on a few model systems, notably primates, pigs, and rabbits. The size, availability, and husbandry requirements of these animals make them excellent laboratory subjects, and they are good models for many processes relating to human dysfunction and disease processes. This selection of species, however, falls short of representing the morphological and functional diversity that exists among living mammals.

Nearly one quarter of all living species of mammals are bats (Wilson and Reeder 2005). As the only mammals capable of powered flight, much of the research on bat morphology has focused on the function and evolution of the flight apparatus and echolocation. The fact that bats arguably possess the broadest array of dietary adaptations and cranial morphologies of any mammalian order is often overlooked by functional morphologists and surprisingly little

experimental research has focused on the functional morphology of feeding in bats. The reason for this omission probably lies in the inherent difficulty of collecting even basic natural history data for small, nocturnal, flying mammals. Aside from the generalization that most bats are insectivorous, we have extremely limited information about diet and foraging behavior for most species (for example Nowak 1999). This is not to suggest that we are not rapidly accumulating a good body of data about bats. The wide availability of mist nets and harp traps has made it easier to study bats in the field, and technological advances are making it possible to undertake successful *in vivo* experiments with very small animals.

There are two convergent clades of plant-visiting bats about which we do have relatively good dietary data (see review by Dumont 2003). The Old World fruit bats (Family Pteropodidae) include the gregarious flying foxes, whose large colonies are hard to miss when visiting the Paleotropics. Not surprisingly, we know relatively little about feeding among the smaller, more elusive species that comprise the bulk of this family. By far the most well-studied group is the New World leaf-nosed bats (Family Phyllostomidae). These animals are ubiquitous in the Neotropics and a spectacular example of an adaptive radiation characterized by dietary divergence.

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Examples of virtually all the dietary adaptations found among bats are represented within this family.

Aside from the inherent appeal of their breadth of dietary adaptations, why study the mechanics of feeding in bats, especially given the potential logistical difficulties of working with them? The extent to which diversity in skull shape among mammals reflects the mechanical demands of feeding is a fundamental question that has yet to be answered and there is reason to believe that bats are a good model system for doing so. Because the energetic cost of flight is high and increases with body mass (for example Thomas and Suthers 1972; Winter and von Helversen 1998), it is logical to hypothesize that bats are under selective pressure to minimize mass while maximizing functional performance. This form of optimization is clearly evident in the post-cranial skeleton of bats (Swartz 1997) and, I submit, is also likely to be at work in the skull. If the loads imposed during feeding have had an impact on the evolution of skull shape in mammals, then the signature of selection for mechanical function is likely to be more apparent in bats than in mammals for which there is a smaller penalty for being “overbuilt.”

Morphological correlates of dietary adaptation

There is a rich history of comparative analyses that use the craniodental morphology of bats as a taxonomic tool (for example Miller 1907; Owen 1987; Wetterer et al. 2000; Simmons and Conway 2001; Giannini and Simmons 2004). Far fewer researchers have looked to the skulls of bats for evidence of functional adaptations. The seminal studies of structure and function in the bat feeding apparatus were Freeman’s (1979; 1981a) analyses of the morphological correlates of specialized insectivory. These studies identified structural similarities in cranial shape among species that have converged on hard-object feeding. Although generations of mammalogists have pointed to associations between skull shape and diet, Freeman’s papers were among the first to attempt to quantify the link between skull shape and the physical properties of food items. As such, they foreshadowed current ideas about hardness of food as a mechanism of resource partitioning in vertebrate communities and the value of bite force as a measure of feeding performance.

Freeman’s work also inspired wider interest in the morphological correlates of skull shape in bats. A number of multivariate studies have correlated cranial morphology and dietary specializations

including faunivory, frugivory, nectarivory, and granivory (Freeman 1981b, 1984, 1988, 1995; Reduker 1983; Dumont 1997, 2004; Nogueira and others 2005). In these studies, the mechanistic links between structure and function are rooted in classic theoretical mechanical models of the mammalian masticatory apparatus (for example Tucker 1954; Maynard Smith and Savage 1959; Davis 1964; Turnbull 1970; Ewer 1973; Greaves 1974; Herring and Herring 1974). Many analyses of feeding mechanics in model mammalian systems have gone beyond correlation and harnessed techniques such as *in vivo* bone strain, electromyography, high speed videography, and x-ray cineradiography to elucidate the mechanisms underlying apparent correlations of structure and function. Given the extreme morphological diversity found among bats and the goal of comparative functional biologists to find the causes behind the correlations, why have not more studies of bat feeding taken that path?

