

Morphological and mechanical determinants of bite force in bats: do muscles matter?

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SUMMARY

Bats are one of the most diverse groups of mammals and have radiated into a wide variety of trophic niches. Accordingly, the cranial structure in bats is unusually variable among mammals and thought to reflect specializations for feeding and echolocation. However, recent analyses of cranial structure, feeding behavior and bite force across a wide range of bats suggest that correlations between morphology and performance and/or ecology are not as clearcut as previously thought. For example, most of the variation in bite force across a wide range of phyllostomid bats was explained by differences in body size rather than specific cranial traits. However, remarkably little is known about the muscular components that are responsible for generating the actual bite forces. We have tested which aspects of the cranial muscular system are good predictors of bite force across a wide range of species using a modeling approach. Model calculations of bite force show good correspondence with *in vivo* data suggesting that they can be used to estimate performance of the cranial system. Moreover, our data show that bite force is strikingly well explained by differences in temporalis muscle mass, temporalis fiber length and masseter muscle mass. Moreover, our data show that evolutionary changes in bite force capacity in bats are associated with evolutionary changes in relative m. temporalis mass and absolute skull length.

Key words: modeling, bite force, bats, muscle, mechanics.

INTRODUCTION

Bats are one of the most diverse groups of mammals (Kunz and Pierson, 1994; Huston, 1994; Simmons, 2005) including species that have specialized for eating fruits, insects, other vertebrates, nectar and even blood (Freeman, 2000). Accordingly, the cranial structure in bats is unusually variable among mammals and is thought to reflect specializations for feeding (Freeman, 2000; Van Cackenberghé et al., 2002) and echolocation (Pedersen, 2000). However, recent analyses of cranial structure, feeding behavior and bite force across a wide range of bats suggest that correlations between morphology and performance (i.e. bite force) and/or ecology are not as clearcut as previously thought (Aguirre et al., 2002; Van Cackenberghé et al., 2002; Dumont, 2004; Dumont and O'Neil, 2004). For example, most of the variation in bite force across a wide range of phyllostomid bats was explained by differences in body size rather than specific cranial traits (Aguirre et al., 2002). This suggests that the evolution towards high bite force capacity and dietary diversity has gone hand in hand with the evolution of large body size, or alternatively, that functionally relevant traits associated with the jaw musculature (rather than cranial shape *per se*) are the principal determinants of bite force capacity in bats.

Remarkably little is known about the muscular traits responsible for generating bite forces in bats. Despite very good descriptive work on the morphology of cranial muscles (McAllister, 1872; Wille, 1954; Storch, 1968; Czarnecki and Kallen, 1980) little attention has been devoted to the functionally relevant components of the cranial system and the jaw musculature such as muscle mass, muscle and fiber orientation, fiber length and physiological cross sectional area (but see De Gueldre and De Vree, 1990).

Consequently, it is currently not known how variation in cranial morphology in general, and muscle morphology in particular, is translated into differential bite performance across species. Moreover, the functional traits and jaw closer muscle groups determining bite force capacity in bats are currently unknown. In mammals in general, however, it has been shown that different muscle groups are important for animals that have to generate bite force at relatively small gape angles (e.g. ungulates) *versus* those that need high bite performance at large gapes (i.e. carnivores) (see Turnbull, 1970). More specifically, herbivores such as ruminants appear to invest most of their jaw muscle mass in the musculus masseter as this allows them to generate high bite forces at these low gape angles. Carnivores, on the other hand, have a relatively larger m. temporalis giving them a performance advantage at large gapes. In accordance, previous data for bats suggest that the m. temporalis complex is relatively larger in fruit eating bats such as *Pteropus* that eat large fruits than in species consuming smaller food items (De Gueldre and De Vree, 1990).

