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Do roost-excavating bats have stronger skulls?

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In addition to feeding, many vertebrates use their skulls for other functions that are highly relevant to fitness. One such function is roost excavation by the bat *Lophostoma silvicolum*. Males of this species use their canines to create cavities inside active termite nests, which are significantly harder than the prey they eat. Here we investigate whether the skull of *L. silvicolum* is specialized for roost excavation relative to the ecologically similar species *Tonatia saurophila* and *Micronycteris hirsuta*, which do not excavate roosts. We conducted a finite element analysis that simulated roost excavating and feeding behaviours. These analyses were informed by our observations of feeding and roost-excavating behaviours, bite force, and dissections of the cranial musculature of the three bat species. During the simulation of roost excavation (bilateral canine biting), our data indicate that most regions of the skull of *L. silvicolum* exhibit less stress than those of *T. saurophila* and *M. hirsuta*; however, the latter exhibited the lowest peak stress at the zygomatic arches. During loads that simulate feeding (bilateral molar biting), the three species exhibit similar stress levels. It is not clear whether *L. silvicolum* has a skull shape that is stronger under the loads imposed by excavation, but it does exhibit relatively higher bilateral canine bite forces that are generated via relatively larger temporalis muscles. Based on the muscle data, our study suggests that the feeding apparatus of mammals can exhibit performance and morphological adaptations to functions other than feeding. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **102**, 1–10.

ADDITIONAL KEYWORDS: biting – cranial morphology – finite element analysis – *Lophostoma silvicolum* – *Micronycteris hirsuta* – Phyllostomidae – *Tonatia saurophila*.

INTRODUCTION

The relationship between cranial morphology and dietary ecology has been studied in a wide variety of taxa spanning all major vertebrate groups (e.g. Perez-Barberia & Gordon, 1999; Verwaijen, Van Damme & Herrel, 2002; Huber *et al*., 2005; Wilga, Motta & Sanford, 2007; Nogueira, Peracchi & Monteiro, 2009); however, in all of these taxa the skull and teeth can also be specialized for functions other than feeding. These functions include grooming (Rosenberger & Strasser, 1985), fighting with conspecifics (Huyghe *et al*., 2005; Husak, Lappin & Van Den Bussche, 2009), sensing the environment (Oelschlager & Stern-Kai, 1990; Pedersen, 1998; Ross & Kirk, 2007), and building shelters (Zuri *et al*., 1999; Hansell & Overhill, 2000; Dechmann, Santana & Dumont, 2009). Of these, shelter building has received the least attention, even though it is clearly relevant to fitness, and is prevalent in groups like birds (reviewed in Hansell & Overhill, 2000).

In comparison with birds, shelter making is relatively rare among mammals (Hansell, 1984). Nonetheless, this behaviour represents an important adaptation that facilitates protection against predators, thermoregulation, and social interactions in mammals (Dyck & MacArthur, 1993; Magoun & Copeland, 1998; Bakker & Hastings, 2002). Whereas most mammals use their forelimbs and claws to modify elements of their environment and create shelters, bats, just like birds, have to use their mouth to create roosts because their forelimbs are highly modified for flight. As a potential consequence, selection

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Within mammals, bats have repeatedly evolved roost-making behaviours that have significant implications for the ecology and fitness of species (Bhat & Kunz, 1995; Hodgkison *et al*., 2003; Kunz & Lumsden, 2003; Dechmann & Kerth, 2008). Most roost-making bats belong to the family Phyllostomidae, the Neotropical leaf-nosed bats (Kunz *et al*., 1994). Roost-making phyllostomids fall into two main categories, tent-making bats and bats that inhabit cavities inside active termite nests. Tent-making phyllostomids include frugivorous species of the subfamily Stenodermatinae, which bite into the veins of leaves or into small branches to create tent-like shelters (Kunz *et al*., 1994; Rodríguez-Herrera, Medellín & Gamba-Ríos, 2006; Rodríguez-Herrera, Medellín & Timm, 2007). Phyllostomids that live inside termite nests have taken the physical challenge of roost making much further. These are insectivorous bats of the genus *Lophostoma* that roost almost exclusively in cavities created inside active, arboreal termite nests (Kalko, Ueberschaer & Dechmann, 2006; but see Handley, 1978; Hice, Velazco & Willig, 2004; Mangolin & Motta, 2009 for reports of *Lophostoma* roosting in houses). The termite nests are made of predigested wood that can be up to 15 times harder than the insects in *Lophostoma*'s diet (Dietz & Snyder, 1924; Dechmann *et al*., 2009). In the only species for which roost-excavating behaviour has been documented, *Lophostoma silvicolum* (d'Orbigny, 1836), single adult males create the cavities using their canines (Dechmann *et al*., 2009).

