

## The effects of gape angle and bite point on bite force in bats

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### Summary

Models of mammalian mastication predict that bite force is affected by both the degree of mouth opening (gape angle) and the point along the tooth row at which force is transferred to a food item (bite point). Despite the widespread use of these models in comparative analyses, experimental data documenting bite force in non-human mammals are extremely limited. The goal of this study is to document variation in non-stimulated bite force associated with change in gape angle and bite point in a broad range of species. We focus on plant-visiting bats because they exhibit a relatively primitive cranial morphology and are good models for generalized mammals. Assessments of the relationship between gape angle and bite force within and among species

demonstrate that bite force decreases significantly as gape angle increases. The relationship between bite force and bite point within each of seven species demonstrates that unilateral molar biting universally generates the highest forces while the unilateral canine biting produces the lowest forces. Bilateral canine biting is intermediate. Beyond these general patterns, differences among species suggest that bite force reflects variation in craniofacial architecture. Finally, these data suggest that behavioral variation in gape angle and bite point may be important variables in comparative, functional analyses of feeding.

Key words: bat, bite force, gape, behavior, performance.

### Introduction

Models of the mammalian masticatory apparatus predict that bite force is affected by both the degree of mouth opening (gape angle) and the location along the tooth row at which force is transferred (bite point). Theoretical analyses of gape angle and empirical studies of muscle function suggest that there is a trade-off between mechanical advantage and gape (Herring and Herring, 1974; Lindauer et al., 1993; Turkawski and van Eijden, 2001). For generalized mammals, larger gape angles require muscles to stretch and are predicted to negatively impact the geometry of their mechanical advantage. Among more specialized taxa, alterations in the geometry of muscle insertions and internal architecture over evolutionary time have resulted in species that can produce high bite forces at high gape angles (carnivores) and other species that are well-suited to producing high bite forces at low gape angles (herbivores). With respect to bite point, models of the lower jaw as a simple class III lever or beam (e.g. Hylander, 1975; Radinsky, 1981; Weishampel, 1993) and constrained lever models that focus on protecting the temporomandibular joint from tensile loading (e.g. Greaves, 1978; Spencer, 1999) predict that bite forces increase at progressively posterior bite points. Constrained lever models further predict that bite forces level off and may decline posterior to an optimal bite point located at or near the first molar.

Despite the widespread use of these models and predictions in discussions of mammalian feeding (e.g. Carraway et al., 1996; Dumont, 1997; Emerson and Radinsky, 1980; Freeman, 1981; Kiltie, 1982; Perez-Barberia and Gordon, 1999; Reduker, 1983; Sicuro and Oliveira, 2002; Stafford and Szalay, 2000), there are surprisingly few experimental data documenting bite force in non-human mammals. Data summarizing maximum bite forces elicited using electrical stimulation are available for macaques, opossums, and rats (Dechow and Carlson, 1983; Robins, 1977; Thomason et al., 1989). Natural, non-stimulated bite forces have been recorded at single (or combined) bite points in possums, hyenas, ferrets and bats (Aguirre et al., 2002; Binder and Van Valkenburgh, 2000; Dessem and Druzinsky, 1992; Thomason et al., 1989). Variation in non-stimulated bite force has been reported only for galagos and macaques (Hylander, 1977, 1979), in which there is a positive relationship between bite force and increasingly posterior bite point.

Humans are the only mammals in which the combined effects of gape and bite point on non-stimulated bite force production have been studied in any detail. Even so, the integrated effects of bite point and gape angle on force production remain unclear (Spencer, 1999). Among experiments in which gape and bite point are altered

simultaneously, bite force is reported either to increase posteriorly (Mansour and Reynick, 1975; Oyen and Tsay, 1991) or to peak at the first molar and then decrease (Pruim et al., 1980). A similar inference was drawn by Spencer (1998), based on associations between muscle activity and bite point. One study reports that when gape angle is held constant, unilateral bite force increases from canine to second molar positions (van Eijden, 1991). In contrast, when bite point is held constant and gape is varied, there appears to be an optimum gape angle at which maximum forces are produced (Fields et al., 1986; Mackenna and Turker, 1983; Manns et al., 1979). The combination of varying results from human studies and lack of experimental data from non-human mammals leaves the relationship between gape angle, bite point and bite force unresolved. With this study, our goal is to document variation in non-stimulated bite force that is associated with changes in gape angle and bite point in a single group of mammals.

Bats are optimal subjects for evaluating the functional relationships among gape angle, bite point and bite force. While the skulls of bats are morphologically diverse, the masticatory apparatus is not so highly derived as to preclude them from being a good model for generalized mammals (e.g. Dumont, 1997; Freeman, 1981, 1988, 2000). Evidence from one species (*Pteropus giganteus*) demonstrates a pattern of muscle activity during mastication that is common to many mammals (De Gueldre and De Vree, 1988; Hylander et al., 2000; Langenbach and van Eijden, 2001). In addition, bats exhibit inter-specific variation in bite force (Aguirre et al., 2002), species-specific variation in preferred bite points during feeding (Dumont, 1999; Dumont and O'Neal, in press), and they eat foods that cover a wide range of size and hardness values (Dumont, 2003). The rapidly growing base of

information about the size and hardness of foods that bats eat facilitates *a priori* predictions about feeding performance, morphology and feeding behavior, making bats an excellent group in which to study mammalian feeding.