Given the importance of the m. temporalis in biting at large gape angles, and the fact that harder prey are also larger on average and *vice versa* (e.g. Aguirre et al., 2003), one would expect the evolution towards high bite force to be associated predominantly with an increase in the cross sectional area of the m. temporalis (Turnbull, 1970). Frugivores, however, might benefit from more powerful m. masseter, allowing them to extensively masticate their food and thus allow them to separate the indigestible fibrous matter from the nutritious juice (Dumont, 2003). Moreover, increased muscle size and force output may allow frugivorous bats to significantly reduce the time and energy spent processing their food or may allow them to incorporate harder fruits into the diet

(Dumont, 1999; Aguirre et al., 2003; Dumont, 2003; Dumont and O’Neil, 2004). As it can be assumed that high bite forces are especially beneficial for bats feeding on hard or large prey, species licking up nectar or blood should show a reduced jaw closer muscle mass.

Assuming that bite force is indeed ecologically relevant, selection could operate on different components of the jaw system. The force generating capacity of a muscle is determined by its cross sectional area which, in turn, is a function of the mass of the muscle, the length of the muscle fibers and the pennation angle. Additionally, the orientation and position of the muscle relative to the jaw joint will affect the moment arm of the muscle and thus also the bite force generated. Given the strong mass constraints for flying animals, one could expect that morphological changes in the system that allow increased force output without an increase in mass would be selected for. Additionally, the suggested trade-off between chewing rate and force generating capacity (i.e. a force–velocity trade-off) may also constrain the evolution of large jaw adductors. Thus we predict that the evolution of high bite force capacity should be associated with changes in the orientation of the muscles and a reduction in fiber length (associated with increased pennation) rather than with increases in the mass of the cranial muscles themselves. Selection for ingestion and biting of large food items, may alternatively constrain fiber length (large mandibular excursions may induce excessive stretch in the jaw adductors if fiber lengths are short, driving muscle to operate away from its plateau on the length–tension curve) (see Gans and De Vree, 1987) thus leading to a relative decrease in bite strength. Alternatively, increases in overall body size, which will result in a relatively rapid increase in bite forces because of the differential scaling of cross sectional area relative to cranial length, may be selected for as suggested previously (Aguirre et al., 2002).

We have tested which components of the jaw adductor system are the best predictors of bite force for a wide diversity of species. To do so, we use a static bite force model that is critically tested using *in vivo* bite force data of an independent sample of the same species (Aguirre et al., 2002; Dumont and Herrel, 2003). To evaluate the importance of body size on bite force capacity we assessed scaling relationships of morphological traits and bite force with cranial length.

MATERIALS AND METHODS

Specimens

Twenty four ethanol-preserved male individuals belonging to 16 species of bats were used in the analysis (Table 1). The majority of the specimens belonged to a single bat community from Northern Bolivia (see Aguirre, 2002). In addition, three old-world species (*Pteropus giganteus* Brünnich 1782; *Eidolon helvum* Kerr 1792; and *Plecotus auritus* Linnaeus 1758) were included in the analysis.

Morphology

Specimens were measured using digital calipers (forearm length and skull length; ±0.01 mm Mitutoyo CD-15B) and cranial muscles (m. masseter superficialis, m. masseter profundus, m. zygomaticomandibularis superficialis, m. zygomaticomandibularis profundus, m. temporalis superficialis, m. temporalis medius, m. temporalis profundus, m. temporalis pars suprazygomatica, m. pterygoideus and the m. digastricus; see Fig. 1A) were removed under a binocular microscope (M5 Wild, Wild Heerbrugg, Gais, Switzerland). Photographs were taken from all stages of the dissection in lateral and dorsal view. Muscles were removed on both sides and transferred to labeled vials containing a 70%