Excavating and maintaining a roost might be energetically costly because of the hardness and constant regrowth of the termite nests around the cavity (Thorne & Haverty, 2000). Nonetheless, there are numerous advantages to the roost-excavating behaviour. First, this strategy may reduce predation and interspecific competition for roosts (Kalko *et al*., 2006). Second, males use the roost as a resource to attract females, and achieve higher fitness through this behaviour (Dechmann *et al*., 2005; Dechmann & Kerth, 2008). Third, active termite nests offer a much more stable and warm microclimate than inactive nests and shelters, such as hollow trees (Dechmann, Kalko & Kerth, 2004). Finally, secretions from the termites have antifungal and insecticidal properties that reduce the ectoparasite load in *L. silvicolum* (Prestwich, 1983; Rosengaus, Lefebvre & Traniello, 2000; Dechmann & Kerth, 2008). Given the advantages of roosting in active termite nests, natural selection should have favoured the evolution of morphological and functional specialization of the feeding apparatus for roost excavation in *Lophostoma*. In fact, we found that *L. silvicolum* has elevated bilateral canine bite forces, which are the bites used during roost making, when compared with closely related and ecologically similar species that do not excavate roosts (Dechmann *et al*., 2009). This suggests some type of specialization in *Lophostoma*'s muscular and/or skeletal system.

Here we investigate whether the skull of *L. silvicolum* is specialized for roost excavation when compared with the ecologically similar species *Tonatia saurophila* (Koopman & Williams, 1951) and *Micronycteris hirsuta* (Peters, 1869), which do not excavate roosts but share a similar diet (Humphrey, Bonaccorso & Zinn, 1983; Kalko *et al*., 1999). Given that the termite nests are harder than the food items consumed by *L. silvicolum*, we predict that these bats will exhibit cranial features that allow them to deal with this physical challenge. First, we explore similarities and differences in the size of the masticatory muscles in these bats. Second, we use finite element analysis to test the prediction that the skull of *L. silvicolum* is stronger under loads that simulate roost-excavating behaviour than the skulls of *T. saurophila* and *M. hirsuta*. We also predict that the skulls of *L. silvicolum*, *T. saurophila*, and *M. hirsuta* are equally strong under loads that simulate feeding. Finite element analysis is a technique borrowed from engineering that is increasingly used in biology to evaluate the functional implications of morphological variation among living and extinct organisms (reviewed in Richmond *et al*., 2005; Rayfield, 2007). Unlike *in vivo* experimentation, finite element modelling provides the opportunity to compare the performance of structures with different shapes while fully controlling for the effects of size differences (Dumont, Grosse & Slater, 2009).

MATERIAL AND METHODS

SPECIMEN, BITE FORCE AND MUSCLE DATA COLLECTION

We caught individuals of *L. silvicolum* (hereafter *Lophostoma*), *T. saurophila* (hereafter *Tonatia*), and *Micronycteris hirsuta* (hereafter *Micronycteris*) by placing mist nets inside forested areas in Venezuela (Caparo forest reserve, 2006, 2007) and Panama (Isla Colon, 2007). We only collected measurements from adult males and adult females that were neither pregnant nor lactating. All procedures used were approved by the Institutional Animal Care and Use Committee at the University of Massachusetts, Amherst, USA (protocol no. 26-10-06).

Shortly after capture, we measured the bite forces of the bats at a 30° gape angle using a piezoelectric force transducer (type 9203, range ± 500 N, accuracy

Table 1. Mass and muscle forces representing the primary jaw adductors of *Lophostoma silvicolum*, *Tonatia saurophila*, and *Micronycteris hirsuta*, and bite forces measured in the field for the three species (means ± standard deviations)

	Mass (mg)	Estimated maximum muscle force (N)	% of total estimated max. muscle force	Measured canine bilateral bite force (N)	Measured molar bilateral bite force (N)
Lophostoma silvicolum				12.49 ± 5.02	15.10 ± 4.11
Temporalis	461.18 ± 87.50	21.92 ± 7.01	81.04		
Masseter	49.70 ± 4.74	2.88 ± 0.54	10.65		
Medial pterygoid	18.65 ± 3.18	1.63 ± 0.35	6.03		
Lateral pterygoid	7.10 ± 0.78	0.63 ± 0.11	2.33		
Total	536.63 ± 96.20	27.05 ± 8.01			
Tonatia saurophila				7.28 ± 2.77	15.41 ± 5.62
Temporalis	406.63 ± 25.19	17.98 ± 1.08	76.84		
Masseter	51.10 ± 2.84	3.12 ± 0.57	13.33		
Medial pterygoid	16.82 ± 5.89	1.61 ± 0.93	6.88		
Lateral pterygoid	4.38 ± 1.16	0.69 ± 0.17	2.95		
Total	478.93 ± 28.60	23.41 ± 2.39			
Micronycteris hirsuta				7.47 ± 1.92	12.48 ± 3.60
Temporalis	207.27 ± 6.08	9.93 ± 0.42	75.17		
Masseter	28.95 ± 4.55	2.00 ± 0.40	15.14		
Medial pterygoid	10.13 ± 0.67	0.89 ± 0.14	6.74		
Lateral pterygoid	2.72 ± 0.85	0.39 ± 0.13	2.95		
Total	249.07 ± 8.45	13.22 ± 0.66			