Here we use three separate data sets collected from plant-visiting bats to investigate the dual impacts of gape angle and bite point on bite force. To study the relationship between gape angle and bite force across species, we assembled data summarizing bite force and gape angle during bilateral canine biting for 11 bat species and tested the prediction that there is a significant negative association between gape angle and bite force across species. The relationship between gape angle and bite force within species was investigated using a second dataset containing bite forces measured at the same bite point but at increasing gape angles within each of four species. Finally, to test the prediction that bite force increases at progressively posterior bite points, we assembled a third data set documenting relative force during unilateral canine and molar biting in seven species in which gape angle increases only slightly from anterior to posterior bite points. During feeding, bats are known to use both unilateral and bilateral canine biting (Dumont, 1999; Dumont and O'Neal, in press). To evaluate the functional implications of symmetrical and asymmetrical canine loading, we also collected unilateral canine bite force for these same seven species.

### Materials and methods

Bite force data were collected from captive bats housed at the Lube Foundation (Gainesville, FL, USA) and from wild bats caught in the field (Dominican Republic) using mist nets. For details of species see Table 1. Animals housed at Lube were captured from their holding cages to measure bite forces,

Table 1. Sample size (N), gape angle during bilateral canine biting, head length, body mass and bite force for species used in the inter-specific analysis of gape angle and bite force

Species	N	Gape angle (degrees)	Head length (mm)	Body mass (g)	Bite force (N)
<i>Pteropus vampyrus</i> <sup>1</sup>	10	16.0	85.3±7.16	1166.6±175.95	84.7±23.44
<i>Pteropus poliocephalus</i> <sup>1</sup>	5	34.1	72.8±2.81	820.0±139.86	63.0±10.05
<i>Eidolon helvum</i> <sup>1</sup>	3	12.8	60.4±2.20	272.0±31.18	77.9±14.87
<i>Rousettus aegyptiacus</i> <sup>1</sup>	5	47.1	45.5±1.32	179.2±16.04	18.81±2.94
<i>Phyllostomus hastatus</i> <sup>1</sup>	9	24.6	35.5±2.15	72.4±5.98	24.9±5.07
<i>Cynopterus brachyotis</i> <sup>1</sup>	5	26.8	28.1±1.71	43.6±2.19	12.3±2.41
<i>Artibeus jamaicensis</i> <sup>1</sup>	5	11.2	28.0±1.41	45.0±9.58	19.2±6.37
<i>Erophylla sezekorni</i> <sup>2</sup>	6	38.3	24.7±1.06	16.9±1.02	2.8±0.96
<i>Monophyllus redmani</i> <sup>2</sup>	2	44.2	22.6±1.08	13.0±0	1.4±0.01
<i>Carollia perspicillata</i> <sup>1</sup>	10	42.3	22.2±0.87	18.4±2.07	4.4±1.06
<i>Glossophaga soricina</i> <sup>1</sup>	10	46.5	21.3±0.57	11.6±1.26	1.37±0.39

<sup>1</sup>Animals housed at the Lube Foundation, Gainesville, FL, USA.

<sup>2</sup>Animals sampled in the field (Dominican Republic, February, 2002).

Values are means ± s.d.

*Pteropus vampyrus* L.; *Pteropus poliocephalus* Temminck; *Eidolon helvum* Kerr; *Rousettus aegyptiacus* Geoffroy; *Phyllostomus hastatus* Pallas; *Cynopterus brachyotis* Müller; *Artibeus jamaicensis* Leach; *Erophylla sezekorni* Gundlach; *Monophyllus redmani* Leach; *Carollia perspicillata* L.; *Glossophaga soricina* Pallas.

and were returned after each trial. Field-caught bats were removed from mist nets and transferred to cloth bags. All animals were released the same evening at the site of their capture. Bite force data are not only relatively simple to collect, but they are non-invasive, necessitate minimal handling of the animals, and provide crucial measurements of *in vivo* bite force. All procedures for collecting bite force data were approved by the Institutional Animal Care and Use Committee (IACUC) at the University of Massachusetts, Amherst, USA.

Bite forces were measured using a piezzo electric force transducer (Kistler, type 9203, range  $\pm 500$  N; Amherst, NY, USA) attached to a handheld charge amplifier (Kistler, type 5995). The transducer is linear across its entire range. Coupled with the charge amplifier, it measures forces at the low end of the sensitivity range with an accuracy of 0.01 N, and at the high end of the sensitivity range with an accuracy of only 0.1 N. Thus the accuracy of the force readings is proportional to the magnitude of the forces. The transducer was mounted between two bite plates as described and illustrated in Herrel et al. (1999) and Aguirre et al. (2002). The distance between the bite plates was varied for different species to adjust gape angles. Using the known distance between the bite plates and the location of the bite point, we calculated gape angles for each species using digital pictures of dry skulls from museum collections. Given a distance between upper and lower teeth, gape angle was measured as the angle subtended by the lines connecting the temporomandibular joint to the tips of the upper and lower canines or first molars.

