

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

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Abstract

The explanation of phenotypic variety and the restrictions imposed by these traits are two key aims of evolutionary biology. *Centurio senex* (Family Phyllostomidae) has a strange and intriguing skull shape. In morphological studies, its very small and broad cranium is a constant outlier, and many scientists have theorized about its purpose. *Centurio*'s distinctive skull shape has been linked to its capacity to produce high bite forces and/or high bite forces at broad gapes. In this study, we test this notion. This is accomplished by comparing field biting force measurements with museum specimen estimations of gape restrictions. It is also possible that *Centurio* feeds in a way that places a unique stress regime onto its face, which we will investigate more in this study. *Centurio* has the strongest bites ever recorded among fruit-eating phyllostomid bats, although its capacity to produce high bite pressures at broad gape angles is likely limited by its small head. We further hypothesize that its powerful bite shows its capacity to eat hard food items when other resources are few, and that these 'resource bottlenecks' may have put substantial selection pressure on its skull shape. Observations of *Centurio*'s eating behavior show that he relies on unilateral biting (loading) in an unusual way. We hypothesize that *Centurio*'s unusually small and broad skull is an adaptation to strong biting pressures and repetitive unilateral loading of the facial bones during feeding.

Keywords

evolution; chiroptera morphology;
feeding behavior; biting force

Introduction

Nature's phenotypic variety has fascinated philosophers and biologists since far before Darwin's time, and understanding why and how it came to be has long been a priority of both. Phenotypic variety has become a fundamental

concern in a wide range of areas nowadays. Physiology and behavior are the driving forces behind an organism's overall performance, according to functional morphologists, who consider anatomical phenotypes as physical frameworks. The range of motion and the capacity to create force and velocity are all constrained by anatomical structures.

It is probable that selection for performance in the face of ecological constraints is driving the evolution of phenotypic

variety by quickly altering anatomical phenotypes within populations (e.g. Losos, Schoener & Spiller, 2004; Phillips & Shine, 2006; Herrel et al., 2008b). Although they are more likely to represent the outer reaches of organismal design, extreme phenotypes may help to bring to light fundamental design principles that may be hidden in more generic forms if they are combined with limited performance envelopes (Adriaens & Herrel, 2008). Here, we examine the skull morphology, eating habits, and biting abilities of an extreme animal in order to better understand the ecological ramifications and possible origins of this phenotypic. When it comes to cranial structure, the wrinkle-faced bat, *Centurio senex* (Gray, 1842), is up there with the best. In studies of cranial morphometrics, its outlier status among bats is often attributed to its unusually foreshortened skull and very broad facial skeleton (Freeman, 1988; Swartz, Freeman & Stockwell, 2003; Stevens, 2005). When it comes to *Centurio*'s appearance, there is a lot of flesh protruding from his face (Fig. 1). However, there is no discernible difference in size or form between sexes in terms of the underlying skull's size and shape, which suggests that sexual selection may be a driving force behind these unusual facial traits (Paradiso, 1967). *Centurio*'s unique cranium, on the other hand, is more likely to be a result of functional adaptations for digesting meals of certain sizes and textures. The

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

Bats of the *Centurio senex* branch of New World leaf-nosed bats are extremely frugivorous and a monotypic species of *Centurio senex* (Phyllostomidae: Stenodermatinae). Mexico, Northern South America, and Trinidad and Tobago are all part of its extensive geographic distribution (Snow, Jones & Webster, 1980). This bat's capture records imply that it migrates periodically and that it prefers undisturbed forest areas (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). Even though it has been found in a wide range of locations, this bat's natural history remains a mystery. *Centurio* seems to be an obligate frugivore, based on the few food records that have been found (Goodwin & Greenhall, 1961; Gardner, 1977; Herrera, Fleming & Sternberg, 1998). In addition to this, there are unconfirmed accounts of the fruits consumed by *Centurio*. It's not unusual for a food item to have two competing challenges to overcome when being fed. The size of many fruits consumed by stenodermatine bats means that they have to extend their jaws wide in order to grip and bite into them, which helps to reduce their exposure to predators that swarm around fruiting trees (Kalko, Herre & Handley, 1996). Furthermore, fruits' varying hardness presents an issue for frugivory. It's possible to pierce some of them with a simple bite, but others are more difficult and take a lot of energy (Dumont, 1999; Aguirre et al., 2002; Dumont, 2003). Frugivores' diets may also be limited by food hardness, which is known to be a problem for insectivorous bats