Table 1. Summary of the morphological data collected in this study

Species	N	Forearm length (mm)	Skull length (mm)	Dig. mass (mg)	Mass. mass (mg)	Temp. mass (mg)	Pt. mass (mg)	Dig. fiber length (mm)	Mass. fiber length (mm)	Temp. fiber length (mm)	Pt fiber length (mm)	Dig. PCSA (mm ²)	Mass. PCSA (mm ²)	Temp. PCSA (mm ²)	Pt. PCSA (mm ²)
<i>Artibeus jamaicensis</i>	2	62.98±1.74	28.49±0.17	33.86±0.41	57.66±5.03	382.59±9.26	47.99±13.74	14.13±2.99	5.03±0.15	6.15±1.35	3.08±1.11	2.43±0.49	4.91±0.67	38.37±9.58	12.41±0.01
<i>Desmodus rotundus</i>	5	59.54±1.54	23.05±0.73	19.32±2.29	20.08±6.23	192.22±56.21	17.81±9.40	8.74±1.24	3.81±0.86	5.80±0.33	2.42±0.12	2.25±0.44	2.62±0.74	20.78±8.209	7.46±3.790
<i>Eidolon helvum</i>	1	94.19	45.54	154.43	283.22	664.26	125.41	12.95	6.58	9.84	5.59	11.93	18.65	37.92	22.43
<i>Glossophaga soricina</i>	1	33.91	20.68	5.28	9.12	49.93	4.63	6.09	3.26	3.37	1.92	0.87	0.85	7.91	2.41
<i>Molossus molossus</i>	1	40.70	16.95	11.97	29.78	142.73	10.95	9.02	2.93	3.42	1.97	1.33	5.59	16.89	5.55
<i>Molossus rufus</i>	1	40.20	16.49	2.01	21.72	97.20	7.65	2.13	3.76	5.67	2.10	0.95	1.67	7.81	3.64
<i>Myotis nigricans</i>	1	40.02	14.39	7.32	16.11	74.17	5.00	6.06	3.14	4.23	1.38	1.21	2.75	8.15	4.10
<i>Myotis simus</i>	1	39.52	14.04	6.54	11.38	54.55	5.00	5.67	2.64	3.96	2.26	1.15	0.99	5.90	2.21
<i>Noctilio albigentris</i>	1	62.33	20.46	32.78	31.71	393.00	30.83	8.64	4.09	6.62	3.04	3.80	2.29	13.95	10.13
<i>Noctilio leporinus</i>	1	86.33	26.28	56.44	78.99	699.92	57.18	10.42	4.15	5.45	5.15	5.42	5.16	43.53	11.10
<i>Phyllostomus discolor</i>	1	61.07	28.09	38.64	69.56	456.41	36.71	9.94	6.31	7.71	5.46	3.89	2.69	42.32	6.72
<i>Phyllostomus elongatus</i>	1	60.31	29.17	21.74	56.02	253.20	28.08	10.14	3.67	4.79	2.54	2.14	10.47	29.39	11.06
<i>Phyllostomus hastatus</i>	1	80.62	34.74	76.25	146.76	809.92	25.07	11.76	4.48	5.66	3.10	6.48	14.01	102.49	8.10
<i>Plecotus auritus</i>	1	39.72	16.61	2.43	7.43	30.24	4.09	7.00	2.25	2.85	1.77	0.35	1.04	6.03	2.31
<i>Pteropus giganteus</i>	4	135.72±0.10	60.11±2.69	259.45±135.75	624.10±297.60	1143.99±548.70	245.66±113.46	15.49±3.84	7.12±1.61	7.45±1.29	4.34±0.82	16.69±5.28	34.90±6.46	63.56±24.89	56.357±12.48
<i>Sturmira litium</i>	1	42.12	22.15	17.91	41.68	216.06	21.83	7.44	3.61	4.87	2.62	2.41	2.41	28.19	8.32

Values are means ± s.d. For mass, fiber lengths and physiological cross sectional area (PCSA), the means for all bundles are represented. Dig. m. digastricus; Mass. m. masseter; Pt. m. pterygoideus; Temp. m. temporalis.

