

Built to bite: cranial design and function in the wrinkle-faced bat

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Introduction

Phenotypic diversity is one of the most intriguing patterns in nature, and understanding why it exists and how it came to be has been a goal of philosophers and biologists since long before Darwin's time. Today, many fields share a fundamental interest in phenotypic diversity. Functional morphologists view anatomical phenotypes as physical frameworks that are animated by physiology and behavior to produce whole-organism performance. Anatomical structures circumscribe capabilities such as range of motion and the ability to generate force and velocity. Selection for performance in the face of ecological challenges can rapidly alter anatomical phenotypes within populations and is likely a driving force in the evolution of phenotypic diversity (e.g. Losos, Schoener & Spiller, 2004; Phillips & Shine, 2006; Herrel *et al.*, 2008b).

Extreme phenotypes are most likely to represent the outer limits of organismal design and, if coupled with narrow performance envelopes, can serve to highlight the basic design principles that may be obscured in more generalized

Abstract

One of the major goals of evolutionary biology is to explain phenotypic diversity and understand the limits imposed by those phenotypes. The cranial morphology of the wrinkle-faced bat *Centurio senex* (Family Phyllostomidae) is bizarre and enigmatic. Its extremely short and wide skull consistently emerges as an outlier in morphological studies and many researchers have speculated about its function. Here, we investigate the hypothesis that the unique skull morphology of *Centurio* is associated with the ability to generate high bite forces and/or high bite forces at wide gapes. We accomplish this by comparing bite force data gathered in the field and estimates of gape limitations gathered from museum specimens. We also examine the possibility that *Centurio* uses unique feeding behaviors that may impose unique loading regimes on the facial skeleton. We found that relative to head size, *Centurio* generates the strongest bites known for any fruit-eating phyllostomid bat, but that its ability to generate high bite forces at wide gape angles is likely limited. We also propose that its exceptionally strong bite indicates the ability to consume hard food items when other resources are limited, and that these 'resource bottlenecks' may have imposed strong selective pressure on its skull morphology. Behavioral data indicate that *Centurio* exhibits a unique reliance on unilateral biting (loading) during feeding. Based on data summarizing bite force, estimates of gape ability and feeding behavior, we suggest that *Centurio*'s exceptionally short and wide skull reflects adaptations for high bite forces and repeated unilateral loading of the facial skeleton during feeding.

forms (Adriaens & Herrel, 2008). Here, we explore the cranial morphology, feeding behavior and biting performance of an extreme mammal with the goal of understanding the ecological implications and potential origins of its unique phenotype.

The wrinkle-faced bat *Centurio senex* (Gray, 1842), exhibits one of the most derived cranial morphologies of any mammal. Its dramatically foreshortened skull and exceptionally wide facial skeleton routinely place it as an outlier among bats in surveys of cranial morphometrics (Freeman, 1988; Swartz, Freeman & Stockwell, 2003; Stevens, 2005). *Centurio*'s unusually naked face is decorated with flaps, folds and protuberances of skin (Fig. 1). The size of the chin lappet and associated secretory glands differs markedly between sexes, suggesting that sexual selection may be a factor driving its extraordinary facial features, but the size and shape of the underlying skull does not differ significantly between the sexes (Paradiso, 1967). Consequently, it seems more likely that the exceptional skull of *Centurio* reflects functional specializations for processing foods of certain sizes and/or textures.



Figure 1 Adult male (left) and female (right) *Centurio senex* (photo by A. H.).

Centurio senex is a monotypic and derived member of the highly frugivorous clade of New World leaf-nosed bats (Phyllostomidae: Stenodermatinae). Its geographic range is broad and extends from Mexico through Northern South America to Trinidad and Tobago (Snow, Jones & Webster, 1980). Capture records indicate that it is most often found in undisturbed forest and suggest that it migrates seasonally (Handley & Leigh, 1991; Fenton *et al.*, 1992; Estrada, Coates-Estrada & Meritt, 1993; Kalko, Handley & Handley, 1996; Medellín, Equihua & Amin, 2000; Schulze, Seavy & Whitacre, 2000; Stoner, 2001). Despite having been reported from many localities, it is an uncommon bat whose natural history is virtually unknown. The limited dietary records available for *Centurio* suggest that unlike most stenodermatines, it is an obligate frugivore (Goodwin & Greenhall, 1961; Gardner, 1977; Herrera, Fleming & Sternberg, 1998). Beyond this, there are anecdotal reports of the type of fruits included in *Centurio*'s diet.

