

2010

Simple predictors of bite force in bats: The good, the better, and the better still

Patricia W. Freeman

University of Nebraska-Lincoln, pfreeman1@unl.edu

Cliff A. Lemen

University of Nebraska-Lincoln, clemen2@unl.edu

Follow this and additional works at: <http://digitalcommons.unl.edu/museummammalogy>



Part of the [Zoology Commons](#)

Freeman, Patricia W. and Lemen, Cliff A., "Simple predictors of bite force in bats: The good, the better, and the better still" (2010).
Mammalogy Papers: University of Nebraska State Museum. 133.
<http://digitalcommons.unl.edu/museummammalogy/133>

This Article is brought to you for free and open access by the Museum, University of Nebraska State at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Mammalogy Papers: University of Nebraska State Museum by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Simple predictors of bite force in bats: The good, the better, and the better still

P. W. Freeman and C. A. Lemen

School of Natural Resources and University of Nebraska State Museum,
University of Nebraska–Lincoln, Lincoln, NE 68583, USA

Corresponding author — Patricia W. Freeman, School of Natural Resources, 428 Hardin Hall,
University of Nebraska–Lincoln, Lincoln, NE, USA 68583-0974. Email: pfreeman1@unl.edu

Abstract

Bite forces of 39 species from six families of New World bats with a variety of diets are quantified with a force meter under field conditions. Using regression approaches we search for a model that is a good morphological predictor of these bite forces. Body mass, an index that ignores differences in skull morphology, has a statistically significant relationship with bite force ($R^2 = 0.76$) but is a relatively poor predictor compared with our best model ($R^2 = 0.94$). The two best models of the eight we examine are one based on an estimate of strength of dentary, which is really simple beam theory; and the other based on muscle mass and jaw mechanics of input and output arms. Both models explain about 90% of the variation in bite force. However, the combination of these variables together in multiple regression works even better, explaining about 94% of the variation. Our model derived from beam theory relies on bony characteristics, which are readily available from museum specimens. This model will be of particular use to students of fossils or ecomorphology for inferring bite force. We also test Freeman's earlier predictions about bite forces of bats with gracile versus robust skulls. These predictions can be only partially confirmed. For species we measured, bats with gracile skulls did have weak bites; however, bats designated by Freeman as having robust skulls did not have particularly strong bites.

Keywords: bite force, beam theory, jaw biomechanics, Chiroptera, ecomorphology, functional morphology

Introduction

Freeman (1979, 1981a) quantified differences in morphology among skulls of molossid bats that she felt reflected differences in bite force. She predicted species specializing in hard-shelled prey items (e.g. beetles) had robust skulls with well-developed cranial crests; short, wide, thick jaws and fewer, larger teeth. Likewise, she felt species eating primarily soft-shelled items (e.g. moths) had less robust skulls and longer, thinner jaws and more, smaller teeth. By comparing extreme forms, she selected a series of shape variables expressed as ratios that characterized the differences in robust and gracile skulls of bats. To find whether these ratios might be useful generally to assess bite force and diet across insectivorous bats, she measured 41 species with at least some dietary information available and performed a PCA (Freeman 1981b). She found that extreme molossid species were on opposite ends of the first principal component (size-removed). Non-molossids also seemed to be positioned in a manner consistent with this robust-gracile axis. At that time neither actual bite force data nor the degree of hardness of fresh insect cuticle was available (but now see Freeman & Lemen, 2007b). With help from entomologists she qualitatively ranked hardness of insects in diets for different species of bats and found a positive correlation between hard-

ness of food item and position on this principal component of robust to gracile-jawed forms. Freeman (1981b) hypothesized that specialization within bats for hard and soft food items is an important factor in the evolutionary diversity of the group because they may prey upon specific portions of the insect community. Now that actual bite force data are available, we can directly test Freeman's (1981b) ecomorphological predictions about insectivorous bats with gracile and robust skulls.

A second goal here is to find an accurate, simple predictor of bite force in bats, much as we did with rodents (Freeman & Lemen, 2008a). Bite force is viewed as a key ecomorphological parameter that impacts the feeding ecology of species (Van Valkenburgh & Ruff, 1987; Thomason, 1991; Aguirre *et al.*, 2002; Meers, 2002; Wroe, McHenry & Thomason, 2005; Herrel *et al.*, 2008; Santana & Dumont, 2009). Many species of bats coexist and have diversified into a variety of dietary preferences making this group ideal as a model system for the study of ecomorphology (Freeman, 1998). Further, the adaptive radiation of bats (Freeman, 1981a,b, 1998, 2000; Dumont, 1997), the coexistence of bats within communities (Black, 1974; LaVal & Fitch, 1977; O'Neill & Taylor, 1989; Gannon & Rácz, 2006; Valdez & Bogan, 2009), and the role of bat feeding behavior and plasticity (Dumont, 1999; Santana & Dumont, 2009) have all been couched in terms of hard and soft foods.