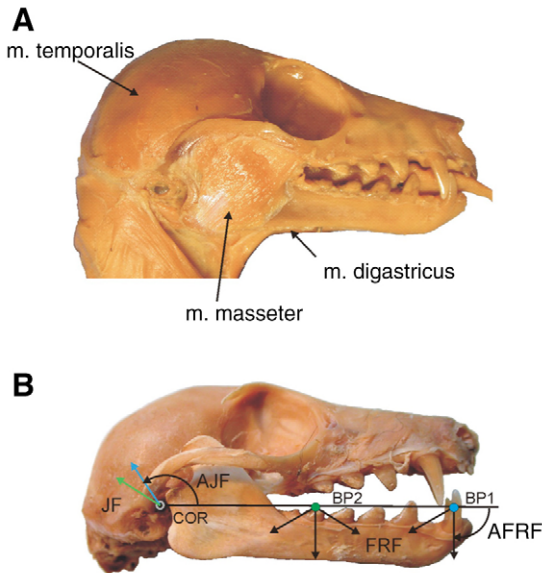


Fig. 1. (A) Photograph of the head of a *Pteropus giganteus* after removal of the skin. The two most important jaw closer groups are the m. temporalis and the m. masseter. The m. digastricus is the jaw opener. For a detailed account of the morphology of the jaw muscles see Storch (Storch, 1968). (B) Skull of the same *Pteropus giganteus* after removal of the jaw muscles. Indicated are the center of rotation (COR), the bite points (BP1 and BP2), and the angle of the food reaction forces (AFRF), which are all defined in the model. The food reaction forces (FRF), the joint forces, and the angle of the joint forces are the variables that are calculated by the model.

aqueous ethanol solution. Muscles were blotted dry and weighed to the nearest 0.01 mg using a microbalance (Mettler Toledo MT5; Mettler-Toledo, Inc., Columbus, OH, USA). Next, muscles were transferred to a 30% aqueous nitric acid solution and left for 20–24 h after which the solution was replaced by a 50% aqueous glycerin solution. Individual fibers were teased apart using blunt-tipped glass needles and 15 fibers were selected randomly and drawn using a binocular microscope with attached camera lucida (MT5 Wild). Drawings were scanned and fiber lengths determined using ImageJ V1.31 software.

Bite model

The model was identical to that previously described (Cleuren et al., 1995; Herrel et al., 1998a; Herrel et al., 1998b) and relies on the computation of the static force equilibrium. As input for the model, the three-dimensional coordinates of origin and insertion and the physiological cross sectional area of the jaw muscles are needed. Additionally, the three-dimensional coordinates of the point of application of the bite force and the center of rotation are needed (Fig. 1B). These were determined on lateral and dorsal pictures taken during the dissection. For muscle bundles with relatively broad areas of origin and insertion, the centroid of the insertion area was used. Physiological cross sectional areas were calculated based on the mass of the muscles, a density of 1.06 g cm^{-3} (Mendez and Keys, 1960), and the average fiber length for each muscle bundle. Since complex pennate muscles were separated into their component parts no correction for pennation was included. Cross sectional areas were scaled using a conservative muscle stress estimate of 25 N cm^{-1} (Herzog, 1994).

For comparative purposes simulations were run at a gape angle of 20 degrees and with all jaw closer muscles set maximally active for all individuals. Published electromyographic data suggest that all jaw closer muscles are indeed maximally or near maximally recruited during biting on hard or tough foods (Kallen and Gans, 1972; De Guedre and De Vree, 1988). Note, however, that maximal activation does not necessarily imply force generation. Bite forces were calculated for a range of orientations of the food reaction forces and at two different bite points (incisor and last molar). Since results were similar for the two bite points (note, however, that absolute forces differ for bites at different locations) (see also Dumont and Herrel, 2003) we report only those for a bite point at the incisor. Model output consists of the magnitude of the bite forces and joint forces and the orientation of the joint forces at any given orientation of the food reaction forces.