Like many food items, fruits pose two opposing challenges during the physical process of feeding. First, the dimensions of many fruits eaten by stenodermatine bats require them to open their mouths widely to grasp and bite into them, as they often carry fruits in their mouths to feeding roosts in order to decrease their exposure to predators that congregate at fruiting trees (Kalko, Herre & Handley, 1996). A second challenge of frugivory is that fruits vary widely in hardness. While some are quite soft and easy to puncture, others are quite resistant and may require high bite forces to penetrate the skin and flesh (Dumont, 1999; Aguirre *et al.*, 2002; Dumont, 2003). Food hardness is known to be a limiting factor in the diets of insectivorous bats and may factor into the diets of frugivores as well (Aguirre *et al.*, 2002, 2003). Given the variation in the size and hardness of fruits, it is reasonable to suggest that both gape and bite force are important aspects of feeding performance for frugivorous bats.

Muscles generate maximum force when they are at the optimal length on their length–tension curve (Rome & Lindstedt, 1997; Burkholder & Lieber, 2001). The extent to which muscles can be stretched and still achieve maximum force production is affected by muscle fiber length and

orientation as well as by the spatial relationship between muscle attachments and the joint(s) that they affect. We know little about the length of muscle fibers in the masticatory muscles of bats. There are no published data on variation in muscle fiber orientation in the jaw adductors of bats, but dissections of 24 species by the two of us (A. H. and S. S.) suggest that variation among species is limited. Overall, there is no evidence of either extreme specialization in fiber lengths or orientations in the jaw adductors of bats.

Assuming that the jaw adductors of bats are near the peak of their length–tension curves at their resting lengths, muscle force is lost to muscle stretching during wide gapes. This loss in bite force is most likely to be compensated for by variation in the placement of the muscle relative to the temporomandibular joint. Such variations have been modeled with respect to the superficial masseter muscle (Herring & Herring, 1974). For this muscle, changes in the location of its origin and insertion relative to the joint may permit wide gapes before the muscle is stretched, and thereby optimize bite force production for wide gape angles. In this paper, we estimate and compare stretch factors for the superficial masseter muscle and present an analogous model for the temporalis muscle. Together, these muscles are the primary jaw adductors in bats (Storch, 1968; Herrel *et al.*, 2008a).

There are reasons to hypothesize that the skull of *Centurio* is specialized for both wide gape and generating high bite forces. Based on a broad morphological assessment of frugivory in bats, Freeman (1988) suggested that *Centurio* and its allies exhibit specializations for gripping fruit with their jaws. Specifically, *Centurio* has exceptionally short and wide jaws, and postcanine teeth that occlude virtually simultaneously to pierce fruits with an exaggerated labial rim of sharp shearing crests relative to less derived stenodermatines. In addition, *Centurio*'s short, broad face may serve to equalize lever to load arm ratios of the masticatory muscles and provide room for relatively large jaw adductors. Both simple class III levers and more complex constrained models of bite force production suggest that these traits would enhance *Centurio*'s ability to generate high bite forces relative to bats with less extreme facial morphology (Greaves, 1998; Spencer, 1999).

It has been difficult to study *Centurio* directly because it is a rare bat. In an attempt to find *Centurio* in southern Mexico, we worked at a field site where, unexpectedly, *Centurio* was the dominant species. Here we take advantage of this unprecedented opportunity to test the hypothesis that the highly derived skull of *Centurio* is specialized for generating high bite forces at high gape angles. We accomplish this by comparing bite force measured in the field from *Centurio* and other phyllostomid bats, and morphological estimates of muscle stretch factors (*sensu* Herring & Herring, 1974) based on museum specimens. We also investigate whether *Centurio* exhibits unique feeding behaviors relative to other stenodermatines. Recent analyses of feeding behavior in phyllostomids illustrate species-specific feeding behaviors that impose different loading regimes on the facial skeleton (Dumont, 1999, 2007; Dumont, Piccirillo & Grosse, 2005), and reconstructions of feeding behavior in

the ancestors of derived stenodermatines exhibited an increase in unilateral loading of the skull during feeding (Santana & Dumont, in press). If the form of the skull reflects adaptations to the forces that are routinely placed upon it, then unique feeding behaviors may be associated with unique cranial morphologies.