Sample sizes and methods for generating muscle forces are described in the text.

0.01–0.1 N; Kistler, Amherst, NY, USA) attached to a handheld charge amplifier (type 5995; Kistler), and mounted between two bite plates (Herrel *et al*., 1999; Dumont & Herrel, 2003). We recorded at least five bite-force measurements for each individual bat at the two bite positions that are used by *Lophostoma*, *Tonatia*, and *Micronycteris* while feeding on insects or excavating termite roosts. Bilateral canine bites, which engage both canines, are the hallmark bite type used by *Lophostoma* during roost excavation (Dechmann *et al*., 2009). Bilateral molar bites, which engage both right and left molar rows simultaneously, are used predominantly by all three species during feeding on insects (Santana & Dumont, 2009). Average maximum bite forces at each of these bite positions were calculated for each species from individual maximum bite-force measurements ($N = 9$ individuals for each of *Lophostoma* and *Tonatia*; $N = 3$ individuals for *Micronycteris*). These average maximum bite forces were used to inform subsequent finite element analyses that simulated roost excavation and feeding.

We retained voucher specimens for each species (sample sizes: *Lophostoma*, 2; *Tonatia*, 3; *Micronycteris*, 3), and conducted dissections of the major cranial muscles (temporalis, masseter, medial, and lateral pterygoid) on both sides of the skull. We documented the locations of muscle attachment, weighed the muscles, and separated individual muscle fibres using nitric acid digestion, following the method described by Biewener (1992). Physiological cross-sectional areas (PCSAs) were calculated for each muscle using the equation: PCSA = muscle mass/(muscle density × fibre length) (Lieber, 2002). Pennation angles were not taken into account, given that our dissections indicated that the muscles were not pennate (see also Herrel *et al*., 2008). We used a mammalian muscle density of 1.06 g cm^{-3} (Mendez & Keys, 1960). The PCSA values were multiplied by a muscle stress value of 25 N cm^{-2} (Herzog, 1994) to obtain muscle force estimates. These data allowed us to determine the relative contribution of each muscle to the total muscle force (Table 1). The skulls of the voucher specimens were cleaned using a dermestid colony, and one skull of each species was used to generate our finite element models.

FINITE ELEMENT MODEL CONSTRUCTION

We constructed finite element (FE) models from micro-computed tomography (CT) scans of dry skulls of one adult male representing each of *Lophostoma*, *Tonatia*, and *Micronycteris* (UMA 5325, 5284, and 5293). These scans were generated at the micro-CT scan facility at Amherst College, MA, USA. The X-ray projection images produced by the micro-CT scanner were converted using filtered back-projection into a volume consisting of a stack of X-ray attenuation cross sections, or slices. This was performed using the reconstruction software NRECON v1.5.1.4 (MicroPhotonics Inc., Allentown, PA, USA). All CT slices for both specimens had the same thickness (0.0354 mm). We transformed the shadow images from the micro-CT scans into FE meshes using two software tools. First, we used MIMICS (Materialise, NV, Leuven, Belgium) to generate and condition three-dimensional surface representations of the skulls. Second, we imported the surface representations into GEOMAGIC STUDIO® (Geomagic Inc., Research Triangle Park, NC, USA), and used this program to position the lower jaw at a gape angle of 30°, and to make minor geometric adjustments to facilitate the construction of solid FE meshes. We then brought the surface representations back into MIMICS, where we adjusted the aspect ratios of the triangular surface elements and generated solid FE models composed of four-noded tetrahedral elements. The completed *Lophostoma* skull model consisted of 354 704 elements, the *Tonatia* skull model consisted of 380 329 elements, and the *Micronycteris* skull model consisted of 469 070 elements.