Analyses

For species where multiple individuals were available, species means were calculated for all morphological traits. For the morphological data, muscles from the different muscle complexes were grouped and means were calculated to improve statistical power. Thus, in our regression models the m. masseter superficialis, m. masseter profundus, m. zygomaticomandibularis superficialis, and the m. zygomaticomandibularis profundus were grouped; the m. temporalis superficialis, m. temporalis medius, m. temporalis profundus, m. temporalis pars suprazygomatica were grouped, and the lateral and medial m. pterygoideus were also grouped. Bite and joint forces were calculated based on individual input data, after which they were averaged to obtain a species mean. All data were \log_{10} -transformed before analyses. First, the scaling of all morphological and functional traits with cranial length was investigated using regression analyses. To test whether slopes differed from those predicted by geometric similarity models *t*-tests were used. Next, calculated bite forces were correlated with *in vivo* bite forces measured for the same species to test the accuracy of the model output where possible (15 out of 16 included in our analysis). Finally, stepwise multiple regression models were run with *in vivo* bite force as the dependent and all morphological traits as independent variables using both raw data and independent contrasts.

As species share their evolutionary history, they cannot be considered independent data points (Felsenstein, 1985; Harvey and Pagel, 1991). Independent contrasts were calculated for all traits using a tree obtained by pruning an existing super tree for bats (Jones et al., 2002) (see Fig. 2). All branch lengths were set to unity since no data are available on divergence times for all species included in the analysis [see Diaz Uriarte and Garland (Diaz Uriarte and Garland, 1998) for the validity of this procedure]. Contrasts were standardized by dividing by the square root of the sum of the branch lengths, and used as input for regression analyses forced through the origin (Garland et al., 1999). We did not use phylogenetically informed analyses to test scaling predictions as regression slopes through the origin represent the evolutionary covariation in traits rather than functional covariation.

RESULTS

Scaling

\log_{10} -transformed muscle masses and physiological cross sectional areas generally scale as predicted by geometric similarity models with slopes of three and two, respectively (Fig. 3). Only the mass of the m. temporalis shows significant negative allometry (Table 2). Fiber lengths either scale isometrically (m. digastricus and m.

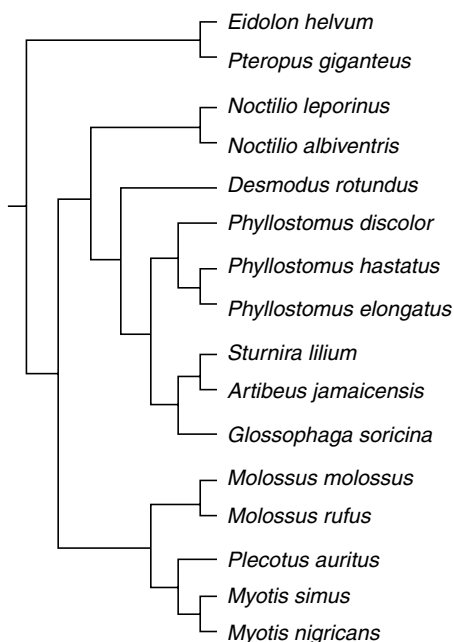


Fig. 2. Phylogenetic relationships between the species included in our analysis. Based on Jones et al. (Jones et al., 2002).

pterygoideus) or with slight negative allometry (m. masseter and m. temporalis). Thus, larger bats tend to have larger jaw muscles with absolutely longer fibers and greater cross sectional areas. Consequently, larger bats are expected to bite harder. Indeed, calculated bite forces scale with a slope not significantly different from the expected slope of two (Table 2). Similarly, temporomandibular joint forces increase across species with a slope not significantly different from the expected slope (Table 2).

Model versus *in vivo* bite forces

Calculated bite forces are a good predictor of *in vivo* bite force data collected for an independent sample of the same species ($r=0.87$; $P<0.01$). The slope of the regression between calculated and measured bite force data (Fig. 4) is not significantly different from

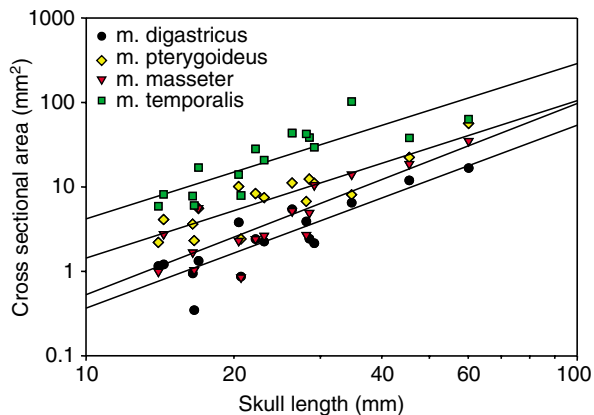


Fig. 3. Scaling of the physiological cross sectional area with cranial length for the different cranial muscles. Cross sectional area scales with a slope not significantly different from the expected slope of two for all muscles (see text for details).