Materials and methods

Field sites

We studied *Centurio* in September 2005 at a field site in a disturbed semideciduous tropical forest near Laguna Silvituc in the South of the State of Campeche, Mexico. Bats were captured over a 1-week period using mist nets set at the ground level around a fruiting *Maclura tinctoria* (Rosales: Moraceae). This tree presented bright green, mulberry-shaped fruits at the axils of leaves on its terminal branches. We estimated that the tree provided a minimum of 1000 ripe fruits at once; fruit production appeared to be stable throughout the week. Nets were opened at dusk and checked at 10-min intervals for 2–3 h. All adult, non-pregnant and non-lactating bats that were captured in the nets were placed individually in cloth holding bags and transported to a base camp roughly 300 m from the netting site; other bats were released immediately. All procedures for capturing, handling, observing and measuring bats were approved by the Institutional Animal Care and Use Committee at the University of Massachusetts, Amherst.

Bite force

We measured bite force from individuals of *Centurio* using a piezoelectric force transducer (Kistler, type 9203, range ± 500 N; Amherst, NY, USA) attached to a handheld charge amplifier (Kistler, type 5995). The transducer was mounted between two bite plates as described in Herrel *et al.* (1999) and Aguirre *et al.* (2002). The tips of both upper and lower bite plates were covered with a layer of cloth medical tape to provide a non-skid surface and to protect the bats' teeth from direct contact with the metal plates. Bite force was measured during unilateral molar biting, a posterior bite position where maximum bite forces have been recorded (Dumont & Herrel, 2003). At least three trials were recorded for each location; animals were allowed 20 min of rest between each set of trials. We used each individual's maximum bite force to calculate the mean maximum bite force value for the species. Following the collection of bite force measurements, we recorded standard field data (body mass, forearm length) and measurements of head length, head width and head height. With the exception of individuals of *Centurio* that were held for behavioral observations, all bats were released at their capture site on the same evening. In all, we measured bite force and head size in 26 adult *Centurio* (means \pm standard deviations; maximum bite force = 10.9 ± 0.85 N, head length = 18.0 ± 0.92 mm, head width = 12.4 ± 1.10 mm, head height = 10.4 ± 0.65 mm).

To test the hypothesis that *Centurio* generates bite forces that are higher than expected for its size, we assembled published data on maximum bite force data from 21 additional phyllostomid species (Aguirre *et al.*, 2002; Dumont & Herrel, 2003, Santana & Dumont, in press) and used least-squares regression to determine whether head length, head width or head height was the best predictor of maximum bite force. We then inspected the residuals from the regression with the highest r^2 and the lowest AIC values to evaluate *Centurio*'s biting performance. All variables were transformed using natural logs before analysis.

Muscle stretch factors

It is impossible to determine the relationship between muscle stretch and force production from live, unanesthetized animals in the field. Therefore, we estimated the ability of animals to generate bite force at wide gapes using measurements of dry skulls from museum collections. Assuming equality in muscle fiber orientations and lengths, the extent to which opening the jaw stretches the superficial masseter, and decreases its ability to generate force, depends on the interplay between the origin–insertion ratio of the muscle and the angle formed between the origin and insertion points and the temporomandibular joint (Fig. 2; Herring & Herring, 1974). According to this model, the extent to which the jaws can be opened without stretching the superficial masseter increases as both the origin–insertion ratio and angle increase. However, high values in one of these variables can compensate for low values in the other, and the overall balance between them can be expressed in a calculated 'stretch factor' (Herring & Herring, 1974). Data summarizing physiological cross-sectional areas of masticatory muscles in bats demonstrate that the temporalis muscle contributes more to masticatory force than does the masseter muscle (Herrel *et al.*, 2008a). Therefore, we adapted the masseter stretch factor calculations for the temporalis muscle. We defined the muscle's origin as the distance from its posteriormost point in lateral view to the temporomandibular joint and its insertion as the distance from the joint to the tip of the coronoid process (Fig. 2). These lengths of these line segments and the dorsal angle between them were substituted into the calculations for the superficial masseter