Bats were usually eager to bite the transducer, and were stimulated to bite by gentle taps at the side of mouth if needed. To protect the bats' teeth and to provide a non-skid surface, the tips of the bite plates were covered with a layer of cloth medical tape. At least five trials were recorded for each individual at each bite position and/or gape angle (note that a single trial can, and usually did, consist of multiple bites). The trial that produced the strongest bite appeared to be random, suggesting that the animals were not accommodating to the texture of the bite plates as the trials progressed. Animals were allowed to rest for at least 20 min between successive trials. The maximal bite force obtained during the trials was considered the maximal bite force for that individual. Many of the bites consisted of repeated 'clenching' of the bite plates between bats' teeth. However, it is important to point out that the bites in this study are most accurately described as defensive and may not reflect bite forces generated during unrestrained feeding. Average bite forces were calculated for each species. Immediately following the collection of bite force data, animals were measured (head length, width, height), weighed and released.

We evaluated the relationship between gape angle and bite force in two ways and with two separate data sets. First, we compared the forces generated during bilateral canine biting at different gape angles across 11 species of bats (Table 1). Because bite force scales with body size (Aguirre et al., 2002; Herrel et al., 2002, 2001, 1999, 1996), we regressed the maximal bite force for each species against a series of size

estimates [ $\ln(\text{body mass})$ ,  $(\text{body mass})^{2/3}$ , head length,  $(\text{head length})^2$ , head width, head height, head width $\times$ height,  $(\text{head volume})^{1/3}$ ] to identify the one with the greatest explanatory power. Head length explained the greatest proportion of the variation in bite force ( $r^2=0.902$ , compared to a maximum of  $r^2=0.855$  for a body mass variable) and residuals were extracted from a regression of bite force on head length. These residual (i.e. size-adjusted) bite forces were then regressed against gape angle using least-squares techniques (Sokal and Rohlf, 1995).

Second, we evaluated the effect of gape angle on bite force during bilateral canine biting for five individuals each of *Rousettus aegyptiacus*, *Cynopterus brachyotis*, *Artibeus jamaicensis* and *Pteropus poliocephalus*. For each species the bite plates were set at different distances, thus inducing variation in gape angle. The difference in angle between the lowest and highest gape positions ranged from 22° to 33°. The effect of species and bite point on bite force was investigated using a two-way, repeated-measures analysis of variance test (ANOVA) (Sokal and Rohlf, 1995).

To investigate the relationship between the point of application of bite force along the tooth row (bite point) and bite force, we assembled a third data set containing bite force measurements collected from three different bite points in seven bat species. The bite points included bilateral canine biting, unilateral canine biting and unilateral molar biting. These bite positions were chosen as they reflect the natural variation in bite points observed in unrestrained feeding trials in bats (Dumont, 1999, 2003; Dumont and O'Neal, in press). Data from these bite points allowed us to evaluate simultaneously the effects of anterior *versus* posterior bite placement and symmetrical and asymmetrical loading of the canines. To collect these data, the distance between the bite plates was set so that gape angle varied by less than 12° between canine and molar bite points and thus minimized potential gape effects. To control the effect of inter-specific variation in body size on absolute bite force, bite force within each species was expressed relative to its maximal bite force. A single classification ANOVA and *post-hoc* multiple-comparisons test was used to document differences in relative bite force between bite positions across species. All analyses were performed using SPSS™ (Version 10, Chicago, IL, USA).

## Results

Regression analysis demonstrates a significant negative relationship between gape angle and size-adjusted force across species (Fig. 1). Given the same bite point, bite force decreases as gape angle increases. Three species fall outside the 95% confidence intervals of the regression. *Eidolon helvum* has higher than expected bite forces for a given gape angle, while bite forces generated by *Pteropus vampyrus* and *Pteropus poliocephalus* are lower than predicted by the regression. The same negative relationship between gape angle and bite force is also true within species (Fig. 2). During bilateral canine