The limited *in vivo* experimental data on the mechanics of feeding in bats is primarily a reflection of the difficulties associated with using bats as experimental animals. In contrast to typical model mammals such as primates and pigs, bats are very small and require specialized housing, light cycles, and, in some cases, special diets. Moreover, many of the most morphologically distinct species are rare (and in some cases migratory), making them very difficult to capture in the wild. All of these factors conspire to make bats a poor choice for experimental studies that require significant surgical manipulations or access to long-lived laboratory colonies.

In all of bat research, only three studies have provided *in vivo* EMG or kinematic data on feeding. Two involved one of the largest bat species, the frugivorous *Pteropus giganteus* (De Guedre and De Vree 1984, 1988). The third made use of one of the most common insectivorous bats in North America, *Myotis lucifugus* (Kallen and Gans 1972). Together these studies demonstrated that movements of the dentaries in these two species fall within the range of basic kinematic patterns seen in other mammals. In contrast, their patterns of muscle firing vary remarkably. These differences are tantalizing, but determining the extent to which they reflect functional divergence in the feeding apparatus will require data from many other closely related and functionally convergent species.

Because it is amenable to modeling experiments, tooth function is one aspect of the functional morphology of feeding in bats that has received a great deal of attention.

Although associations between the form and function teeth have been recognized for centuries, explicit mechanical models linking tooth structure and the material properties of foods first appeared in the 1970s (Kay and Hiiemae 1974; Kay 1975; Lucas 1979, 1982; Lucas and Luke 1984). These studies sparked a renaissance in comparative functional analyses of mammal teeth that recently culminated in carefully controlled experimental and model-based studies of tooth function in insectivorous bats (Evans 2005, 2006; Evans and Sanson 2003, 2005b). This work is an urgent reminder that tooth design, not simply cranial structure or muscle function, is a significant component in the feeding systems of mammals. Although understanding how all these variables work together will be a monumental task, it is the last critical step toward being able to characterize the fundamental mechanical components in the feeding system of any given species.

Relatively few investigations into the evolution of feeding mechanisms in bats have made use of modern comparative techniques. Several studies have investigated dietary shifts in a phylogenetic context for the exceptionally diverse New World leaf-nosed bats (Family Phyllostomidae). Two have mapped diet onto a generic-level phyllostomid phylogeny and used parsimony to hypothesize a sequence of dietary transitions from an ancestral state of insectivory through omnivory to feeding on nectar and fruit-feeding (Ferrarezzi and Gimenez 1996; Wetterer et al. 2000). A third study took a more qualitative approach to linking morphological diversity to the questions of the adaptive radiation of phyllostomids (Freeman 2000). All three studies came to a similar conclusion: that the ability to make use of plant resources somehow played a key role in the phyllostomid radiation.

Aside from these large-scale investigations of evolutionary transitions in diet, only a few morphological studies of the feeding apparatus of bats have incorporated evolutionary data using modern comparative techniques (Aguirre et al. 2002; Van Cakenburghe et al. 2002; Dumont 2006; Dumont and Nicolay 2006). One relatively simple step toward linking the evolution of cranial morphology and diet is to evaluate morphological/behavioral correlations within a clearly defined phylogenetic framework. For example, Fig. 1 presents a phylogeny for 53 species of phyllostomid bats (and two outgroups) illustrating a parsimonious reconstruction of diet. A simple analysis of variance using independent contrasts of 18 variables describing cranial shape demonstrates that the evolution

of dedicated frugivory is significantly associated with a decrease in relative length of the face and increase width of the palate ($P < 0.05$). The opposite trends occurred in the evolution of nectar-feeding ($P < 0.05$). In addition, the evolution of both nectar-feeding and blood-feeding is significantly associated with a decrease in the relative surface area of the molar teeth ($P < 0.05$). Although very basic, this kind of analysis allows quantification of the strength of association between morphology and dietary adaptation. It also points to a subset of morphological features whose functions should be investigated more thoroughly with the goal of elucidating the mechanical basis of ecological transitions such as the shift from insectivory to a plant-based diet.