Table 2. Scaling of morphological traits against cranial length across all species included in our analysis

	R	P	Slope	Intercept
Mass				
m. digastricus	0.89	0.47	3.02	-2.87
m. masseter	0.92	0.24	2.77	-2.20
m. temporalis	0.84	0.04	2.28	-0.80
m. pterygoideus	0.91	0.17	2.67	-2.37
Fiber length				
m. digastricus	0.73	0.49	0.85	-2.25
m. masseter	0.86	<0.01	0.69	-0.35
m. temporalis	0.72	0.01	0.59	-0.09
m. pterygoideus	0.77	0.13	0.79	-0.64
Physiological cross section				
m. digastricus	0.87	0.31	2.12	-2.60
m. masseter	0.85	0.24	2.27	-2.54
m. temporalis	0.84	0.31	1.84	-1.22
m. pterygoideus	0.88	0.31	1.87	-1.71
Bite force	0.75	0.24	1.71	-1.59
Joint force	0.78	0.15	1.63	-1.02

Slope values in bold type differ significantly from the slope predicted by geometric similarity models (1 for linear dimensions, 2 for areas and forces and 3 for mass).

1.0 (slope=1.25, $t=1.25$, $P=0.23$). Thus our model accurately predicts bite force capacity across a wide range of species with different morphologies and phylogenetic histories. The correlation is not merely a consequence of body size as a correlation between residual calculated bite force and residual *in vivo* bite force was highly significant ($r=0.67$; $P=0.006$).

Functional determinants of bite force

A multiple regression with calculated bite forces at bite point 1 (food reaction force orientation of 90°, gape angle of 20°) as dependent variable and all morphological traits as independents retained a significant model with skull length ($\beta=0.75$), residual m. temporalis mass ($\beta=0.62$), m. temporalis fiber length ($\beta=-0.21$) and m. masseter mass ($\beta=0.16$) as best predictors ($r^2=0.93$; $P<0.01$). When taking into account the phylogenetic relationships among species a significant model with the independent contrasts of residual m. temporalis mass ($\beta=0.89$), the contrasts of skull

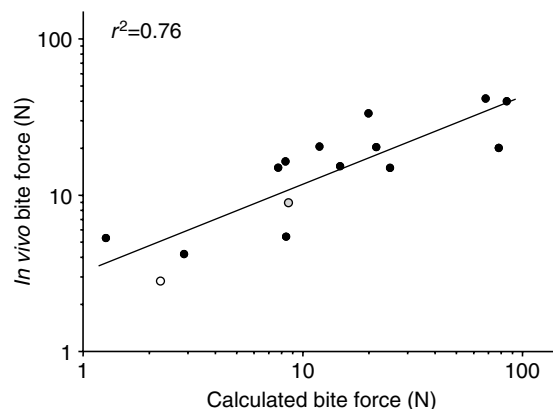


Fig. 4. Plot showing the correlation between calculated and *in vivo* bite forces. Both are strongly correlated ($r=0.87$; $P<0.01$) and the slope is not significantly different from one. Thus calculated bite forces are a good approximation of *in vivo* bite forces. The white circle represents *Glossophaga soricina*, a nectar eater and the gray one *Desmodus rotundus*, a blood-licking bat.

length ($\beta=0.63$) and the contrasts of m. temporalis fiber length ($\beta=-0.32$) is retained ($r^2=0.96$; $P<0.01$).