Using STRAND7 (Strand7 Pty Ltd, Sydney, Australia), the three models were assigned average isotropic material property values for cortical bone in mammals (Young's modulus = 2.512×10^4 MPa, Poisson's ratio = 0.3; Erickson, Catanese & Keaveny, 2002; Dumont *et al*., 2009). Each model was constrained from rigid body motion by fixing four nodes. The first two nodes represented the contacts between the dentary and skull along the temporomandibular joint (TMJ) axis. To avoid over-constraining the model, one of the TMJ nodes was fixed in all directions, and the other was fixed only in two directions, such that deformation was permitted along the TMJ axis. In the roost excavation simulation, one additional node was constrained at the tip of each upper canine in the plane perpendicular to a plane passing through the occlusal surfaces of the upper M1. These constraints represented the contacts between the canines and a termite nest. For the feeding simulation, the canine constraints were released and one node was constrained on each upper M1 paraconids, again only in the plane perpendicular to a plane passing through the occlusal surfaces of the upper M1. These constraints represented the contacts between the upper molars and a food item. Following methods laid out in previous FE analyses of mammalian masticatory systems, forces representing the masticatory muscles were added to pull the skull ventrally onto these constraints, generating reaction forces at the TMJ and bite reaction forces at the teeth (Strait *et al*., 2002, 2005; Dumont, Piccirillo & Grosse, 2005; Dumont *et al*., 2009).

We used a modified version of BONELOAD (Grosse *et al*., 2007; Dumont *et al*., 2009) to apply muscle forces to the skulls in their correct proportions (Table 1) for *Lophostoma*, and then scaled the *Tonatia* and *Micronycteris* skulls (see below). All muscles were assumed to contract maximally and simultaneously, based on studies of muscle activity at maximum occlusion in another large bat, and in primates (De Gueldre & De Vree, 1988; Hylander, Ravosa & Ross, 2004). Using the gradient pressure method of applying forces (Dumont *et al*., 2010), the force generated by each cranial muscle was distributed over its attachment area on the skull. The resultant force vector for each muscle pointed directly to its centroid of the muscle insertion region in the lower jaw.

Metrics that are commonly used to assess the performance of FE models (e.g. stress and strain energy) are affected by both model size and model shape (Dumont *et al*., 2009). As our question was whether or not the shape of the *Lophostoma* skull reflects its roost-excavating habits, we controlled for the effects of size by scaling the three models to have the same calculated muscle force to surface area ratios (Dumont *et al*., 2009). For each model we assumed maximum, bilateral force production in proportion to each muscle's contribution to total muscle force (Table 1; De Gueldre & De Vree, 1988; Hylander *et al*., 2004). For the roost-excavation simulation (bilateral canine biting), the three models were loaded with the muscle force to surface area ratio required for the *Lophostoma* model to return a total bite reaction force at the canines of 12.49 N in the plane passing through the tips of the upper and lower canines (Santana & Dumont, 2009). Similarly, for feeding simulation (bilateral molar biting) the three models were loaded with the muscle force to surface area ratio required for the *Lophostoma* model to return a bite reaction force at the first molars of 15.09 N perpendicular to the occlusal plane of the P3 and M1 paraconids (Santana & Dumont, 2009).

We compared the performance of the FE models using von Mises stress (Dumont *et al*., 2009). Stress values were contrasted among the three models by visual inspection of colour-coded contour plots, and by comparing the maximum stress values in five anatomical regions: the zygomatic arches, the infratemporal fossae, the dorsum of the rostrum, the posterior region of the palate, and the basioccipital bone (Fig. 1). For bilateral structures (i.e. the zygomatic arches and infratemporal fossae), we calculated the average of maximum stress from the left and right sides. We report the average because it is not uncommon for FE models, or indeed skulls, to contain small geometric asymmetries that result in small stress asymmetries. The von Mises stress data provided an estimate of the strength of the two models. Specifi-