Feeding performance and the material properties of foods

The ecomorphological concept of linking form to function through variables in performance has transformed the way that many functional morphologists think about feeding. No longer is research focused solely on identifying the mechanistic links between form and function, it also aims at understanding the evolutionary processes that have guided the expression of functional traits. There are many ways to assess feeding performance and the choice depends upon the selective regime that is hypothesized to drive functional adaptations. For example, if food is a limiting resource, then morphologies or behaviors that maximize nutrient extraction and minimize energy expenditure may be useful performance variables. Alternatively, if high densities of predators increase the risk of predation, then morphologies or behaviors that minimize the time food is handled could be critical performance variables.

Many comparative morphologists interested in the mechanics of skull function have turned to bite force as a measure of feeding performance. Not only does biting impose loads that must be resisted by the skull and jaws, but the hardness of food items (and the bite force required to process them) can also play a role in the partitioning of resources within vertebrate communities (for example Freeman 1979, 1981a; Toft 1980; Wainwright 1987; Van Valkenburgh 1996; Aguirre et al. 2003).

To date, bite force has been documented for more species of bats than for any other group of mammals (Aguirre et al. 2002, 2003; Dumont and Herrel 2003; Dumont et al. in review). While bats are not optimal laboratory animals, they are relatively easy to capture