There are now models of jaw mechanics to predict bite force of bats (Herrel *et al.*, 2008; Santana, Dumont & Davis, 2010). These authors use detailed analysis of muscle mass, muscle fiber lengths and muscle insertion points to create detailed biomechanical models of jaws to predict bite force in bats. In our view, the ultimate and laudable goal of these studies is to contribute towards a general model of biomechanics. Such a model is based on mechanistically modeling the interaction of muscle and bone in vertebrates. In contrast we simply want to predict bite force to facilitate eco-morphological research and not the underlying mechanisms of the jaw. For practical reasons we do not wish to use the descriptive biomechanics approach. The measurements require fresh material, careful, skilled dissection and sometimes CT scans (Santana & Dumont, 2009). We prefer a method that is easy to use when only dried skulls and fossils are available. Second, we hoped to develop models with great accuracy in predicting bite force. The R^2 value between measured bite force and the predictions from the descriptive biomechanical models of bite forces in bats in Santana *et al.* (2010) is $R^2 = 0.66$ and in Herrel *et al.* (2008) is $R^2 = 0.75$. These correlations are highly significant, but we felt there was room for improvement.

All the models we built are put through a model-selection procedure using the AIC method (Burnham & Anderson, 2002). Conceptually the simplest model we have is based on body size. When there are large differences in body size among species in a study, body size might be expected to be a fair predictor of bite force. For example in this study bats range in size from 4 to 90 g, and the R^2 of body mass and bite force is about 0.75 (results below). Therefore almost any morphological measurement from these bats will have high correlation with bite force because most measurements are size related. Size is clearly an important eco-morphological variable and was one of the first used (Hutchinson, 1959), however it does not give insights into the interesting variation in the diverse shapes of skulls seen in bats (Freeman, 1984, 1998, 2000).

Finally, we wished to compare our method of measuring bite force with the approach used by Aguirre *et al.* (2002). Although the details of the sensors we each used are different, both methods involve a captive bat biting a sensor. However, our previous work with rodents impressed us that obtaining bites from animals is not always easy. Because of problems associated with maximal performance (see Anderson, McBrayer & Herrel, 2008), we were curious how results from Aguirre *et al.* (2002) would compare with ours.

Materials and methods

Our bite force detector has two components, a piezoresistive sensor and an electronic device to track changes in the resistance of the sensor (description in Freeman & Lemmen, 2008b). The one-plate sensor itself is a strip of thin plastic 10 mm wide, 150 mm long, and only 0.2 mm thick. We used a variety of coverings to protect the thin sensors from being penetrated by teeth. For smaller bats (<6 g) we used a layer of liquid plastic. For larger species we added

thin (0.25 mm) stainless-steel disks under the liquid plastic to protect the top and bottom surfaces.

Because of the design of our bite force sensor, we could not easily control gape angle as other authors have (Dumont & Herrel, 2003). The thickness of the sensors used on smaller bats (<9 g) was about 1.4 mm and on larger species about 2.2 mm. The gape angle would be a function of this thickness, canine length and jaw length. However because of the relative thinness of the sensor, gape angles were relatively low.

Each sensor was calibrated separately to determine the relationship between applied force in newtons and conductance. With the possibility of damage to the sensor with each bite, we continually calibrated with a hand-held force device (Chatillion force gauge to 10 N) as measurements were taken in the field.

We always took bite force so that both canines make contact with the sensor at the same time. We normally measured bite force within a few minutes of capture. In a few cases we held bats overnight and measured bite force in the morning after they had warmed up. For bats willing to bite, we recorded the maximum bite force that the bat produced. The mean bite force (biteForce) for a species was the average of the strongest bite for each individual (Table 1). As presented below, our method produces bite forces similar to those of Aguirre *et al.* (2002). With this in mind, we used their bite force data for two species, *Phyllostomus hastatus* and *Noctilio leporinus*, because we had muscle and jaw measurements for these species, but not bite forces.

We performed our research on live animals following guidelines set by ASM, and approved by the University of Nebraska's committee on animal care and use (IACUC). Our standard protocol for testing bite force is that no pain stimulation is used, and second, testing is brief and lasts about a minute.

Voucher specimens of each species were collected for identification, muscle dissection and measurement. All measurements used here were taken on this sample (normally two adults, a male and female) for each species and averaged. Species and sample sizes of measured individuals of the 39 species included in this study are presented in Table 1. Lengths measured and illustrated in Figure 1 include: length from mandibular condyle to tip of coronoid (inputArm), length from mandibular condyle to tip of canine (outputArm), length from rear of last molar to tip of canine (loadArm), height of dentary at rear of last molar (htDent), width of dentary just posterior to last molar (widDent). Masses measured include: mass of freshly caught animals (bodyMass), mass of skull including dentary (skullMass, of cleaned and dried bone), sum of masses of left and right temporalis, masseter and pterygoideus jaw muscles dissected from freshly caught specimens (jawmusMass). We also measured width across the zygomatic arches (zygoWidth) on the cranium. All variables were log (base 10) transformed before analysis.