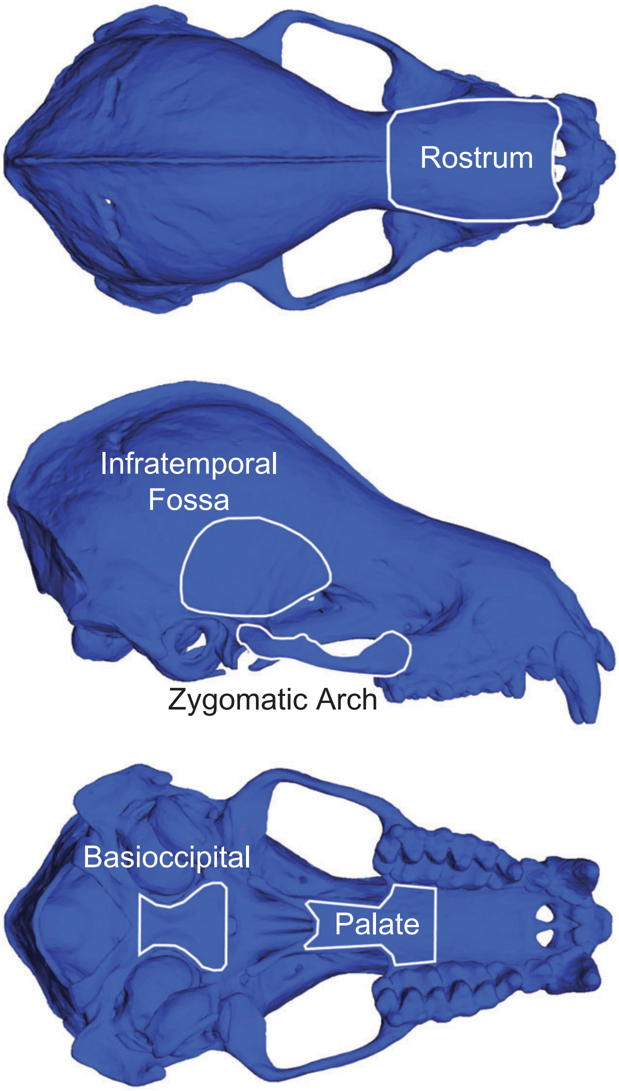

Figure 1. Regions of elevated von Mises stress during finite element analyses. Peak values from these areas are reported in Table 2.

cally, given identical loading regimes, the stronger model exhibits the least stress, and is therefore capable of withstanding a higher load before it fractures.

RESULTS

MUSCLE DISSECTIONS

Results from muscle dissections indicated that the temporalis muscle in *Lophostoma* contributes to a higher percentage of the total muscle force in *Lophostoma* than in *Tonatia* and *Micronycteris* (Table 1). Conversely, the masseter seems to contribute the lowest percentage of total muscle force in *Lophostoma* when compared with the other two species. Across all three species the pterygoid muscles made a similar contribution to the total muscle force.

ROOST-EXCAVATION SIMULATION (BILATERAL CANINE BITING)

Stress contour maps for the roost excavation load revealed similar patterns in the topographic distribution of stress in the *Lophostoma*, *Tonatia*, and *Micronycteris* models (Fig. 2). In lateral view, all three models exhibited elevated stress along the rostrum, zygomatic arches, the infratemporal fossae and the region surrounding the glenoid fossae. Ventral views further illustrated elevated stress in the posterior regions of the palate, basisphenoid and basioccipital bones. The zygomatic arches were the regions of highest stress in all models, indicating that these areas have the lowest safety factor and are most susceptible to failure. The quantitative data confirmed that, on average, most regions of the *Lophostoma* model performed better (i.e. exhibited lower stress) under the roost-excavation load than did the *Tonatia* and *Micronycteris* models (Table 2). Compared with *Lophostoma*, the average maximum von Mises stress in the zygomatic arches of *Tonatia* and *Micronycteris* were 12.19 and 7.95% higher, respectively. Other regions of the skull demonstrated even greater differences in average von Mises stress, with up to 83% more stress in the infratemporal fossae of *Micronycteris*. The only exception to this pattern was that the lowest absolute peak stress in the zygomatic arch occurred in *Micronycteris*, not in *Lophostoma* (values in parentheses in Table 2).

FEEDING SIMULATION (BILATERAL MOLAR BITING)

The three models exhibited similar topographic distributions of von Mises stress under loads that simulated biting with the molar teeth (Fig. 3). In lateral view, the infratemporal fossa and the region surrounding the glenoid fossa are highly stressed. The ventral view illustrates elevated stress in the posterior edge of the palate and anterior edge surrounding the auditory bullae. Again, the zygomatic arches were the regions with the highest stress values. Overall, the stress contour maps suggested that *Lophostoma* experienced slightly lower stress levels than *Tonatia* and *Micronycteris*. Nevertheless, the quantitative data indicated that the three models performed similarly under the feeding load. *Lophostoma* presented intermediate values of von Mises stress in the zygomatic arches, with *Tonatia* having 3.86% higher values and *Micronycteris* having 3.96% lower values. Peak stress values in other regions of the skull were lowest for *Tonatia*. In the majority of the skull regions, the percentage stress difference between