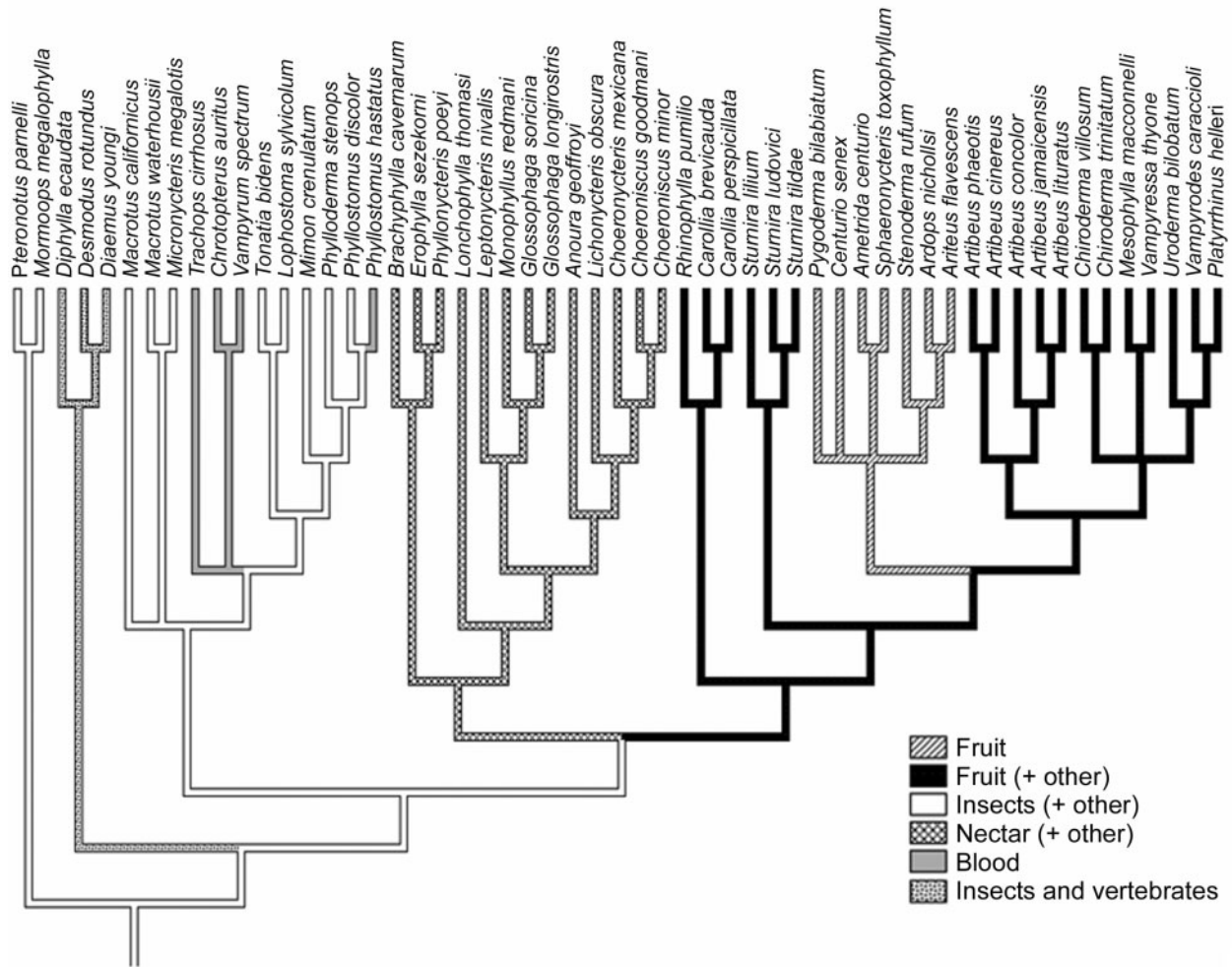


Fig. 1 Parsimonious reconstruction of feeding behavior in 53 New World leaf-nosed bats (Family Phyllostomidae) and two outgroup taxa. Data from Jones et al. (2002) and Wetterer et al. (2000).

and work with in the field. This is especially true in the tropics where many different species often can be sampled at single localities. As in other vertebrates, bite force in bats increases with body size, but there is significant scatter around the regression line (Fig. 2). That nectar feeders and the single vampire bat have relatively low bite forces while bite force appears to be relatively high among frugivores suggests that the residual variation is associated with some aspect of functional divergence. While comparative morphologists find this possibility intuitively pleasing, neither of the two studies that have investigated residual variation in bite force among bats found an association between that variation and simple measures of skull shape (Aguirre et al. 2002; Dumont et al. in review). There are at least three possible interpretations of these data.

First, the data could suggest that departures of bite force from expectations based on body mass are

random and, in fact, contain no useful information. Second, the regression residuals could reflect measurement error. There is evidence suggesting that this is not the case. All studies of bite force in bats have used identical instrumentation to measure maximum voluntary bite force at similar tooth positions (Aguirre et al. 2002). While bite force for some species is represented by values from single individuals, larger samples exist for most species and comparative studies have found statistically significant differences among them in bite force values when individual variation is taken into account (Aguirre et al. 2002; Dumont and Herrel 2003). Finally, field studies are beginning to demonstrate a good fit between bite force and the hardness of foods that bats eat, suggesting that the available data on bite force are accurate (Aguirre et al. 2003). The third possible explanation for the deviation of average bite force from expectations based on size is that they are associated with more complex

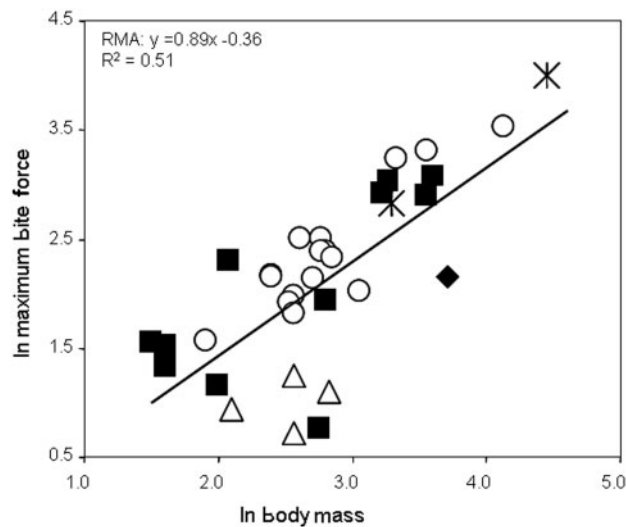


Fig. 2 Reduced major axis (RMA) regression of ln bite force on ln body mass for 35 species of bats. Symbols represent species means: ○ = frugivore, ■ = insectivore, △ = nectar-feeder, ◆ = blood-feeder, ⊠ = consumes small vertebrates. Data from Aguirre et al. (2002, 2003), Dumont and Herrel (2003), Dumont et al. (in review) and Santana, unpublished. Sample sizes for species range from 1 to 26 individuals; the average sample size is five individual per species.