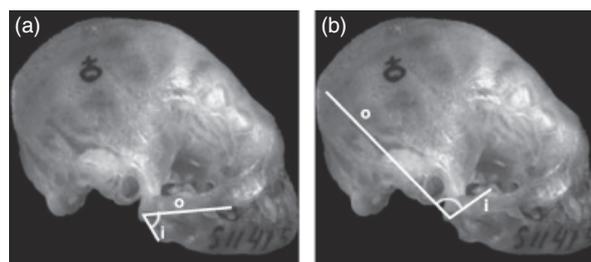


Figure 2 Linear distances and angles used in the calculation of superficial masseter (left) and temporalis (right) stretch factors. All measurements were taken from lateral photographs of articulated crania and dentaries. o, origin; i, insertion.

developed by Herring & Herring (1974). We calculated stretch factors for the masseter and temporalis muscles based on a wide gape angle of 60° for 16 species of phyllostomid bats (Table 1).

Feeding behavior

We studied *Centurio*'s feeding behavior to determine whether it differs significantly from that of other stenodermatines. First, we determined whether *Centurio*, like other stenodermatines (Dumont, 1999), uses different feeding behaviors when eating soft and hard fruits. Second, we compared the feeding behavior of *Centurio* and other stenodermatines when they were feeding on hard objects. We focused on hard-object feeding because it presents a physical challenge that elicits higher bite forces (loads to the facial skeleton) and sometimes different biting behaviors (loading regimes) than those used during soft-object feeding.

Seven individuals were retained after netting in order to observe their feeding behavior. Bats were filmed at night using a digital video camera (Sony TRV-900, New York, NY, USA) and low-level, white spotlight illumination. Bats were housed singly or in groups of up to three individuals in portable (40 cm³) cages. The back wall and ceiling of each cage was made from shade cloth (a loosely woven, screen-like plastic fabric), which allowed the bats to move around the cage easily and protected them from damaging their claws. Varnished plywood was used for cage floor for ease of daily cleaning. Two permanent side walls and a sliding front wall were made of plexiglass. These ensured that the bats

were visible from a wide range of vantages and that the insides of the cages were easily accessible. Similar procedures were used to collect the previously published behavioral data for the other stenodermatines included in this analysis (Dumont, 1999; Santana & Dumont, in press).

To evaluate the effect of food hardness on feeding behavior in *Centurio*, all individuals were offered ripe fruits of *M. tinctoria* (length = 18 ± 2.1 mm, width = 19 ± 2.6 mm, *n* = 10) and pieces of apple that were carved to mimic the size and shape of the native fruits, but differed significantly in puncture resistance [one-way analysis of variance (ANOVA), *P* < 0.001]. *Machura tinctoria* is a relatively soft fruit that can be punctured with 0.4 ± 0.10 N mm⁻² (*n* = 10), while apple is harder (1.1 ± 0.19 N mm⁻², *n* = 25). All individuals readily ate both *M. tinctoria* and apple, despite the fact that apple is not a normal part of *Centurio*'s diet and is absent from the field site and other ecosystems within its range.

Upon return from the field, approximately 16 h of video tape were reviewed at normal and slow speeds to document biting behavior. Observations were limited to the early stages of feeding, when the fruits were no less than one half of their initial size. Following previous studies (Dumont, 1999; Dumont & O'Neal, 2004), each biting event was placed in one of four descriptive categories based on which teeth were used to bite into the fruit: shallow unilateral bites, shallow bilateral bites, deep unilateral bites and deep bilateral bites. Shallow bites were centered on the canines whereas deep bites were centered on the postcanine teeth. We also carefully reviewed the taped feeding events to determine whether *Centurio* used pulling or tearing motions

Table 1 Sample sizes (*n*), means and standard deviations of superficial masseter and temporalis stretch factors