Our first model uses just bodyMass, a general measure of size, to predict bite force. Next are three models that are based on head size: zygoWidth, jawmusMass and skullMass. Because the head produces the bites we reasoned

Table 1. Bite force for species used in this study

| Species | Diet | Jaw muscle (n) | Bites (n) | biteForce (N) | Bite (SD) |
|---|------|----------------|-----------|---------------|-----------|
| <i>Anoura geoffroyi</i> ^T | N | 3 | 2 | 2.7 | 1.17 |
| <i>Antrozous pallidus</i> ^B | I | 2 | 4 | 6.4 | 0.93 |
| <i>Artibeus glaucus</i> ^T | F | 2 | 8 | 6.1 | 1.83 |
| <i>Artibeus jamaicensis</i> ^T | F | 2 | 9 | 16.4 | 2.36 |
| <i>Artibeus lituratus</i> ^T | F | 2 | 4 | 48.8 | 6.20 |
| <i>Carollia perspicillata</i> ^T | F | 5 | 16 | 5.6 | 1.69 |
| <i>Chiroderma trinitatum</i> ^T | F | 1 | 1 | 4.3 | – |
| <i>Chiroderma villosum</i> ^T | F | 3 | 8 | 10.1 | 1.12 |
| <i>Corynorhinus townsendii</i> ^B | Ig | 2 | 1 | 1.25 | – |
| <i>Eptesicus brasiliensis</i> ^T | I | 1 | 1 | 3.8 | – |
| <i>Eptesicus fuscus</i> ^{NE} | I | 1 | 9 | 8.7 | 1.50 |
| <i>Eumops perotis</i> ^B | Ig | 1 | 1 | 9.3 | – |
| <i>Glossophaga soricina</i> ^T | N | 4 | 5 | 1.8 | 0.54 |
| <i>Lasiurus borealis</i> ^{NE} | lr | 1 | 5 | 3.4 | 0.27 |
| <i>Lasiurus cinereus</i> ^{NM} | lr | 1 | 18 | 6.8 | 0.79 |
| <i>Micronycteris megalotis</i> ^T | I | 3 | 6 | 2.4 | 0.52 |
| <i>Micronycteris minuta</i> ^T | I | 1 | 1 | 2.2 | – |
| <i>Molossus ater</i> ^T | lr | 4 | 8 | 9.1 | 1.86 |
| <i>Molossus molossus</i> ^T | lr | 3 | 28 | 3.7 | 1.86 |
| <i>Mormoops megalophylla</i> ^T | Ig | 2 | 5 | 3.7 | 0.12 |
| <i>Myotis velifer</i> ^B | I | 2 | 2 | 2.2 | 0.30 |
| <i>Noctilio leporinus</i> ^T | lr | 1 | a | 19.9 | – |
| <i>Nycticeius humeralis</i> ^{NE} | I | 1 | 6 | 4.2 | 0.57 |
| <i>Nyctinomops femorosaccus</i> ^B | Ig | 1 | 1 | 1.5 | – |
| <i>Nyctinomops macrotis</i> ^{U, NM, B} | Ig | 2 | 8 | 2.6 | 0.45 |
| <i>Phyllostomus discolor</i> ^T | O | 3 | 1 | 17.4 | – |
| <i>Phyllostomus hastatus</i> ^T | O | 2 | a | 68.0 | – |
| <i>Platyrrhinus helleri</i> ^T | F | 4 | 7 | 3.9 | 1.01 |
| <i>Pteronotus davyi</i> ^T | I | 1 | 1 | 1.7 | – |
| <i>Pteronotus parnellii</i> ^T | I | 2 | 8 | 5.1 | 1.82 |
| <i>Rhynchonycteris naso</i> ^T | I | 3 | 1 | 0.9 | – |
| <i>Saccopteryx bilineata</i> ^T | I | 1 | 4 | 2.9 | 0.99 |
| <i>Saccopteryx leptura</i> ^T | I | 1 | 1 | 1.3 | – |
| <i>Sturnira lilium</i> ^T | F | 2 | 7 | 6.6 | 1.81 |
| <i>Sturnira tildae</i> ^T | F | 3 | 8 | 8.7 | 1.75 |
| <i>Tadarida brasiliensis</i> ^{B, NM} | I | 4 | 2 | 2.0 | 0.36 |
| <i>Trinycteris nicefori</i> ^T | I | 1 | 1 | 1.8 | – |
| <i>Uroderma bilobatum</i> ^T | F | 4 | 15 | 5.8 | 1.37 |
| <i>Vampyroides caraccioli</i> ^T | F | 1 | 1 | 13.0 | – |

a. Bite force data from Aguirre *et al.* (2002).