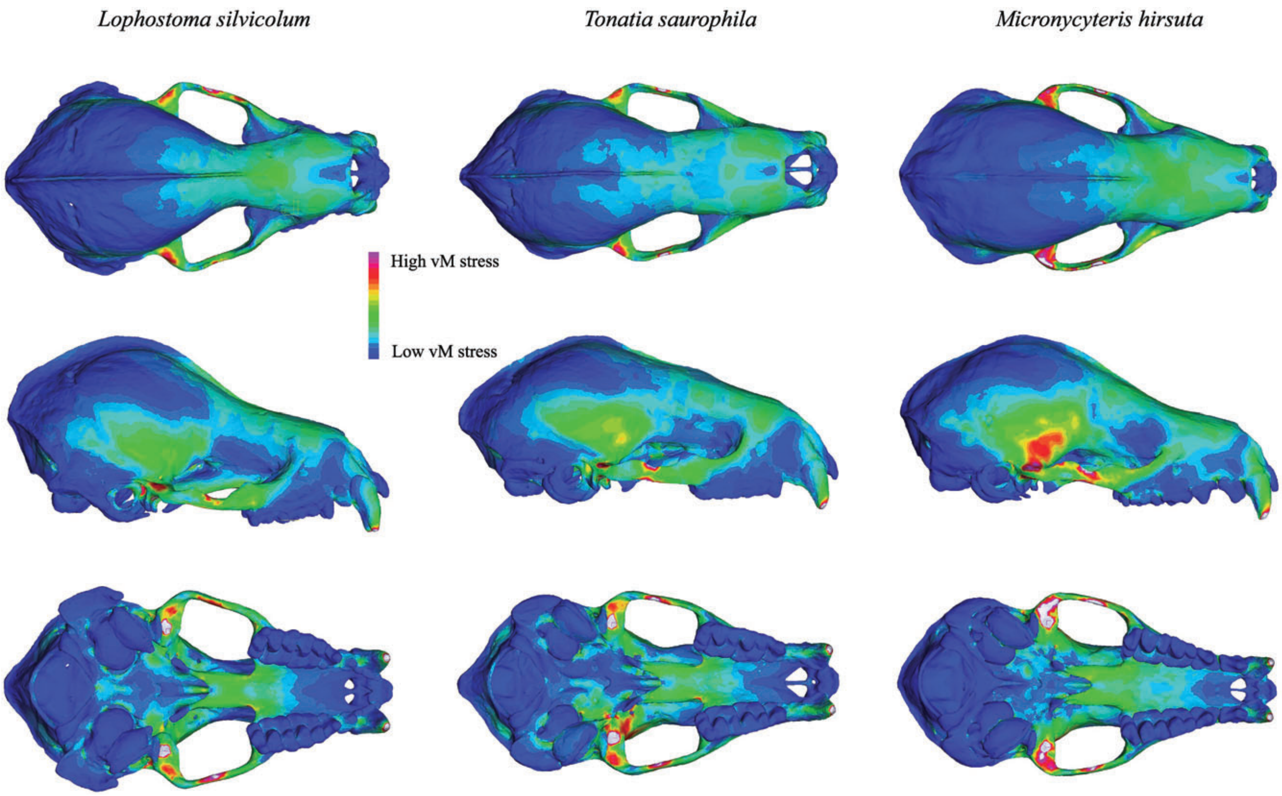

Figure 2. The predicted distribution of von Mises stress in finite element models of *Lophostoma silvicolum*, *Tonatia saurophila*, and *Micronycteris hirsuta* under a bilateral canine load, which simulates roost excavation. Warm colours indicate high von Mises stress and cool colours indicate regions of low stress. White areas indicate stresses that exceed the range contained in the histogram.

Lophostoma and the other two species was greater in the roost-excavation simulation than in the feeding simulation (Table 2).

DISCUSSION

Our FE analysis results did not provide overwhelming evidence that the skull of *Lophostoma* is specialized for roost excavation. When considering average stresses, the shape of the skull in *Lophostoma* renders it stronger than the two non-excavators under loads generated during the roost-excavation simulation (bilateral canine biting) and across all skull regions. The differences in average stress among the three species are within the ranges documented for other comparative FE studies, some of which deal with species with much greater shape differences (e.g. Tseng, 2009; Dumont *et al.*, 2005; Slater, Dumont & Van Valkenburgh, 2009). Nonetheless, in terms of peak stress at the zygomatic arches (values in parentheses in Table 2), *Micronycteris* has the strongest skull during bilateral canine biting. This result suggests that skull strength in *Lophostoma* is not specialized for roost excavation behaviour. However, interpretations made from stress values at the zygomatic arches should be taken with caution. *In vivo* studies have registered elevated strain values at the zygomatic arches (e.g. Wang *et al.*, 2008), but the anatomy of these areas is probably not modelled realistically with current FE techniques. In particular, ligaments and fascia are not included, which could make the arches appear to be weaker than they actually are. Further tests for cranial specialization in *Lophostoma* are necessary, and should either include models from more individuals in order to account for intraspecific variation in skull shape or, once methods are developed, assess the probability of structural failure across the three species.