Subfamily and species	<i>n</i>	Temporalis stretch factor	Masseter stretch factor	Diet
Carollinae				
<i>Carollia perspicillata</i> ^a	9	1.12 ± 0.018	1.28 ± 0.023	Fruit + insects
<i>Rhinophylla pumilio</i>	6	1.12 ± 0.014	1.31 ± 0.042	Fruit + insects
Brachyphyllinae				
<i>Brachyphylla cavernarum</i>	5	1.15 ± 0.022	1.46 ± 0.048	Fruit + insects
Phyllonycterinae				
<i>Erophylla sezekorni</i> ^a	3	1.06 ± 0.022	1.36 ± 0.012	Nectar
Glossophaginae				
<i>Anoura geoffroyi</i>	10	1.08 ± 0.037	1.18 ± 0.065	Nectar
<i>Glossophaga soricina</i> ^a	9	1.06 ± 0.022	1.42 ± 0.044	Nectar
Phyllostominae				
<i>Macrotus waterhousii</i>	6	1.15 ± 0.020	1.43 ± 0.040	Insects
<i>Micronycteris megalotis</i>	4	1.09 ± 0.070	1.41 ± 0.043	Insects
<i>Vampyrum spectrum</i>	6	1.09 ± 0.045	1.22 ± 0.112	Insects + vertebrates
Stenodermatinae				
<i>Ariteus flavescens</i>	6	1.14 ± 0.022	1.28 ± 0.034	Fruit
<i>Artibeus jamaicensis</i> ^a	11	1.16 ± 0.033	1.30 ± 0.029	Fruit + insects
<i>Artibeus phaeotis</i> ^a	11	1.13 ± 0.015	1.31 ± 0.042	Fruit
<i>Centurio senex</i> ^a	9	1.14 ± 0.012	1.44 ± 0.086	Fruit
<i>Platyrrhinus helleri</i> ^a	5	1.12 ± 0.033	1.43 ± 0.042	Fruit + insects
<i>Pygoderma bilabiatum</i>	3	1.16 ± 0.027	1.22 ± 0.021	Fruit
<i>Sturnira lilium</i> ^a	15	1.11 ± 0.018	1.30 ± 0.061	Fruit + insects

^aMean maximum bite forces for these species are included in Fig. 3.

Dietary categories follow Wetterer *et al.* (2000) and Swanepoel & Genoways (1983).

during feeding that were different from those observed in other phyllostomids (Dumont, 1999).

For each bat species in our sample, we used a three-way ANOVA to investigate whether 'fruit type' (soft or hard) had a significant impact on 'bite type' (proportions of shallow unilateral, shallow bilateral, deep unilateral and deep bilateral bites). In the ANOVA model, 'fruit type' and 'bite type' were designated as fixed factors and 'individual' was defined as a random factor in order to include variation among individuals in the construction of error terms. For each species, the analysis was limited to the individuals for which we had feeding data for both types of fruit. The four 'bite types' were expressed as percentages for each individual and fruit. This made it impossible to test for the significance of 'fruit type' and, more importantly, to generate accurate error terms. Therefore, we arbitrarily deleted the shallow unilateral bite type category before analysis. Note that this did not affect the results of the ANOVA as information about this bite type was inevitably reflected in the values for the three remaining categories. An arcsine transformation was applied to the percentages representing each bite type before analysis (Sokal & Rohlf, 1995).

Results

The regression of ln maximum bite force against the three head size variables identified head height as the best predictor of bite force for this sample ($r^2_{\text{head height}} = 0.59$, $b = 2.46$, $P < 0.00$, $\text{AIC} = -29.69$; $r^2_{\text{head length}} = 0.29$, $b = 1.87$, $P = 0.009$, $\text{AIC} = -17.48$; $r^2_{\text{head width}} = 0.38$, $b = 1.87$, $P = 0.005$, $\text{AIC} = -19.72$). *Centurio* exhibited the highest positive residuals of any species of fruit-eating bat (Fig. 3). The scatterplot of calculated masseter and temporalis stretch factors illustrates that *Centurio* has relatively high values on both axes (Fig. 4). Overall, frugivores have the highest temporalis stretch factors and the nectarivores the lowest. This suggests that the gross anatomy of the masticatory system in frugivores favors high force production at low gape angles. In contrast, these data suggest that most insectivores and nectar feeders are capable of sustaining bite force at wider gape angles than can frugivores. This is not to say that bite force in nectar and insect feeders is highest at wider gapes, only that it is predicted to drop less precipitously than in frugivores as gape increases. There is no clear pattern of association between diet and superficial masseter stretch factors. The range of masseter stretch factor values spans from those reported for generalized mammals (~ 1.2) to those of dedicated herbivores (~ 1.7) (Herring & Herring, 1974). None of these bats exhibited the very low stretch factors characteristic of carnivores that are specialized to produce high bite forces at wide gapes.