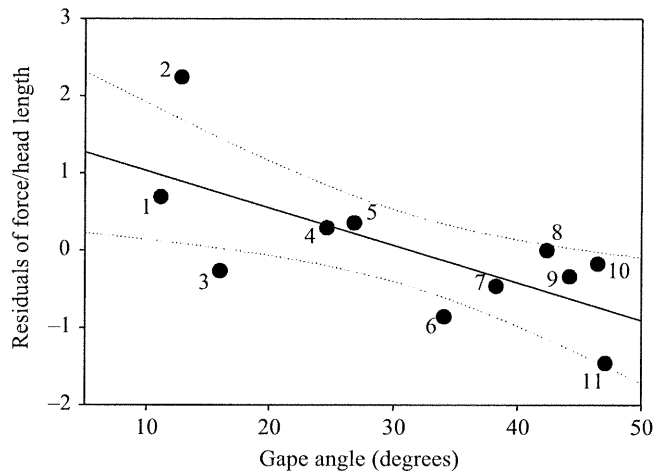


Fig. 1. Least-squares regression of size-adjusted bite force (residuals of maximum bite force against head length) against gape angle during bilateral canine biting (slope=-1.51,  $r^2=0.49$ ,  $P=0.017$ ). The dotted lines represent 95% confidence intervals. Each point represents a species mean: <sup>1</sup>*Artibeus jamaicensis*; <sup>2</sup>*Eidolon helvum*; <sup>3</sup>*Pteropus vampyrus*; <sup>4</sup>*Phyllostomus hastatus*; <sup>5</sup>*Cynopterus brachyotis*; <sup>6</sup>*Pteropus poliocephalus*; <sup>7</sup>*Erophylla sezekorni*; <sup>8</sup>*Carollia perspicillata*; <sup>9</sup>*Monophyllus redmani*; <sup>10</sup>*Glossophaga soricina*; <sup>11</sup>*Rousettus aegyptiacus*.

biting in each of four species, absolute bite force tends to decrease with increasing gape angle. The only exception is *Pteropus poliocephalus*, in which bite force is identical between medium and high gape angles. Nevertheless, a two-way repeated-measures ANOVA demonstrates that the trend toward decreasing bite force with increasing gape angle is significant ( $F_{(2,6)}=37.31$ ,  $P<0.001$ ). Species overlap broadly in bite force measures and the interaction between species and bite point is not significant ( $F_{(6,32)}=15.37$ ,  $P=0.19$ ).

All species exhibit a substantial increase in relative bite force as animals shift from unilateral canine biting to unilateral molar biting (Fig. 3). Molar biting consistently produces the

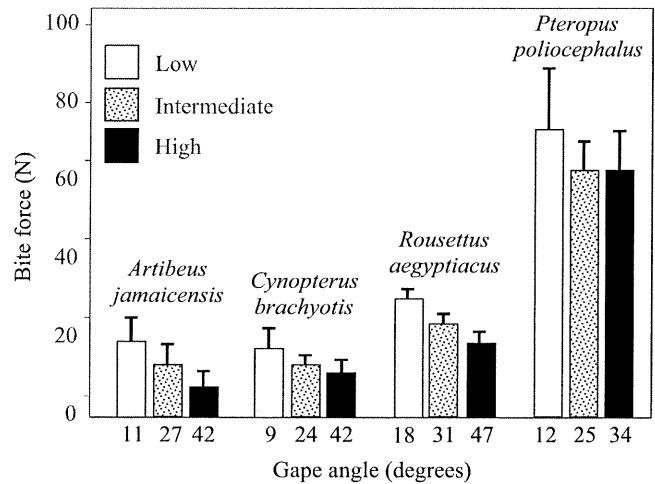


Fig. 2. Absolute bite force (means  $\pm$  S.D.) during bilateral canine biting at increasing gape angles in four species of bats. Species are arranged from left to right in order of increasing head length (Table 1). Gape angles are given below each bar.

highest bite forces while unilateral canine biting universally results in the lowest forces. *Pteropus poliocephalus* is unique in producing very similar forces during bilateral and unilateral canine biting. Across species, relative bite force differs significantly among the three bite positions ( $F_{(2,18)}=23.40$ ,  $P<0.001$ ) and between all pairs of bite positions (Tukey's HSD test,  $P<0.05$  in all comparisons). Untransformed bite forces and gape angles for these seven species are presented in Table 2.

### Discussion

The data presented here lend support to all models predicting that gape angle and bite point influence bite force. With respect to gape, there is a general pattern of decreasing bite force with increasing gape angle both within and between species. The significant, negative association between gape angle and bite

Table 2. Gape angles for canine and molar bites and absolute magnitude of bite forces during bilateral canine, unilateral canine and unilateral molar bite points in seven species

	N	Gape angle (degrees)		Bite force (N)		
		Canine	Molar	Bilateral canine	Unilateral canine	Unilateral molar
<i>Pteropus vampyrus</i> <sup>1</sup>	10	16	24	84.7 $\pm$ 23.44	52.4 $\pm$ 13.70	163.0 $\pm$ 34.26
<i>Pteropus poliocephalus</i> <sup>1</sup>	10	12	16	73.5 $\pm$ 15.34	70.7 $\pm$ 11.62	117.4 $\pm$ 18.15
<i>Eidolon helvum</i> <sup>1</sup>	3	13	17	77.9 $\pm$ 14.87	63.8 $\pm$ 13.81	92.2 $\pm$ 18.80
<i>Rousettus aegyptiacus</i> <sup>1</sup>	10	18	26	24.5 $\pm$ 3.97	19.7 $\pm$ 3.92	32.2 $\pm$ 7.66
<i>Phyllostomus hastatus</i> <sup>1</sup>	9	25	33	24.9 $\pm$ 5.07	20.4 $\pm$ 5.60	31.1 $\pm$ 6.76
<i>Erophylla sezekorni</i> <sup>2</sup>	6	38	50	2.8 $\pm$ 0.96	2.0 $\pm$ 0.70	3.0 $\pm$ 1.09
<i>Monophyllus redmani</i> <sup>2</sup>	2	44	53	1.4 $\pm$ 0.01	1.0 $\pm$ 0.26	2.1 $\pm$ 0.01

<sup>1</sup>Animals housed at the Lube Foundation, Gainesville, FL, USA.