Superscript initials indicate where in the New World bite data for each species came from: T, Trinidad; B, Big Bend National Park, Texas.; NE, Nebraska; NM, New Mexico; U, Utah.

Initials in the diet column correspond with the diet list and symbols in Figure 2a.

For the remaining columns: *n* jaw muscle is the number of individual bats for which fresh jaw-closing muscles were extracted, *n* bites is the total number bats from which we recorded maximum bites, biteForce is the mean of the maximum bite force given by each bat within a species. Bite SD is the standard deviation of the bite force.

head-size models might be more closely correlated with bite force, especially if relative head size varies among species.

Our next model is more complex because it includes both a measure of size and mechanical advantage in the form of input and output arms. This model is an index of bite force based on mass of fresh jaw muscles and a lever (force × input arm/output arm):

$$\text{muscleCalc} = \frac{\text{jawmusMass}^{2/3} \times \text{inputArm}}{\text{outputArm}}$$

Mass of jaw muscle (jawmusMass) is raised to the 2/3 power to obtain a measure linearly related to cross-sectional area. Although the muscleCalc model is a step up in complexity from the jawmusMass model, it is simpler than the biomechanical models that include fiber lengths of muscles and insertion points for each muscle (Herrel *et al.*, 2008; Santana *et al.*, 2010).

The next model incorporates a different approach from the typical jaw mechanics model by calculating the expected strength of the jaw. The relative strength of a beam can be thought of as the ratio of its sectional modulus

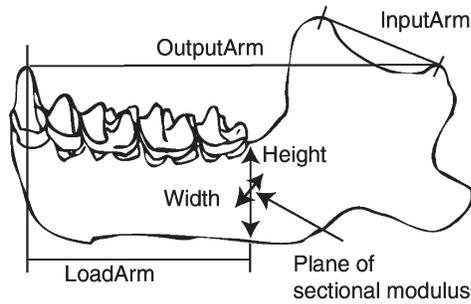


Figure 1. Dentary measurements used in this study. Height and width of the dentary are taken just posterior to the last, lower molar and is our plane of sectional modulus.

and the bending moment (load \times beam length). If we assume a rectangular beam, the sectional modulus is $htDent^2 \times widDent/6$ where $htDent$ and $widDent$ are the height and width of the beam (mm). Of course, dentaries are not perfect rectangles in cross-section, and species do vary in shape (Dumont & Nicolay, 2006). However, in keeping with our goal of simplicity, we still made this assumption rather than measure the cross-sectional outlines. An example where a problem might arise is the comparison of beam strength in long bones of birds versus mammals. Here the large internal vacuities in avian bone might affect strength in comparison with mammals. Our assumption is that dentaries of bats are roughly similar in cross-sectional shape. If our assumption were incorrect then our model would be a relatively poor predictor of bite force. This turned out not to be the case. The bending moment is the length of the beam times the load applied. Because we want to compare relative resistance to bending, a load of one can be used in all cases (Van Valkenburgh & Ruff, 1987; Van Valkenburgh & Koepfli, 1993). These calculations do not include an attempt to calculate an absolute stress produced by a load or the maximum load possible in a jaw as was done for teeth in Freeman and Lemen (2007a). Here we are calculating a relative index of strength using:

$$beamCalc = \frac{htDent^2 \times widDent/6}{loadArm}$$

where $loadArm$ is the length from the section of interest (just posterior to the last molar) to the end of the load (at the tip of the canine). Also, we combine $muscleCalc$ and $beamCalc$ (including an interaction term) into a multiple regression model to predict bite force ($comboModel$).

Another approach using museum skeletal material to predict bite force was taken by Thomason (1991) who estimated bite force in carnivores from measurements on photographs of skulls. His method uses the area of the opening in the skull formed by the zygomatic arch and the braincase in an effort to quantify the cross-sectional area of the jaw-closing muscles. This area coupled with input and output arms of the dentary should be an index of bite force. Although there may be differences, areas and landmarks needed to calculate this index are measurable in microchiropterans with the result that we include the Thoma-

son model for comparison with our models. Related to the Thomason model is our simplified $zygoWidth$ model. The idea behind this model is that large jaw muscles can affect the width of the skull and are correlated with bite force. Unlike the Thomason model, our $zygoWidth$ model makes no allowance for lever input and output arms.

Using Freeman's (1979, 1981a,b, 1984) research we could classify five insectivorous species in this study as having robust skulls (*Lasiurus borealis*, *Lasiurus cinereus*, *Molossus molossus*, *Molossus ater* and *Noctilio leporinus*). Six species are classified as having gracile skulls (*Corinorhinus townsendi*, *Molossus megalophylla*, *Noctilio macrotis*, *Noctilio femorasaccus*, *Eumops perotis* and *Tadarida brasiliensis*). The other species were either seen as intermediate in robustness or not studied in Freeman's earlier research. The relative bite force of the bats with robust and gracile skulls were compared with a t -test. Relative bite force was defined as the residual from the bite force to body mass regression for all species in the study.