assessments of lever/load arm values, muscle morphology, or aspects of skull shape that have not yet been identified. Thus far, analyses of bite-force residuals have looked for correlations with simple linear measurements. Recent advances in geometric morphometric analysis open the possibility of investigating correlations with more complex morphologies that have the potential to convey greater functional signal.

To accompany studies of bite force and resource partitioning in bats, there is a small but growing body of literature summarizing the physical properties of the fruits and insects that bats eat. Most field-based assessments of physical properties have reported the “hardness” of food items as measured by their resistance to puncture (Dumont 1999, 2003; Aguirre et al. 2003; Dumont and O’Neal 2004). From a materials science perspective, this is an imprecise measurement as the term “hardness” refers to the resistance of the surface of a material to deformation while fracture behaviors of materials are mediated by the properties of strength, stiffness, plasticity, and toughness (see reviews in Strait 1997; Vincent 2004). These properties have been measured for a number of insects and commercially produced fruits using sophisticated laboratory equipment (for example Vincent 1991; Strait and Vincent 1998; Grotte et al. 2001; Vincent and Wegst 2004; Wang 2004). More recently, field kits with tools for making

some of these more complex measurements have become available (Lucas et al. 2001). A recent study by Aguirre et al. (2003), however, demonstrated a good fit between bite force and simple measures of puncture resistance. This suggests that puncture resistance provides an adequate assessment of the physical properties of food for the purposes of investigating the ecological implications of feeding performance in bats.

Perhaps the biggest challenge facing studies of food hardness and bite force is that we know very little about the diets of most bats. Data on stomach contents and fecal composition have long been used to document the diets of insectivorous species, but the results are complicated by the difficulty of identifying fragments of insects to family, much less to genus or species. On a brighter note, a recent experimental study illustrated that cuticle thickness is correlated with insect hardness (Evans and Sanson 2005a), opening the possibility of evaluating dietary hardness without identifying insect fragments. Unfortunately, none of these techniques are useful for assessing the diets of plant-visiting species, which typically swallow only nectar or fruit pulp. In these cases, only field-based natural history studies can document diet with any useful level of detail.

Field-based studies of feeding behavior

Field-based studies of feeding behavior are a relatively new development in the study of feeding mechanisms in bats (Dumont 1999; Dumont and O’Neal 2004; Dumont et al. in review). The seed of this work was sown by Van Valkenburgh’s (1996) study of feeding behavior in free-ranging carnivores, that documented differences within and among African wild dogs, lions, spotted hyenas, and cheetahs in which teeth were used to process prey items. She associated these differences with the consistency of food items as well as with the structure of the teeth and skulls. This work highlighted several important points about feeding in mammals: (1) different species bite and chew foods in different ways, (2) different biting and chewing behaviors impose different patterns of loading on the skull during feeding, and (3) biting and chewing behavior is plastic in the face of changing hardness of food. In essence, Van Valkenburgh demonstrated that there is enough variation in feeding behavior among closely related species to support investigations into the evolutionary relationship between cranial morphology and feeding behavior in mammals.

Work on feeding behavior in bats has focused on two families that have converged on frugivory and nectarivory, the New World leaf-nosed bats (Family Phyllostomidae) and the Old World fruit bats (Family Pteropodidae) (see review by Dumont 2003). Not only do these two lineages provide a “natural experiment,” but they also offer the advantage that plant-visiting bats are much easier to capture and eat much more slowly than is true of insectivorous species. In these studies, bats were captured in the field, placed in temporary caging, and fed fruits of known size and hardness (that is, puncture resistance). Feeding events were recorded on video tape and then analyzed in the laboratory to determine the proportions of four different bite types: unilateral canine, unilateral molar, bilateral canine, and bilateral molar. Because it is relatively simple to measure bite force in bats, we have been able to document how bite force varies across tooth positions (Dumont and Herrel 2003). Not unexpectedly, bite force increases posteriorly as the dentary load arm approximates the lever arm and muscle forces are transmitted more efficiently to the teeth. Anteriorly, unilateral canine biting evokes lower bite forces than does bilateral canine biting. It is not clear why this occurs but one interesting possibility is that bite force is modulated by proprioceptive feedback that limits strain on the teeth or facial skeleton. Data summarizing strain during unilateral and bilateral biting would be useful in addressing this hypothesis.