With respect to biting behavior during feeding, *Centurio* broadly resembled other stenodermatines in that it used multiple bites to remove a mouthful of food, spent an extended period of time chewing the bolus, spat out a wad of relatively dry fiber and then repeated the process. Analyses of biting sequences revealed that *Centurio* used primarily deep unilateral bites during feeding on both soft and hard

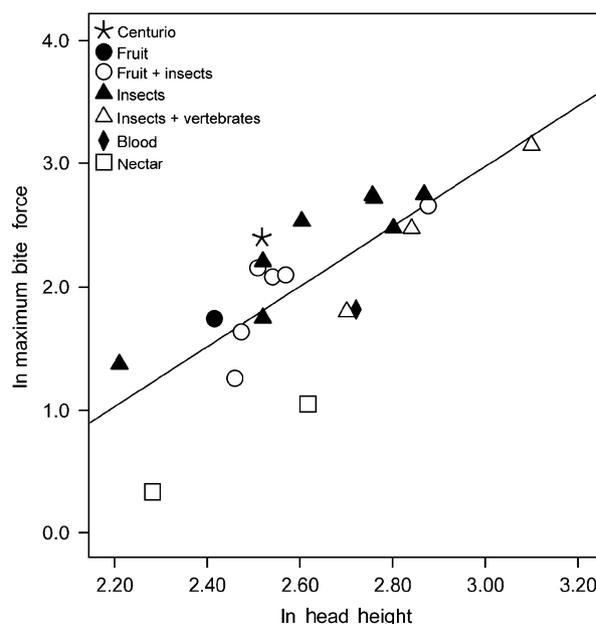


Figure 3 Regression of ln maximum unilateral molar bite force on ln head height ($b = 2.46$, $r^2 = 0.59$, $P < 0.001$). Symbols represent species means. Dietary classifications follow Wetterer *et al.* (2000). Bite force data represent a blood feeder *Desmodus rotundus*, a fruit feeder *Artibeus phaeotis*, fruit and insect feeders (*Artibeus jamaicensis*, *Carollia brevicauda*, *Carollia perspicillata*, *Platyrrhinus helleri*, *Sturnira lilium* and *Uroderma bilobatum*), insectivores (*Lophostoma brasiliense*, *Lophostoma silvicolum*, *Micronycteris hirsuta*, *Micronycteris minuta*, *Mimon crenulatum*, *Phyllostoma stenops*, *Phyllostoma elongatus* and *Tonatia saurophila*), species that eat insects and vertebrates (*Phyllostoma discolor*, *Phyllostoma hastatus* and *Trachops cirrhosus*) and nectar feeders (*Erophylla sezekorni* and *Glossophaga soricina*) (Aguirre *et al.*, 2002; Dumont & Herrel, 2003; Santana & Dumont, in press).

fruits (Table 2). Shallow unilateral bites were also common, especially when the bats were feeding on the soft *M. tinctoria* fruits. *Centurio* rarely used bilateral bites. The three-way ANOVA demonstrated that there was a significant shift in the proportions of bite types when *Centurio* ate soft and harder fruits (fruit type \times bite type interaction term, $F_{2,10} = 4.65$, $P = 0.037$). As food hardness increased, shallow unilateral canine bites were replaced with deep unilateral bites. Most other stenodermatines also exhibited significant changes in feeding behavior with increasing food hardness (Table 2). The exception was *Platyrrhinus helleri*, but this result should be viewed with caution as only two individuals were available for study.

During the final stage of removing a mouthful of fruit, *Centurio* commonly used a series of quick side-to-side head movements to detach the bolus. The frequencies of these movements did not differ significantly between soft- and hard-object feeding (paired *t*-test, $t = 1.44$, $P = 0.20$). Based on our observations of the videotaped feeding events, neither *P. helleri* nor *Uroderma bilobatum* exhibited discernible head movements during feeding. Previously, *Sturnira lilium* was the only other bat known to consistently use head

movements while securing a mouthful of food (Dumont, 1999). Unlike *Centurio*, *S. lilium* uses significantly more head movements when it feeds on hard fruit than when it feeds on soft fruit. In addition, the details of the movements used by the two bats differ substantially. *Centurio* typically grasps the fruit with its forelimbs and thumb claws, secures it with a unilateral bite and then uses a series of rapid prying motions to remove a bolus. *Sturnira lilium* uses a combination of pulling and tearing by gripping the fruit with a

bilateral bite and rocking the head from side to side (laterally) while pushing the fruit away with its wings and shoulders.