We dissected jaw-closing muscles from skulls and weighed them on either an a Denver Instruments scale (model XE-50) or an O'Haus Scout II (in the field) with an accuracy of at least 0.01 g. To make sure of similar levels of hydration, we soaked all muscles in saline (0.9% NaCl) for 24 h before lightly blotting and weighing.

For area and landmark measurements for the Thomason (1991) index, we took photographs of the skulls in three orientations with a digital camera with a scale included in each for calibration. All measurements were taken from these digital images with ImageJ (Abramoff, Magelhaes & Ram, 2004).

All linear regressions to predict bite force from our predictor variables were run in R (R Development Core Team, 2009; using the lm function). We compared our regression model for body mass with bite force with those of Aguirre *et al.* (2002). We performed an ANCOVA analysis within R (R Development Core Team, 2009; using the lm function). A class variable, $Study$, was created and scored a 1 for our data from our study and 0 for results from Aguirre *et al.* (2002). We tested for a difference in the relationship of bite force and body mass by looking at the significance of the interaction term of $Study$ and $bodyMass$ (slopes of regression) and the $Study$ variable (intercepts).

Because these species share an evolutionary history, our data are not considered statistically independent (Felsenstein, 1985). We tested for the effects that phylogeny may impose by using BayesTraits (Pagel & Meade, 2007). We used a pruned version of the bat supertree produced by Jones *et al.* (2002) and Jones, Bininda-Emonds, & Gittleman (2005). We made only slight adjustments to this tree based on more recent information from Baker *et al.* (2003) and Hoofer *et al.* (2003). The importance of phylogenetic effects can be estimated by using the parameter, λ , and its likelihood that is calculated with BayesTraits.

Results

Using the relationship between $bodyMass$ and $biteForce$, we compared the regression models of our data to

Table 2. A comparison of results from regression analyses for models to predict bite force in bats

| Model | R^2 | AIC | δ |
|---------------|-------|--------|----------|
| comboModel | 0.94 | -56.3 | 0 |
| beamCalc | 0.91 | -44.18 | 12.12 |
| muscleCalc | 0.89 | -34.09 | 22.21 |
| muscleMass | 0.86 | -29.2 | 27.1 |
| skullMass | 0.88 | -27.7 | 28.6 |
| zygoWidth | 0.83 | -19.85 | 36.45 |
| ThomasonIndex | 0.80 | -14.49 | 51.6 |
| bodyMass | 0.75 | -5.49 | 50.81 |

All models are highly significant. Calculation of δ values is relative to comboModel. Order is based on small to large AIC values.

those of Aguirre *et al.* (2002); our regression slope = 1.169, intercept = -0.745; Aguirre slope = 1.083, intercept = -0.484. There was not a statistical difference in the slopes or intercepts from these regressions (interaction of Study \times bodyMass was not significant, $P < 0.5$; Study was not significant, $P < 0.9$).

We found it difficult to get some species to bite our sensor. This was a source of considerable frustration because of the problem of small samples sizes. The two-plate sensor used in Aguirre *et al.* (2003) and Santana & Dumont (2009) has been reported to have good success getting most bats to bite and resistant bats could easily be made to bite with some gentle stimulation. A more careful comparison of our two sensors (one plate vs. two plate) may reveal some behavioral differences in the willingness of bats to bite.

To find the most accurate method of predicting bite force, we used the AIC method to compare results (Table 2). All regressions are highly significant. However, some models are better than others. The best single-variable model of bite force was beamCalc ($R^2 = 0.91$; Figure 2b).

We combined beamCalc and muscleCalc in a multiple regression (with interaction term) called comboModel. All terms in comboModel [beamCalc ($P \ll 0.01$), muscleCalc ($P < 0.01$) and the interaction term ($P < 0.01$)] were highly significant with an R^2 of 0.94 (biteForce = $2.40 + 1.06$ beamCalc + 1.23 muscleCalc + 0.47 beamCalc \times muscleCalc; all variable are log transformed). The AIC value for this analysis was 12 lower than beamCalc and has the lowest AIC value of all the models (Table 2).

In testing for the impact of phylogeny on our three best models we found λ was not significantly different from 0 (meaning phylogeny has no effect) in beamCalc and combo-Model. For the muscleCalc model there was a phylogenetic effect ($P < 0.01$) but analysis within Bayes-Traits indicated that even when using the estimated optimum value of λ (0.80), there was a highly significant relationship between muscleCalc and bite force ($P < 0.01$).