As in carnivores, there is significant variation among bat species in the types of bites that are used during feeding. In addition, different species exhibit different levels of behavioral plasticity in biting styles. This is most apparent among the New World plant-visiting species where moderately derived fruit specialists shift to mechanically efficient biting styles during feeding on hard fruit. In contrast, less derived species consistently use less efficient bites and the most derived frugivores consistently use the most efficient bites during feeding on hard objects. In an effort to more tightly link cranial form and function in New World plant-visiting bats, independent contrasts and squared-change parsimony have been used to evaluate the correlated evolution of cranial morphology and loading behavior (Dumont 2006). The results were encouraging; there were significant associations between unilateral biting and the depth of the dentary and the width of the mandibular condyle and palate. Similar evolutionary analyses are underway for the Old World fruit bats, which appear to exhibit very different associations between morphology and behavior.

These studies of feeding behavior in bats offer tantalizing glimpses into associations between cranial morphology and feeding behavior. There is strong evidence that the evolution of form and function are linked in these animals. What remains missing is a clear picture of the underlying mechanistic connections between loads that are imposed during feeding and variation in the shape of the skull. Identifying those connections would help us to understand if, and how, the interplay between cranial morphology and feeding behavior has guided the evolution of diversity in feeding mechanisms among bats and other mammals.

The search for mechanistic links

Functional morphologists have a large set of tools for investigating the mechanics of feeding. Techniques including electromyography, sonomicrometry, cineradiography, strain analysis, and particle image velocimetry offer fundamental, real-time data summarizing how animals accomplish feeding tasks. Unfortunately, for reasons outlined earlier, few of these methods can be used effectively to study feeding in bats. In the search for methods of visualizing the mechanics of feeding in bats, a recent study has turned to finite element analysis (FEA) (Dumont et al. 2005).

FEA is an *in silico* modeling and analysis tool (that is, it is performed via computer simulation) that engineers use to understand the behavior of “physical systems,” which are interconnected entities whose behavior is governed by Newtonian physics. Physical systems that have been modeled using FEA range from interacting molecules in the atmosphere to ocean currents, geological processes, and manufactured structures and products. Very recently, comparative biologists have recognized the utility of FEA for predicting the behavior of complex systems and are beginning to use it to investigate the functional adaptations of living and extinct organisms (Fastnacht et al. 2002; Wootton et al. 2003; Preuschoft and Witzel 2004; Dumont et al. 2005; Metzger et al. 2005; Rayfield 2005; Richmond et al. 2005; Strait et al. 2005).

FEA offers several advantages over traditional *in vitro* techniques. First, in contrast to strain gages, FEA provides an instantaneous snapshot of the stress/strain state throughout entire structures. This allows researchers to visualize stress pathways and to evaluate stress/strain in anatomical regions that are not surgically accessible. Second, FE models and analyses can be precisely manipulated and controlled, allowing researchers to design experiments that are not possible

in living animals. Finally, thanks to ongoing improvement in model-building techniques (Grosse et al. in review), FEA opens the possibility of building comparative data sets that otherwise would be extremely difficult, if not impossible, to accumulate in any reasonable timeframe.

FEA begins with the construction of a finite element model. Briefly, serial image stacks such as CT scans are the raw material for FE models of most biological systems. These images are first reassembled to generate a 3D surface representation of the object being modeled. This 3D surface is then imported into finite element software where it is transformed into a solid model that is composed of hundreds or thousands of blocks, plates, or tetrahedrons called finite elements. Elements are connected at their corners (nodes) to form a unified mesh of finite elements. Researchers assign material properties to each element, define the forces and kinematic constraints acting on the model, and subject the model to an FEA. By solving for system static equilibrium, the analysis calculates displacements for each node and returns data on stress and strain for each element in the model.