It is noteworthy that the stress values reported for all three species are well below the value at which bone fails (140 MPa; Nordin & Frankel, 2001; Dumont *et al.*, 2005). Consequently, the skulls of *Tonatia* and *Micronycteris* should be able to withstand the stress generated during roost excavation, and these bats possess bite forces that are strong enough to excavate termite nests at the low end of the hardness spectrum (Dechmann *et al.*, 2009; Santana & Dumont, 2009). Despite this, only *Lophostoma* is

Table 2. Average and range of von Mises stress in several skull regions (see Fig. 1) from the *Lophostoma silvicolum*, *Tonatia saurophila*, and *Micronycteris hirsuta* finite element models under simulated roost excavation (bilateral canine) and feeding (bilateral molar) biting loads

	Average and maximum stress (MPa)				
Loading condition	Zygomatic arches	Infratemporal fossae	Rostrum	Basioccipital	Palate
Roost excavation					
Lophostoma silvicolum	**56.207** (43.713–68.701)	**20.404** (18.604–**22.204**)	**14.512**	**14.725**	**22.765**
Tonatia saurophila	63.163 (54.540–71.787)	25.118 (22.389–27.847)	21.903	15.412	28.089
Micronycteris hirsuta	61.259 (60.445–**62.072**)	37.504 (35.692–39.316)	21.222	17.464	23.445
% Difference *Lophostoma–Tonatia*	–12.37%	–23.10%	–50.93%	–4.67%	–23.43%
% Difference *Lophostoma–Micronycteris*	–8.98%	–83.81%	–46.24%	–18.60%	–3.025%
Feeding					
Lophostoma silvicolum	41.910 (31.643–52.178)	**13.823** (14.212–**13.434**)	7.909	10.485	11.360
Tonatia saurophila	43.529 (35.193–51.866)	15.077 (13.824–16.329)	**6.613**	9.609	**10.195**
Micronycteris hirsuta	**40.254** (39.472–**41.035**)	19.055 (17.848–20.261)	9.667	**8.714**	11.878
% Difference *Lophostoma–Tonatia*	3.86%	–9.071%	16.382%	8.355%	10.25%
% Difference *Lophostoma–Micronycteris*	3.95%	–37.849%	–22.228%	12.226%	–4.55%

The ranges, corresponding to the left and right side of the skull, are given in parentheses for bilaterally symmetrical structures. Values in bold indicate better performance (i.e. lowest average or maximum stress).

known to excavate termite nests. One could speculate that a combination of interspecific competition for roosting resources, and morphological and behavioural pre-adaptations could have fostered the evolution of such a unique roosting strategy in *Lophostoma*. For example, ancestral state reconstructions suggest that the ancestor of *Lophostoma* and *Tonatia* exhibited a relatively high proportion of shallow bites during feeding (Santana & Dumont, 2009), and this biting style may have been later co-opted for roost making in *Lophostoma*.

Whether or not selection has favoured stronger skulls in *Lophostoma*, these bats do have increased bilateral canine bite forces than ecologically similar species (Dechmann *et al.*, 2009). A recent study of masticatory muscle morphology in phyllostomid bats suggests that *Lophostoma* can generate these higher canine bite forces because its temporalis muscles have relatively high PCSA values (Santana, Dumont & Davis, 2010; Table 1). Many other mammals that specialize in biting hard objects, including other phyllostomids, also invest in large temporalis muscles that allow them to produce high forces at large gape angles (Smith & Savage, 1959; Davis, 1964; Greaves, 1985; Perez-Barberia & Gordon, 1999; Slater *et al.*, 2009). This could be a specialization of the feeding apparatus towards roost excavation in *Lophostoma*. Male *Lophostoma* spend prolonged periods of time biting into the termite nests to maintain their cavities (Dechmann *et al.*, 2005), and thus their cranial apparatus needs to constantly produce high bilateral canine forces and withstand the stress produced by these loads. As these roost-excavating males tend to sire more offspring (Dechmann & Kerth, 2008), and cranial morphology is likely to be highly heritable, the patterns described here in muscle morphology, bite force, and possibly skull stress could be the result of selection for roost-excavating behaviour.

Lophostoma, *Tonatia*, and *Micronycteris* are similarly strong under loads that simulate feeding, as illustrated by the smaller differences in stress values across regions of the skull relative to the roost-excavation simulation. All three species feed mostly on katydids (bush crickets) and other large arthropods gleaned from the ground or vegetation (Humphrey *et al.*, 1983; Kalko *et al.*, 1999), and use their molars to crush and chew these insects (Santana & Dumont, 2009). As katydids are relatively soft and do not require the highest molar bite forces that the bats can produce (Dechmann *et al.*, 2009; Santana & Dumont, 2009), it is not surprising that the skulls of these species all exhibited similar and low levels of stress under this loading regime.