<sup>2</sup>Animals sampled in the field (Dominican Republic, February, 2002).

Values are means  $\pm$  S.D.

Gape angle within species varies by a maximum of 12°.

force across bat species (Fig. 1), coupled with data from humans (Fields et al., 1986; Mackenna and Turker, 1983; Manns et al., 1979), suggests that this relationship is common among mammals with generalized cranial morphology. However, the presence of outliers and a relatively low coefficient of determination for the regression ( $r^2=0.49$ ) indicate that bite force is also affected by factors other than gape angle.

Variation among species in their motivation to bite the apparatus may explain some of the scatter in this regression. Although we could not discern clear interspecific differences in behavior, this potential source of variation cannot be ruled out and, indeed, must be accepted in exchange for voluntary (non-stimulated) bite force data. The fact that these species exhibit a wide variety of cranial shapes is another factor that may underlie the scatter in this regression. Although the bite forces used in this inter-specific regression are size-adjusted, they are not shape-adjusted. Among humans, subtle differences in absolute bite force production have been associated with variation in face shape (Proffit et al., 1983). The cranial morphology of bats is extremely diverse, even among plant-visiting species (Dumont, 1997; Freeman, 1988; Storch, 1968). It is likely that architectural details of the skull, including muscle size, muscle fiber orientation and bony morphology, contribute to variation in bite force. Based on skull anatomy alone it is not clear why *Eidolon helvum*, *Pteropus vampyrus* and *Pteropus poliocephalus* are outliers in this analysis. However, the anatomy of the masticatory musculature is unknown for these species and may have a critical influence on their ability to produce bite forces.

The influence of gape angle on bite force is underscored by intra-specific comparisons (Fig. 2), where again there is a significant trend toward decreased bite force with increasing gape angle. Among these species, *P. poliocephalus* is unique in exerting equal bite forces at medium and high gape angles. One possible explanation is that the change in gape angle between medium and high gape was less in *P. poliocephalus* than in other species ( $9^\circ$  versus  $15\text{--}16^\circ$ ). The smaller change in angle, and consequent lower gape angle during biting at a wide gape, may have moderated the effect of gape on bite force at the widest gape position. In addition, *P. poliocephalus* was the most aggressive species that we sampled and appeared to be highly motivated to bite.

Finally, the shape of the bony skull and dentary in *P. poliocephalus* differs substantially from that of *Artibeus jamaicensis*, *Cynopterus brachyotis*, and *Rousettus aegyptiacus*. Relative to these other species, *P. poliocephalus* may be optimized for strong biting at high gape angles. Additional data documenting muscle size and orientation, bite force and feeding behavior in this and other species of *Pteropus* are needed to fully investigate these alternatives.

With respect to unilateral canine versus molar biting, regardless of body size, maximum bite forces are produced during unilateral molar biting. Across species, forces produced during unilateral canine biting vary between 30% and roughly 70% of those produced during unilateral molar biting. The

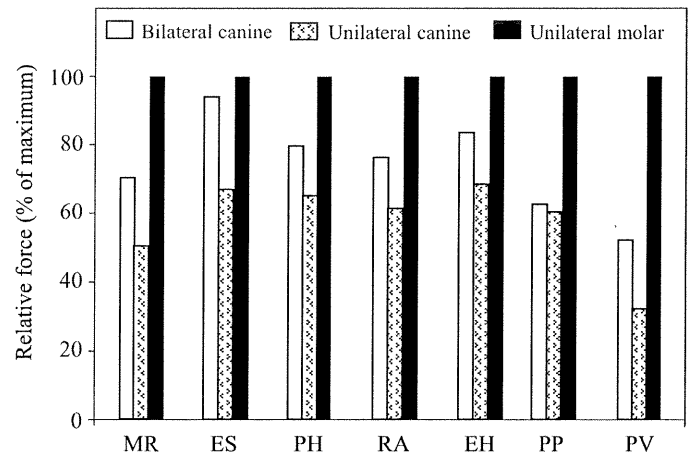


Fig. 3. The relationship between bite point and relative bite force (with respect to maximum bite force) within each of seven bat species. Bars represent species means. Species are arranged from left to right in order of increasing head length (Table 1). MR, *Monophyllus redmani*; ES, *Erophylla sezekorni*; PH, *Phyllostomus hastatus*; RA, *Rousettus aegyptiacus*; EH, *Eidolon helvum*; PP, *Pteropus poliocephalus*; PV, *Pteropus vampyrus*.

pattern of variation among species does not track differences in body size, dietary habits or family membership. Again we suggest that the relationship between interspecific variation in patterns of bite force production and variation in bony and muscular architecture deserves further investigation. Despite variation in the relative magnitude of unilateral canine bite forces, the overall pattern of higher bite force during unilateral molar biting accords well with the general prediction of both constrained and unconstrained lever models of the mammalian masticatory apparatus that bite force increases as bite point shifts posteriorly. Testing the detailed predictions of these models (i.e. that bite force increases incrementally or that it peaks near the first molar and then decreases or remains constant at second and third molar positions) can only be accomplished with bite force data from each tooth position within the post-canine tooth row.