Discussion

Our goal was to investigate whether the exceptional shape of the skull in *Centurio* is associated with the ability to generate high bite forces and/or a high bite force at high gape angles. Relative to the size of its head, *Centurio* has the highest bite force of any fruit-eating bats sampled thus far and is clearly an outlier in this regard (Fig. 3). However, based on our gape estimates, *Centurio*'s ability to generate high bite forces does not appear to be coupled with the ability to do so at exceptionally wide gapes.

As a group, the bats sampled here exhibit elevated, herbivore-like values of masseter stretch factors (Fig. 4). Values that depart from 1.0 suggest that opening the mouth widely stretches the muscle beyond the length at which it can generate the maximum muscle force (Herring & Herring, 1974). Based on this variable, phyllostomid bats as a group, particularly *Centurio*, are best suited to producing high bite forces at low gapes. Our calculations of temporalis stretch factors are novel and broader comparative data for carnivores and herbivores are not available. Nevertheless, these values indicate that the location of temporalis origins and insertions in fruit-eating phyllostomids favor high bite force production at low gape angles as well. The emphasis on bite force at low gapes in fruit-eating phyllostomids fits well with what we know about how they process fruits. Many of these animals spend prolonged periods of time chewing relatively low-quality fruits at low gape angles to extract all of the available nutritive contents (Bonaccorso & Gush, 1987; Dumont, 1999).

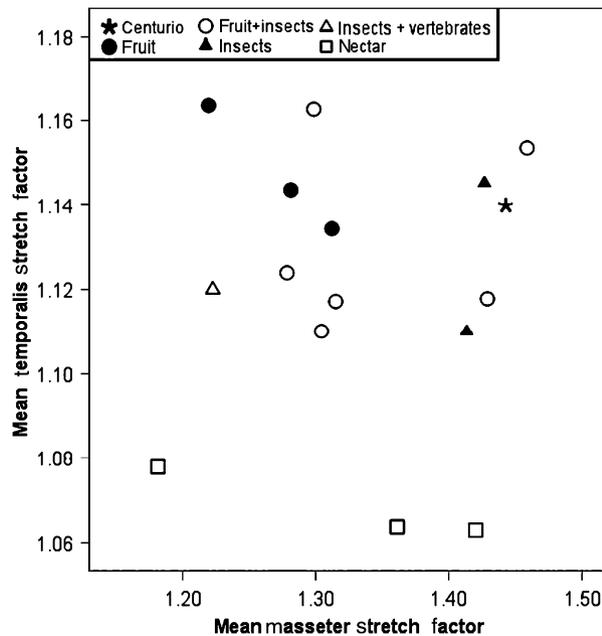


Figure 4 Scatterplot of mean masseter and temporalis stretch factors at a 60° gape angle. High values suggest that muscles are more stretched. Symbols represent species means.

Table 2 Biting behavior during soft- and hard-object feeding

Species	Fruit texture	<i>n</i>	Bite sequences	Shallow bilateral	Shallow unilateral	Deep bilateral	Deep unilateral	<i>P</i>
<i>Artibeus jamaicensis</i> ^a	Hard	7	264	1.01 ± 0.56	11.13 ± 2.53	11.27 ± 3.56	76.57 ± 4.64	< 0.001
	Soft	9	282	14.33 ± 4.89	18.99 ± 7.48	40.31 ± 10.69	26.37 ± 8.17	
<i>Artibeus phaeotis</i> ^a	Hard	3	156	7.53 ± 2.36	19.76 ± 6.27	8.37 ± 3.42	64.33 ± 5.51	0.033
	Soft	2	55	25.65 ± 22.35	17.00 ± 3.00	33.65 ± 0.35	23.65 ± 19.65	
<i>Centurio senex</i>	Hard	7	170	2.10 ± 0.99	12.57 ± 4.73	7.70 ± 2.59	77.64 ± 3.06	0.008
	Soft	7	185	5.54 ± 2.36	37.11 ± 7.75	4.69 ± 1.26	52.64 ± 8.96	
<i>Platyrrhinus helleri</i>	Hard	2	35	0.00–32.5	0.00–1.60	14.30–14.30	51.60–85.70	0.657
	Soft	2	18	0.00–50.00	0.00–0.00	16.70–50.00	0.00–83.30	
<i>Sturnira lilium</i> ^a	Hard	3	75	14.00 ± 5.29	6.00 ± 3.05	62.67 ± 5.33	17.33 ± 4.81	0.038
	Soft	3	61	44.07 ± 8.12	16.67 ± 12.74	39.27 ± 18.41	0.00 ± 0.00	
<i>Uroderma bilobatum</i>	Hard	4	102	14.82 ± 8.17	2.50 ± 2.50	1.80 ± 0.92	80.92 ± 9.30	0.014
	Soft	3	22	26.50 ± 13.76	10.70 ± 5.36	27.37 ± 20.16	35.47 ± 7.84	

^aDumont (1999).