In vivo bite forces for the same set of species are best explained by residual m. temporalis mass and skull length. These results are identical when using traditional ($r^2=0.86$; $P<0.01$; skull length: $\beta=0.77$, temporalis mass: $\beta=0.51$) or phylogenetically informed ($r^2=0.90$; $P<0.01$; skull length: $\beta=0.94$, temporalis mass: $\beta=0.33$) analyses.

To test the role of muscle mass *versus* muscle fiber length in generating bite forces, we ran two regression models: one with only the residual muscle masses and a second one with both muscle masses and fiber lengths. Our first model explained 63% of the total variation in residual bite force; our second model explained an additional 13% of the variation in bite force in our data set.

DISCUSSION

Our static bite force model turns out to be a good predictor of *in vivo* bite forces despite all the assumptions and limitations involved. Although there is a slight tendency for the model to under predict bite forces in large animals, the two data sets are highly correlated and the slope is not different from one. Thus the underlying morphology of the musculoskeletal system appears to be a good predictor of *in vivo* performance. This allows the assessment of performance consequences of extreme morphological specializations in species that are not easily collected in the wild (e.g. *Musonycteris* with an extremely elongated rostrum or *Centurio* with a very short rostrum). Interestingly, our results suggest that, despite the wide variety of cranial shapes among the species included in our data set, the scaling of bite and joint forces does not differ from the predictions of geometric similarity models. Thus large animals load their skulls to similar degrees as smaller animals.

Although comparative data sets on scaling of functionally relevant muscle properties, such as physiological cross sectional area, moment arms and fiber lengths, are limited, the available data suggests that bats may be divergent from other vertebrates. In fish (Herrel et al., 2005), rodents (Druzinsky, 1993), primates (Anapol et al., in press) and humans (Weijs and Hillen, 1985) the physiological cross sectional area of the jaw muscles scales with strong positive allometry. In accordance, analyses of bite force scaling in different vertebrate groups also suggest strong positive allometry of the force generation capacity of the jaw system (e.g. Herrel et al., 2002; Herrel and O'Reilly, 2006). A comparison of the data presented here with those provided by Herrel and coworkers (Herrel et al., 2005) on the scaling of fish muscles suggests that the difference in scaling in muscle cross sectional area between the two groups is largely due to the strong positive allometry of muscle mass in fish. As an exception, the scaling relationships of physiological cross sectional area and muscle fiber length were similar in bats and strepsirrhine primates (Perry and Hartstone-Rose, 2007). Although this may suggest similar constraints on the cranial system in the two groups (maintenance of fiber length; constraints on cranial mass), it should be noted that the data for the strepsirrhines were scaled to body mass and may potentially be confounded by allometric changes in cranial length.

Interestingly, our interspecific analysis shows that across all species, overall cranial size, muscle masses and the fiber length of the m. temporalis are the best predictors of bite force as calculated by our model. Species with a larger cranium, a larger m. temporalis mass and shorter m. temporalis fiber lengths bite harder. Moreover, these results are identical when taking into account the phylogenetic relationships between species. Evolutionary changes

in bite force are thus associated with changes in cranial length, m. temporalis mass and m. temporalis fiber length. Given that fiber length may constrain the gape angles at which force can be optimally produced (Taylor and Vinyard, 2004), this suggests that animals that have evolved high bite forces may be restricted to eat relatively smaller prey. Our data do, however, suggest a discrepancy between analyses run with calculated *versus in vivo* bite forces, with m. temporalis fiber length no longer contributing to variation in bite force in the latter analysis. Although this may be a sample size issue, more data are needed for a wider range of species to test the relevance of this finding.

In summary, our data suggest an important role for cranial size and the m. temporalis muscle in the evolution towards increased bite performance in bats. Although our analyses suggest no constraint on mass as predicted *a priori*, scaling analyses suggest that mass constraints may operate for larger-bodied animals. Moreover, our data hint at a potential trade-off between increased bite performance and food size as m. temporalis fiber length is an important determinant of bite force in bats. Finally, the results of this study demonstrate the usefulness and applicability of simple mechanical models in testing morphology–performance relationships across species and suggest that such models may also be used to test hypotheses of cranial design variation associated with differences in feeding strategy in bats.

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