The fact that forces generated during unilateral canine biting are almost universally lower than forces generated during bilateral canine biting suggests that there is a constraint on unilateral canine bite force production. There are at least two potentially limiting factors. First, the decreased forces produced during unilateral canine biting may be a means of protecting the canines from damage. During bilateral canine biting the force of biting is spread across the tips of all four canines. In contrast, the force of biting is concentrated on the tips of only two canines during unilateral canine biting. If equal forces were generated in both unilateral and bilateral canine biting, the canine teeth involved in unilateral biting would experience much higher concentrations of stress. In contrast to the canines of carnivorans, the canine teeth of bats are relatively long, thin and exhibit sharp crests along their length (Freeman, 1992). While this morphology may enhance the

ability of these teeth to initiate and propagate cracks in food items (Freeman, 1992), it is not well suited to resist breaking under high loads (Van Valkenburgh and Ruff, 1987). Given the shape of bat canine teeth and the concentration of forces on fewer teeth during unilateral biting, we suggest that sensory feedback from the canine alveoli may serve as a signal to decrease bite force during unilateral canine biting and thus protect these teeth from high stresses and potential damage. A detailed investigation of canine shape and relative bite force during unilateral and bilateral loading would be a reasonable first step toward testing this hypothesis.

A second factor that could serve to constrain force production during unilateral canine biting is the twisting of the face that would result from high unilateral forces applied near the front of the mouth. With respect to the skeleton of the lower face, unilateral loading during mastication (i.e. unilateral molar biting) in primates produces patterns of strain consistent with torsion (e.g. Ravosa et al., 2000; Ross, 2001; Ross and Hylander, 1996). By extension, unilateral canine biting is also likely to result in twisting of the facial skeleton. Relative to the molar teeth, the greater distance of the canine from the temporomandibular joint may even exaggerate twisting strains. All other things being equal, unilateral canine biting forces equal to those produced during bilateral canine biting could produce a much higher strain than that imposed by unilateral molar activity during mastication. Although safety factors in the facial skeleton appear to be quite high (Hylander and Johnson, 1997), it remains a possibility that bite forces (at all bite points) are modulated *via* proprioceptive feedback from regions of the facial skeleton experiencing strain. Strain analysis of the bat facial skeleton during feeding would constitute a first step toward evaluating this hypothesis. Interestingly, differences in unilateral and bilateral canine bite forces are not associated with gross variation in the morphology of the lower jaw. Although we sampled only one species with an unfused symphysis (*Phyllostomus hastatus*), the relative magnitudes of unilateral and bilateral bite forces do not appear to differ between this species and the others in the sample.

Variation in bite force production between symmetrical and asymmetrical loading is an interesting issue that has received very little attention. In contrast to the data reported here, the only other studies comparing unilateral and bilateral biting report that bite forces are equal during unilateral and bilateral molar biting in humans (Mansour and Reynick, 1975; van Eijden, 1991). Whether the same is true during unilateral and bilateral molar biting in bats and whether there are differences in bite force during unilateral and bilateral canine biting in humans is not known. We are currently designing modified bite plates to gather these data.

Overall, the data presented here constitute the most comprehensive assessment of variation in bite force available for mammals and support existing models of bite force production in species with generalized cranial morphology. Both bite point and gape angle significantly impact bite force. The interaction between these two variables has important implications for ecomorphological analyses of feeding in

mammals. From an ecomorphological perspective, bite force provides a measure of feeding performance because it circumscribes the range of food items that animals can use (Aguirre et al., 2002; Binder and Van Valkenburgh, 2000). Mammals use many different, species-specific combinations of bite points and gape angles during feeding (Dumont, 1999; Dumont, 2003; Dumont and O'Neal, in press; Van Valkenburgh, 1996). The data presented here suggest that it is important to account for behavioral variation if the goal is to make ecologically relevant functional comparisons among species. These data also highlight interspecific differences in bite force production that are likely to be associated with variation in the bony and muscular architecture of the masticatory system. The evolutionary relationships between bite force, feeding behavior and craniofacial morphology are intriguing avenues of research that have the potential to highlight patterns of adaptation and constraint in the evolution of feeding in mammals.