A *t*-test of relative bite force and skull robustness found that the five species with robust skulls had relatively strong bites as compared with the six gracile species ($t = 6.62$, $P < 0.01$). The estimate of λ for these data was not significantly different from zero with the result that no phylogenetic adjustments were statistically required. For completeness

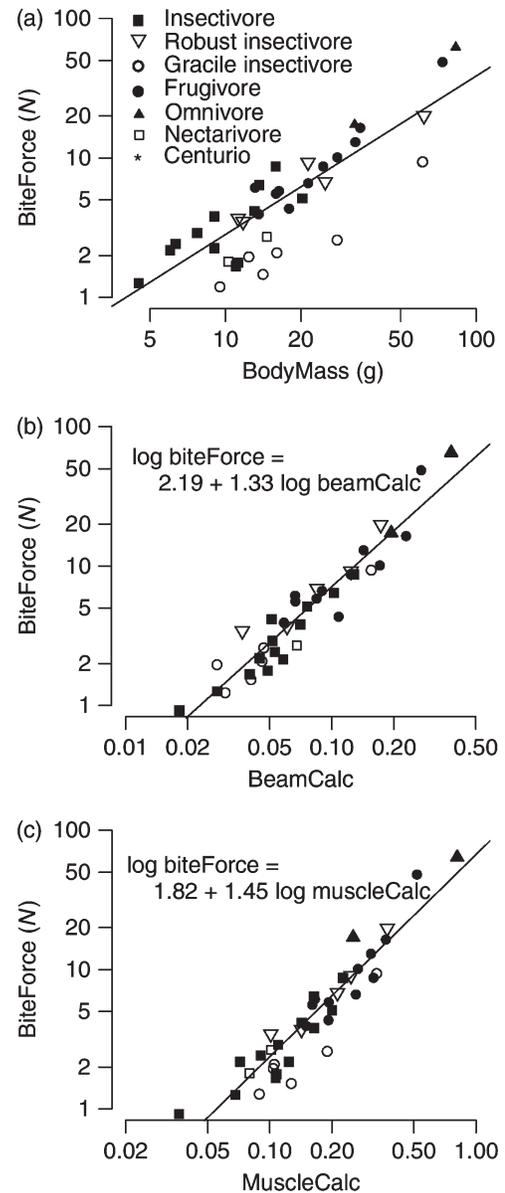


Figure 2. Actual bite force reconciled with different models derived from morphology of the lower jaw in bats. (a) Regression of bodyMass to biteForce (mean bite force) is based on bats listed in Table 1. Body mass (bodyMass; $R^2 = 0.75$) is not the best predictor of bite force compared with our other models; (b) a tight scattergram of beamCalc and biteForce with regression equation and line ($R^2 = 0.91$); (c) a tight scattergram of muscleCalc and biteForce with regression equation and line ($R^2 = 0.89$). However, the best index is comboModel derived from the addition of beamCalc and muscleCalc ($R^2 = 0.94$; Table 2).

we tested the significance of this relationship by using BayesTraits with the most likely λ (0.11) and found the correlation between bite force and skull robustness was still highly significant ($P < 0.01$).

Discussion

Several alternative models for predicting bite force are shown in Table 2. The best single-variable model is beam-

Calc, which is based on a beam theory approach. Initially it might seem surprising that this variable, that is not based on classic jaw mechanics, should be such a good predictor of bite force. However from a structural engineering point of view, this measurement makes a good deal of sense. It is taken at a point posterior to the last molar between the complex posterior portion of the dentary with the condyle (hinge), coronoid and angular processes (muscle attachments) and the anterior tooth-bearing portion. We think this point, where our plane of sectional modulus was taken, serves primarily as a structural linkage between the key functional elements of the jaw (Figure 1). Its size and shape would largely be a function of the need for strength alone and not an interaction with strength, muscle attachment or tooth bearing.

Our other results for single-variable models can be understood in light of the fact that the closer the models came to realistically modeling the mechanism of bite generation, the better they worked. The models based on head size (zygo-Width, muscleMass and skullMass) outperformed a model of overall size, bodyMass (Table 2). This is reasonable to us because size of head, the apparatus responsible for bite force, should be a better predictor of bite force than body size. Within the head size models the simple zygoWidth did not predict as well as muscleMass or skullMass. The muscleCalc model worked better than the either skullMass or muscleMass, which might be expected because muscleCalc takes into account the input and output arms of the jaw. The possible exception to this rule is the modest success of the Thomason model, which was clearly better than body size, but otherwise the worst predictor.

Our two-variable model, comboModel, is a clear winner over the next best model, beamCalc, with an AIC difference of 12. However on a practical note, the advantage of using beamCalc alone is that not only is it reasonably effective compared with the best model (beamCalc explains 91% of the variation in bite force while comboModel explains 94%) but also can be measured easily on a museum specimen or fossil. In comboModel the component, muscleCalc, requires dissecting fresh muscles. Further, although beamCalc and comboModel are free of phylogenetic effects, the muscleCalc model is influenced by phylogeny. We recommend the beamCalc model as the most practical method to predict bite force because it combines simplicity of measurement and predictive power. However if fresh material is available the comboModel would be preferred.