Once FE models are constructed, FE analysis can be used to test hypotheses about the mechanistic links between cranial morphology and feeding behavior. For example, the Jamaican fruit bat, *Artibeus jamaicensis*, is a derived frugivore within the New World family Phyllostomatidae. As noted earlier, the evolution of dedicated frugivory in this clade is significantly associated with an increased palate width and a shorter face. Increased palate width is also linked to an increase in the frequency of unilateral biting during feeding (Dumont 2006). Indeed, field-based studies of feeding behavior demonstrate that the Jamaican fruit bat uses primarily unilateral molar biting when feeding on hard fruits (Dumont 1999). One hypothesis about why this bat focuses on unilateral molar biting is that the skull is more resistant to unilateral molar loading than it is to less frequently used biting strategies, such as bilateral canine biting. FEA provides an excellent means of testing this hypothesis.

Figure 3 illustrates the results of an experiment in which an FE model of a Jamaican fruit bat (*Artibeus jamaicensis*) was loaded to simulate average bite forces generated during bilateral canine and unilateral molar biting (18.8N and 22.2N, respectively). [See Dumont et al. (2005) and Grosse et al. (in review) for a description of kinematic constraints and muscle-loading algorithms.] The stress histograms indicate that the relative magnitude of stress is highest under bilateral canine biting. During bilateral

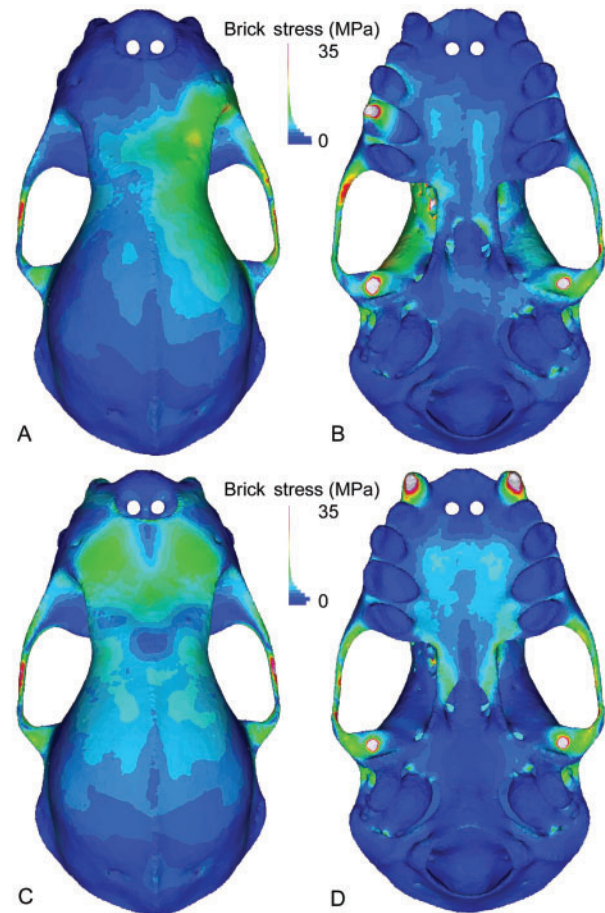


Fig. 3 Finite element analyses of average bite force produced under unilateral molar (A, B) and bilateral canine (C, D) biting in *Artibeus jamaicensis* (bite forces are 22.5N and 18.8N, respectively). The skull of *Artibeus* is least stressed (or most resistant) under unilateral canine biting, the most commonly used biting strategy during feeding on hard objects.

canine biting, the superior surface of the rostrum, palate, and zygomatic arches are markedly stressed. Under bilateral canine biting, stress is largely confined to the superior and lateral surfaces of the rostrum on the right (working side) of the skull. FEAs solve for static equilibrium; thus, more energy is going into the model of bilateral canine biting. Indeed, the muscle forces needed to produce 18.8N of bite force under bilateral canine biting are 22% higher than the forces required to produce 22.5N of bite force under unilateral molar biting. In other words, unilateral molar biting is more efficient than bilateral canine biting (that is a larger proportion of total muscle force is transferred to bite force).