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## References

- Aguirre, L. F., Herrel, A., van Damme, R. and Matthyssen, E. (2002). Ecomorphological analysis of trophic niche partitioning in a tropical savannah bat community. *Proc. R. Soc. Lond. B* **269**, 1271-1278.
- Binder, W. J. and Van Valkenburgh, B. (2000). Development of bite strength and feeding behaviour in juvenile spotted hyenas (*Crocuta crocuta*). *J. Zool.* **252**, 273-283.
- Carraway, L. N., Verts, B. J., Jones, M. L. and Whitaker, J. O. (1996). A search for age-related changes in bite force and diet in shrews. *Amer. Midland Nat.* **135**, 231-240.
- De Gueldre, G. and De Vree, F. (1988). Quantitative electromyography of the masticatory muscles of *Pteropus giganteus* (Megachiroptera). *J. Morphol.* **196**, 73-106.
- Dechow, P. C. and Carlson, D. S. (1983). A method of bite force measurement in primates. *J. Biomech.* **16**, 797-802.
- Dessem, D. and Druzinsky, R. E. (1992). Jaw muscle activity in ferrets, *Mustela putorius furo*. *J. Morphol.* **213**, 275-286.
- Dumont, E. R. (1997). Cranial shape in fruit, nectar, and exudate feeders: Implications for interpreting the fossil record. *Am. J. Phys. Anthropol.* **102**, 187-202.
- Dumont, E. R. (1999). The effect of food hardness on feeding behaviour in frugivorous bats (Phyllostomidae): An experimental study. *J. Zool., Lond.* **248**, 219-229.
- Dumont, E. R. (2003). Bats and fruit: an ecomorphological approach. In *Bat Ecology* (ed. T. H. Kunz and M. B. Fenton), pp. 398-429. Chicago: University of Chicago Press.
- Dumont, E. R. and O'Neal, R. (in press). Food hardness and feeding behavior in Old World fruit bats. *J. Mammal.*
- Emerson, S. B. and Radinsky, L. B. (1980). Functional analysis of sabertooth cranial morphology. *Paleobiol.* **6**, 295-312.
- Fields, H. W., Proffitt, W. R., Case, J. C. and Vig, K. W. L. (1986). Variables affecting measurements of vertical occlusal force. *J. Dental Res.* **62**, 135-138.
- Freeman, P. W. (1981). Correspondence of food habits and morphology in insectivorous bats. *J. Mammal.* **62**, 166-173.
- Freeman, P. W. (1988). Frugivorous and animalivorous bats (Microchiroptera) – dental and cranial adaptations. *Biol. J. Linn. Soc.* **33**, 249-272.