Phyllostomid bats present one of the most outstanding morphological radiations within mammals

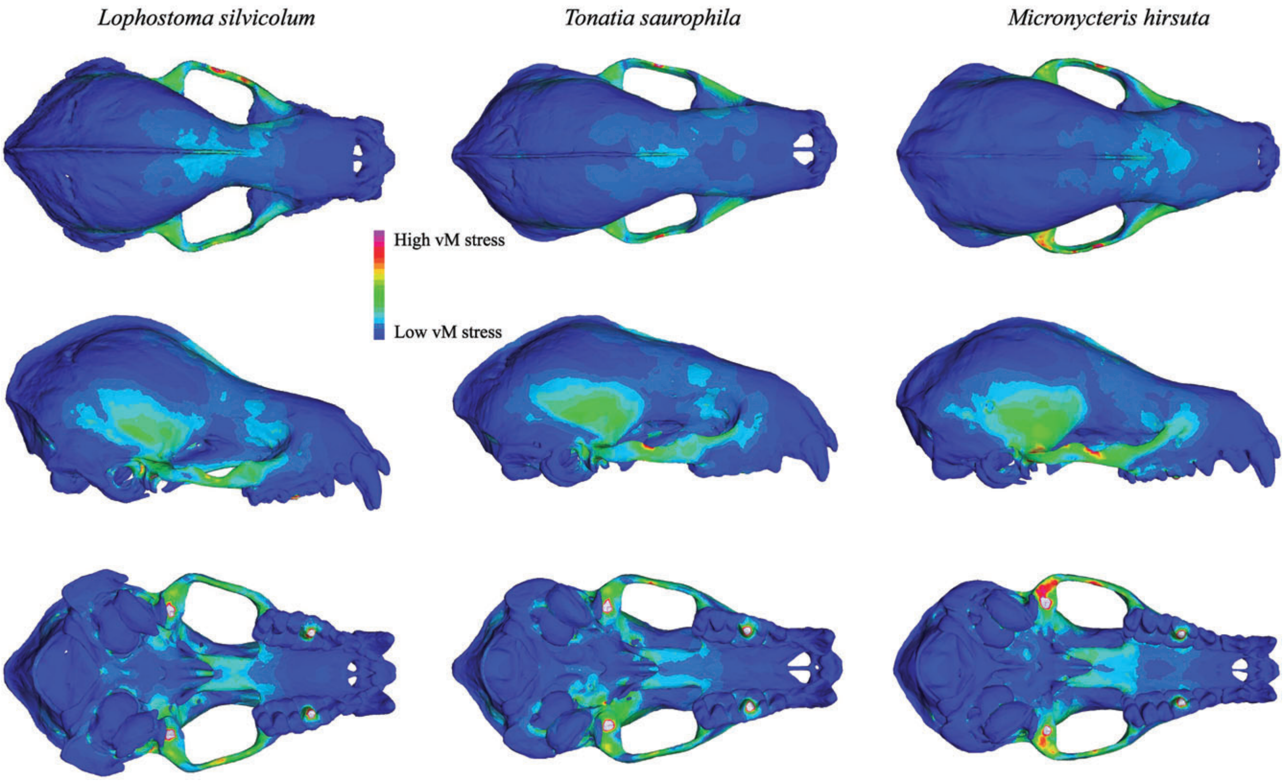

Figure 3. The predicted distribution of von Mises stress in finite element models of *Lophostoma silvicolum*, *Tonatia saurophila*, and *Micronycteris hirsuta* under a bilateral molar load, which simulates feeding. Warm colours indicate high von Mises stress and cool colours indicate regions of low stress. White areas indicate stresses that exceed the range contained in the histogram.

(Freeman, 2000). The diversity in the shape and function of phyllostomid skulls is clearly associated with different dietary niches (Freeman, 2000; Nogueira *et al.*, 2009; Santana *et al.*, 2010). However, the construction of shelters is also widespread in phyllostomids and, because of the fitness advantages of this behaviour and its importance in determining species distributions (reviewed in Kunz & Lumsden, 2003), it may also have played a role in shaping the morphology and function of the skulls of these bats. The fact that both roost excavation and feeding are associated with fitness in *Lophostoma* makes this a unique system for studies of specializations of the masticatory apparatus with respect to these two behaviours. We provide evidence for specializations in bite performance, muscle size, and possibly skull morphology in the skull of male bats that have to perform a physically demanding function that is highly relevant to their ecology. This study sets the stage to further explore the possibility that the feeding apparatus of mammals can exhibit performance and morphological adaptations to functions other than feeding, such as building roosts.

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