Freeman's (1979, 1981a,b) view of eco-morphological space was that bats exist on a continuum from robust bats with relatively strong biting species for their size that are eating hard-bodied insects, to gracile bats that have relatively weak bites and consume soft prey. Our results do not totally support this view of ecomorphology in insectivorous bats. She maintained that gracile forms such as *Corynorhinus*, *Tadarida*, *Nyctinomops*, *Eumops*, and *Mormoops* should be weak-biting bats (Freeman, 1979, 1981a,b). In Figure 2 we plotted the six gracile species as open circles. These bats are indeed weak biters for their body mass. She also predicted that *Molossus*, *Lasiurus* and *Noctilio*, would have powerful bites (they are plotted as open triangles

in Figure 2), but these bats have only average bite forces. Therefore we can verify Freeman's inference for gracile, weak-biting bats, but not for hard-biting species. However, several species that Freeman predicted should have strong bites have not yet been measured for bite force. Perhaps other species will yet fill the role of a hard-biting insectivorous bat. Further research will be needed to understand the relative importance of this robust-gracile axis in the adaptive radiation of bats as bite force information becomes available for a broader array of insectivorous bats.

Acknowledgments

We particularly thank our colleagues K. Geluso, M.J. Harner, K.N. Geluso, M. Bogan, and T. Mollhagen for help in the field and spirited discussions of natural history. For our work in Trinidad we are grateful to J. Rasweiler, III, S. (Patsy) Williams, R. Hernandez, H. Nelson, the Asa Wright Nature Center, and the William Beebe Tropical Research Station (Simla). David Boodoo and B. Ramoutar, expedited our permits in Trinidad, and A. Ramsey, in Tobago. Our colleague at UNL, S. Thomas, gave us important traveling, working and living tips at Simla. At Big Bend National Park, R. Skiles permitted our fieldwork and assisted in housing. Funding for Trinidad was obtained by Freeman from the Maude Hammond Fling Fellowship awarded by the Research Council, University of Nebraska- Lincoln and a Putney Award from the University of Nebraska State Museum. Funding from University of Nebraska-Kearney to K. Geluso helped support our trip to Tobago. Further, general support came from the Museum, and additional travel support to Big Bend came from the School of Natural Resources and the University of Nebraska Agricultural Research Division. This project was conducted in accordance with and approved by the Institutional Animal Care and Use Committee at UNL.

References

- Abramoff, M. D., Magelhaes, P. J., and Ram, S. J. (2004). Image Processing with ImageJ. *Biophotonics Int.* **11**, 36–42.
- Aguirre, L. F., Herrel, A., Van Damme, R., and Matthyssen, E. (2002). Ecomorphological analysis of trophic niche partitioning in a tropical savanna bat community. *Proc. Roy. Soc. Lond. Ser. B* **269**, 1271–1278.
- Aguirre, L. F., Herrel, A., Van Damme, R., and Matthyssen, E. (2003). The implications of food hardness for diet in bats. *Funct. Ecol.* **17**, 201–212.
- Anderson, R. A., McBrayer, L. D., and Herrel, A. (2008). Bite force in vertebrates: Opportunities and caveats for use of a nonpareil whole-animal performance measure. *Biol. J. Linn. Soc.* **93**, 709–720.
- Baker, R. J., Hooper, S. R., Porter, C. A., and Van Den Bussche, R. A. (2003). Diversification among New World leaf-nosed bats: An evolutionary hypothesis and classification inferred from digenomic congruence of DNA sequence. *Occas. Pap. Mus. Tex. Tech Univ.* **230**, i+1–32.