Columns report species, number of sampled individuals (*n*), total number of bite sequences analyzed, means and standard deviations of percentages of the four bite types (shallow bilateral, shallow unilateral, deep bilateral and deep unilateral) and the probability that biting behaviors differ significantly between soft- and hard-object feeding within each species (*P*; 'food type × bite type' interaction from three-way ANOVA). Ranges rather than means and standard deviations are reported for *Platyrrhinus helleri*.

Our proposition that *Centurio* generates high bite forces but not at high gape angles is consistent with what we know of its diet. The few existing reports speculate that *Centurio* feeds on soft, mushy fruits or ripe, juicy fruits from which these bats suck the juices (Goodwin & Greenhall, 1961; Snow, Jones & Webster, 1980; Emmons & Freer, 1997; Reid, 1997; Nowak, 1999). Only two link *Centurio* with a specific food, one of them known only by the common name azulillo (Ramirez-Pulido & Lopez-Forment, 1979), and the other being *Guettarda foliacea* (Family Rubiaceae; Gianini & Kalko, 2004). The size and consistency of these fruits is unknown. We captured *Centurio* as it approached a large *M. tinctoria* that was producing large quantities of soft (Vargas-Contreras *et al.*, 2009), juicy fruits that were eaten by *Centurio* and other stenodermatines, lending additional circumstantial evidence to the claim that it is primarily a soft-fruit feeder.

Centurio's wide jaws and postcanine teeth with sharp labial shearing crests that occlude virtually simultaneously are well suited for grasping fruits (Freeman, 1988). If those fruits are soft, then even low bite forces at wide gape angles may be sufficient to accomplish this task. However, given *Centurio*'s ability to produce a very strong bite, we predict that it feeds on relatively hard food items that require a strong bite either seasonally or over a limited part of its range. These foods could have had a profound influence on the evolution of *Centurio*'s extreme craniofacial morphology if they represent what was (and perhaps is) available during resource 'bottlenecks'. Two stenodermatine bats, *Chiroderma doriae* and *Chiroderma villosum*, were identified recently as seed predators (Nogueira & Peracchi, 2003; Nogueira *et al.*, 2005). We saw no evidence that *Centurio* damaged the 1–2 mm seeds of *M. tinctoria* during our feeding trials, but this does not preclude the possibility that *Centurio* can break apart seeds. We predict that the hard food items in *Centurio*'s diet are either fruits or seeds that are consumed either seasonally or in certain localities along its migratory path.

Like most stenodermatines, *Centurio* exhibits a significant shift in its biting behavior when it is confronted with hard food items (Table 2). However, from a broader evolutionary perspective, this behavioral plasticity is reduced in *Centurio*, *U. bilobatum* and *P. helleri* (Santana & Dumont, in press). Of these three species, the feeding behavior of *Centurio* is unique in that it relies heavily on unilateral biting during both hard- and soft-object feeding. This may capitalize on the well-developed shearing surfaces along the labial rim of the upper molars, premolars and canines that are characteristic of derived stenodermatines (Freeman, 1988; Freeman, 1992).

This study illustrates that *Centurio*'s extreme morphology is associated with a greater than expected bite force and distinctive feeding behaviors. In comparison with its close relatives, *Centurio* has a strong bite relative to its head size, emphasizes unilateral biting and uses a unique prying movement of the head when acquiring a mouthful of food. *Centurio* is also likely exposed to unilateral loading significantly more frequently than are the faces of other bats. We further suggest that *Centurio*'s exceptionally short and wide

skull reflects adaptations for withstanding this loading regime. Testing this hypothesis will require additional investigation into the mechanical link between loading and skull form in a broad range of taxa with known loading behaviors and bite forces.

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