- Freeman, P. W. (1992). Canine teeth of bats (Microchiroptera): size, shape and role in crack propagation. *Biol. J. Linn. Soc.* **45**, 97-115.
- Freeman, P. W. (2000). Macroevolution in microchiroptera: recoupling morphology and ecology with phylogeny. *Evol. Ecol. Res.* **2**, 317-335.
- Greaves, W. S. (1978). The jaw lever system in ungulates: A new model. *J. Zool., Lond.* **184**, 271-285.
- Herrel, A., De Grauw, E. and Lemos-Espinal, J. A. (2001). Head shape and bite performance in xenosaurid lizards. *J. Exp. Zool.* **290**, 101-107.
- Herrel, A., O'Reilly, J. C. and Richmond, A. M. (2002). Evolution of bite performance in turtles. *J. Evol. Biol.* **15**, 1083-1094.
- Herrel, A., Spithoven, L., Van Damme, R. and De Vree, F. (1999). Sexual dimorphism of head size in *Gallotia galloti*: Testing the niche divergence hypothesis by functional analyses. *Funct. Ecol.* **13**, 289-297.
- Herrel, A., Van Damme, R. and De Vree, F. (1996). Testing the niche divergence hypothesis by bite force analysis. *Neth. J. Zool.* **46**, 253-262.
- Herring, S. W. and Herring, S. E. (1974). The superficial masseter and gape in mammals. *Amer. Nat.* **108**, 561-576.
- Hylander, W. L. (1975). The human mandible: lever or link? *Am. J. Phys. Anthropol.* **43**, 227-242.
- Hylander, W. L. (1977). *In vivo* bone strain in the mandible of *Galago crassicaudatus*. *Am. J. Phys. Anthropol.* **46**, 309-326.
- Hylander, W. L. (1979). Mandibular function in *Galago crassicaudatus* and *Macaca fascicularis*: An *in vivo* approach to stress analysis of the mandible. *J. Morphol.* **159**, 253-296.
- Hylander, W. L. and Johnson, K. R. (1997). *In vivo* bone strain patterns in the zygomatic arch of macaques and the significance of these patterns for functional interpretations of craniofacial form. *Am. J. Phys. Anthropol.* **102**, 203-232.
- Hylander, W. L., Ravosa, M. J., Ross, C. F., Wall, C. E. and Johnson, K. R. (2000). Jaw-muscle recruitment patterns during mastication in anthropoids and prosimians. *Am. J. Phys. Anthropol.* **112**, 469-492.
- Kiltie, R. A. (1982). Bite force as a basis for niche differentiation between rain forest peccaries (*Tayassu tajacu* and *T. pecari*). *Biotropica* **14**, 188-195.
- Langenbach, G. E. J. and van Eijden, T. (2001). Mammalian feeding motor patterns. *Am. Zool.* **41**, 1338-1351.
- Lindauer, S. J., Gay, T. and Rendell, J. (1993). Effect of jaw opening on masticatory muscle EMG-force characteristics. *J. Dental Res.* **72**, 51-55.
- Mackenna, B. R. and Turker, K. S. (1983). Jaw separation and maximum incising force. *J. Pros. Dent.* **49**, 726-730.
- Manns, A., Miralles, R. and Palazzi, C. (1979). EMG, bite force, and elongation of masseter muscle under isometric voluntary contractions of the human masseter muscle. *J. Pros. Dent.* **42**, 674-682.
- Mansour, R. M. and Reynick, R. J. (1975). *In vivo* occlusal forces and moments: I, Forces measured in terminal hinge position and associated moments. *J. Dental Res.* **54**, 114-120.
- Oyen, O. J. and Tsay, T. P. (1991). A biomechanical analysis of craniofacial form and bite force. *Am. J. Orthodont. Dentofacial Orthoped.* **99**, 298-309.
- Perez-Barberia, F. J. and Gordon, J. J. (1999). The functional relationship between feeding type and jaw and cranial morphology in ungulates. *Oecologia* **118**, 157-165.
- Proffit, W. R., Fields, H. W. and Nixon, W. L. (1983). Occlusal forces in normal and long-face adults. *J. Dental Res.* **62**, 566-571.
- Pruim, G. J., De Jongh, H. J. and Ten Bosch, J. J. (1980). Forces acting on the mandible during bilateral static biting at different bite force levels. *J. Biomech.* **13**, 755-763.
- Radinsky, L. B. (1981). Evolution of skull shape in carnivores I. representative modern carnivores. *Biol. J. Linn. Soc.* **15**, 369-388.
- Ravosa, M. J., Johnson, K. R. and Hylander, W. L. (2000). Strain in the galago facial skull. *J. Morphol.* **245**, 51-66.
- Reduker, D. W. (1983). Functional analysis of the masticatory apparatus in two species of *Myotis*. *J. Mammal.* **64**, 277-286.
- Robins, M. W. (1977). Biting loads generated by the laboratory rat. *Arch. Oral Biol.* **22**, 43-47.
- Ross, C. F. (2001). *In vivo* function of the craniofacial haft: The interorbital 'pillar'. *Am. J. Phys. Anthropol.* **116**, 108-139.
- Ross, C. F. and Hylander, W. L. (1996). *In vivo* and *in vitro* bone strain in the owl monkey circumorbital region and the function of the postorbital septum. *Am. J. Phys. Anthropol.* **101**, 183-215.
- Sicuro, F. L. and Oliveira, L. F. B. (2002). Coexistence of peccaries and feral hogs in the Brazilian pantanal wetland: An ecomorphological view. *J. Mammal.* **83**, 207-217.
- Sokal, R. R. and Rohlf, F. J. (1995). *Biometry: The Principles and Practice of Statistics in Biological Research*: W. H. Freeman and Company.
- Spencer, M. A. (1998). Force production in the primate masticatory system: Electromyographic tests of biomechanical hypotheses. *J. Hum. Evol.* **34**, 25-54.
- Spencer, M. A. (1999). Constraints on masticatory system evolution in anthropoid primates. *Am. J. Phys. Anthropol.* **108**, 483-506.
- Stafford, B. J. and Szalay, F. S. (2000). Craniodental functional morphology and taxonomy of dermopterans. *J. Mammal.* **81**, 360-385.
- Storch, G. (1968). Funktionsmorphologische Untersuchungen an der Kaumuskelatur und an kerrelierten schadelstrukturen der chiropteren. *Abh. Senckenberg. Natur. Gesell.* **51**, 1-92.
- Thomason, J. J., Russell, A. P. and Morgeli, M. (1989). Forces of biting, body size, and masticatory muscle tension in the opossum *Didelphis virginiana*. *Can. J. Zool.* **68**, 318-324.
- Turkawski, S. J. J. and van Eijden, T. (2001). Mechanical properties of single motor units in the rabbit masseter muscle as a function of jaw position. *Exp. Brain Res.* **138**, 153-162.
- van Eijden, T. M. G. J. (1991). Three-dimensional analyses of human bite-force magnitude and moment. *Arch. Oral Biol.* **36**, 535-539.
- Van Valkenburgh, B. (1996). Feeding behavior in free-ranging large African carnivores. *J. Mammal.* **77**, 240-254.
- Van Valkenburgh, B. and Ruff, C. B. (1987). Canine tooth strength and killing behavior in large carnivores. *J. Zool., Lond.* **212**, 379-397.
- Weishampel, D. B. (1993). Beams and machines: modeling approaches to the analysis of skull form and function. In *The Skull: Functional and Evolutionary Mechanisms*, vol. 1 (ed. J. Hanken and B. K. Hall), pp. 303-344. Chicago: University of Chicago Press.