- Black, H. L. (1974). A north temperate bat community: Structure and prey populations. *J. Mammal.* **55**, 138–157.
- Burnham, K. P., and Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York: Springer-Verlag.
- Dumont, E. R. (1997). Cranial shape in fruit, nectar and exudate feeding mammals: Implications for interpreting the fossil record. *Am. J. Physiol. Anthropol.* **76**, 1127–1136.
- Dumont, E. R. (1999). The effect of food hardness on feeding behaviour in frugivorous bats (Phyllostomidae): An experiment study. *J. Zool. (Lond.)* **248**, 219–229.
- Dumont, E. R., and Herrel, A. (2003). The effects of gape angle and bite point on bite force in bats. *J. Exp. Biol.* **206**, 2117–2123.
- Dumont, E. R., and Nicolay, C. W. (2006). Cross-sectional geometry of the dentary in plant-visiting bats. *Zoology* **109**, 66–74.
- Felsenstein, J. (1985). Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* **39**, 783–791.
- Freeman, P. W. (1979). Specialized insectivory: Beetle-eating and moth-eating molossid bats. *J. Mammal.* **60**, 467–479.
- Freeman, P. W. (1981a). A multivariate study of the family Molossidae (Mammalia, Chiroptera): Morphology, ecology, evolution. *Fieldiana: Zool. (New Series)* **7**, vii–173.
- Freeman, P. W. (1981b). Correspondence of food habits and morphology in insectivorous bats. *J. Mammal.* **62**, 166–173.
- Freeman, P. W. (1984). Functional cranial analysis of large animalivorous bats (Microchiroptera). *Biol. J. Linn. Soc.* **21**, 387–408.
- Freeman, P. W. (1998). Form, function, and evolution in the skulls and teeth of bats. In Kunz, T. H., and Racey, P. A. (Eds), *Bat biology and conservation*: 140–156. Washington: Smithsonian Institution Press.
- Freeman, P. W. (2000). Macroevolution in Microchiroptera: Recoupling morphology and ecology with phylogeny. *Evol. Ecol. Res.* **2**, 317–335.
- Freeman, P. W., and Lemen, C. A. (2007a). An experimental approach to modeling strength of canine teeth. *J. Zool. (Lond.)* **271**, 162–169.
- Freeman, P. W., and Lemen, C. A. (2007b). Using scissors to quantify hardness of insects: Do bats select for size or hardness? *J. Zool. (Lond.)* **271**, 469–476.
- Freeman, P. W., and Lemen, C. A. (2008a). A simple morphological predictor of bite force in rodents. *J. Zool. (Lond.)* **275**, 418–422.
- Freeman, P. W., and Lemen, C. A. (2008b). Measuring bite force in small mammals with a piezo-resistive sensor. *J. Mammal.* **89**, 513–517.
- Gannon, W. L., and Rácz, G. R. (2006). Character displacement and ecomorphological analysis of two long-eared *Myotis* (*M. auricolus* and *M. evotis*). *J. Mammal.* **87**, 171–179.
- Herrel, A., De Smet, A., Aguirre, L. F., and Aerts, P. (2008). Morphological and mechanical determinants of bite force in bats: Do muscles matter? *J. Exp. Zool.* **211**, 86–91.
- Hoofer, S. R., Reeder, S. A., Hansen, E. W., and Van Den Bussche, R. A. (2003). Molecular phylogenetics and taxonomic review of noctilionoid and vespertilionoid bats (Chiroptera: Yangochiroptera). *J. Mammal.* **84**, 809–821.
- Hutchinson, G. E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *Amer. Nat.* **93**, 145–159.
- Jones, K. E., Bininda-Emonds, O. R. P., and Gittleman, J. L. (2005). Bats, clocks, and rocks: Diversification patterns of Chiroptera. *Evolution* **59**, 2243–2255.
- Jones, K. E., Purvis, A., MacLarnon, A., Bininda-Emonds, O. R. P., and Simmons, N. B. (2002). A phylogenetic supertree of the bats (Mammalia: Chiroptera). *Quart. Rev. Biol.* **77**, 223–259.
- LaVal, R. K., and Fitch, H. S. (1977). Structure, movements, and reproduction in three Costa Rican bat communities. *Occas. Pap. Mus. Nat. Hist. Univ. Kansas* **69**, 1–28.
- Meers, M. B. (2002). Maximum bite force and prey size of *Tyrannosaurus rex* and their relationships to the inference of feeding behavior. *Hist. Biol.* **16**, 1–12.
- O'Neill, M. G. and Taylor, R. J. (1989). Feeding ecology of Tasmanian bat assemblages. *Aust. J. Ecol.* **14**, 19–31.
- Pagel, M., and Meade, A. (2007). *Bayestraits, version 1.0 – Draft Manual*. Available at <http://www.evolution.rdg.ac.uk> (accessed May 2010).
- R Development Core Team (2009). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available at <http://www.R-project.org>
- Santana, S. E., and Dumont, E. R. (2009). Connecting behavior and performance: The evolution of biting behaviour and bite performance in bats. *J. Ecol. Biol.* **22**, 2131–2145.
- Santana, S. E., Dumont, E. R., and Davis, J. L. (2010). Mechanics of bite force production and its relationship to diet in bats. *Funct. Ecol.* **24**, 776–784.
- Thomason, J. J. (1991). Cranial strength in relation to estimated biting forces in some mammals. *Can. J. Zool.* **69**, 2326–2333.
- Valdez, E. W., and Bogan, M. A. (2009). Does variation in cranial morphology of *Myotis occultus* (Chiroptera: Vespertilionidae) reflect a greater reliance on certain prey types? *Acta Chiropterol.* **11**, 443–450.
- Van Valkenburgh, B., and Koepfli, K. (1993). Cranial and dental adaptations to predation in canids. In Dunstone, N., and Gorman, M. L. (Eds), *Mammals as predators, Symposia of the Zoological Society of London*, 65: 15–37. Oxford: Oxford Science Publications.
- Van Valkenburgh, B., and Ruff, C. B. (1987). Canine tooth strength and killing behaviour in large carnivores. *J. Zool. (Lond.)* **212**, 379–397.
- Wroe, S., McHenry, C., and Thomason, J. (2005). Bite club: Comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. *Proc. Roy. Soc. Lond. Ser. B* **272**, 619–625.