Although the simplest models of the mammalian masticatory apparatus predict that molar biting is more efficient than incisor biting, there is evidence that unilateral molar biting is particularly

efficient in *Artibeus*. A recent comparison of FEAs of *Artibeus* and an ecologically convergent Old World fruit bat, *Cynopterus brachyotis*, demonstrated that the efficiency of unilateral molar biting relative to bilateral canine biting is much higher in *Artibeus* than in *Cynopterus* (Dumont et al. 2005). These analyses suggest that the high preponderance of unilateral molar biting by *Artibeus* during feeding is associated with structural specializations for efficient transmission of muscle forces. Additional FEAs of biting behavior in other species will help to pinpoint exactly what those specializations are.

FEA can be a powerful tool for comparative functional morphologists *if it is used properly*. It is essential to keep in mind that FEA is a modeling technique and, as such, the results are only as good as the assumptions that are made in building and analyzing the model. Assumptions enter FEAs at every single step. During the modeling process, one can control the level of anatomical detail portrayed by the model by varying the number of elements. More elements yield a more detailed model but significantly increase computational demands of the analysis. The complexities of biological structures also frequently require that some anatomical details be simplified in order for mesh generation to proceed. For example, the spaces that house the inner ear structures are filled and treated as bone in the model of the Jamaican fruit bat (Fig. 3).

There is a method on the horizon that may ultimately address these first two modeling assumptions. Voxel-based modeling takes the 3D volumetric (solid) models that are commonly built from stacks of CT scans and converts each voxel into a finite element. In voxel-based models of bone, each element is then assigned material properties data based on voxel density (a greyscale value). This modeling technique produces highly detailed and anatomically accurate models with very little input from the researcher. The tradeoff is that the models contain millions of elements and, even with the help of many powerful processors working in concert, can require thousands of hours of CPU time and weeks to solve (Van Reitbergen et al. 2003). Voxel-based modeling will almost certainly become more attractive as computational power continues to increase. At the moment, however, it is not a practical approach to comparative FEA studies.

No matter how an FE model is generated, further assumptions are required when assigning material properties and kinematic constraints and when applying loads. Advances in nanotechnology are providing biologists with tools to define the material properties of biological tissues, and *in vivo* kinematic

studies can provide excellent data for determining loads and constraints for FE models. As FEA continues to increase in popularity among vertebrate biologists, it will be essential to step up efforts to validate FE models with *in vivo* experimental data. As with all modeling techniques, FEA is only useful to the extent that it offers a reasonable approximation of biological reality.

Future directions

Investigations into the evolution of feeding mechanisms in bats are clearly in their infancy. Nevertheless, they are already offering tantalizing insights into the functional and evolutionary relationships among feeding behavior, feeding performance, and cranial morphology. Several different types of information and analyses are critically needed before we can combine data from each of these perspectives and generate a holistic view of the evolution of feeding in bats. First, there is a pressing need for more field-based studies not only to document feeding performance and behavior in more species, but also to collect basic data about diets and the physical properties of food items. Long-term dietary data will be particularly important for evaluating the role of hardness of food as a selective agent in the evolution of dietary diversity. Second, there is a need to integrate data summarizing tooth function and the material properties of foods into measures of feeding performance. This seems particularly important for studies of feeding in mammals, where tooth structure plays a fundamental functional role in feeding. Third, as morphological, behavioral, and mechanical data are accumulating for more species, comparative studies should take advantage of modern comparative techniques. Coupled with advances in phylogenetic resolution, such analyses will allow us to identify broad evolutionary patterns in the relationship of form and function. Fourth, perhaps the most challenging need is for additional, focused mechanical analyses of feeding. Techniques such as FE modeling and analysis will no doubt play an important role in accomplishing these analyses but it will also be important to keep model-based studies rooted in data generated using more traditional methods. In sum, given recent advances in the power of affordable computer technology, many exciting avenues for research into the function and evolution of feeding mechanisms in bats and other mammals are wide open and ready to be explored.

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