(Aguirre et al., 2002, 2003). It is plausible to assume that gape and biting force are major factors in feeding performance for frugivorous bats, given the wide range of fruit sizes and hardnesses. When muscles are

at their ideal length on the length– tension curve, they produce the most force (Rome & Lindstedt, 1997; Burkholder & Lieber, 2001). Muscle fiber length and orientation, as well as the spatial connection between muscle attachments and the joints they impact, influence the amount to which muscles may be stretched and yet achieve maximal force generation. The length of bats' masticatory muscles' muscle fibers is a mystery to us. Dissections of 24 bat species by A. H. and S. S. (A. H. and S. S.) reveal that there is little diversity in muscle fiber orientation in the jaw adductors. Overall, there is little indication that the jaw adductors of bats have a highly specialized structure in terms of fiber lengths or orientations. Muscle force is lost during big gaps in bats' jaw adductors, which are assumed to be around the apex of their length–tension curves at rest. Muscle variation in relationship with the temporomandibular joint is most likely to offset this reduction in biting power. The superficial masseter muscle has been modified to accommodate these variances (Herring & Herring, 1974). The origin and insertion points of this muscle, in relation to the joint, may allow for large gapes before the muscle is stretched, hence optimizing biting force output for large gape angles for this particular muscle. For the superficial masseter muscle, we estimate and compare stretch factors and offer a model for the temporalis muscle. Bats' major jaw adductors are these muscles (Storch, 1968; Herrel et al., 2008a). For *Centurio*, it's possible that the skull is designed for both a broad gape and a powerful bite. According to Freeman (1988), a morphological evaluation of bats' fruit-eating habits, *Centurio* and its associates have jaw specializations. When it comes to *Centurio*'s jaws, they're extraordinarily small, broad, and have postcanine teeth that almost occlude simultaneously to puncture fruits with an accentuated labial rim of sharp shearing crests. As a result, *Centurio*'s slender, wide face may help balance the masticatory muscles' lever-to-load arm ratios and allow for comparatively big jaw adductors. Constrained models of bite force generation imply that *Centurio* has the capacity to create higher bite forces than bat species with less severe facial morphology because of its class III levers and constrained models (Greaves, 1998; Spencer, 1999). *Centurio*, a rare bat, has made it impossible to examine it firsthand. We went to a field location in southern Mexico in search of *Centurio* and were surprised to discover that *Centurio* was the dominating species there. To test the idea that *Centurio*'s highly evolved skull is specialized for producing strong bite forces at high gape angles, we take advantage of this once-in-a-lifetime chance. With bite force measurements from *Centurio* and other

phyllostomid bats, as well as morphological estimations of muscle stretch factors (see Herring & Herring, 1974), we've arrived at this conclusion. As part of our study, we examine if *Centurio*'s eating habits differ from those of other stenodermatines. *Centurio senex* adult male and female facial skeletons are subjected to various loading regimes during eating (Dumont, 1999, 2007; Dumont, Piccirillo & Grosse, 2005) based on recent assessments of feeding behavior in phyllostomids (photo by A. H.). The skulls of the progenitors of evolved stenodermatines were more heavily loaded on one side when they were fed (Santana & Dumont, in press). Unusual eating habits may be linked to unusual cranial morphologies if the shape of the skull reflects adaptations to the pressures acting on it on a regular basis.

Materials and methods

In September 2005, we performed *Centurio* field study in Laguna Silvi tuc in southern Campeche, Mexico. Mist nets were erected around a *Maclura tinctoria* fruiting location for a week at ground level (Rosales: Moraceae). Bright green mulberry-shaped fruits adorned the tree's terminal branches. At any one time, there may be as many as 1000 ripe fruits gathered, and this production seemed to be consistent throughout the week. They opened their nets every ten minutes for two to three hours after nightfall. Adult, non-pregnant, and non-lactating bats found in the nets were sent to a base camp approximately 300 meters distant from the netting spot, and the rest were released immediately. All procedures for trapping, handling, observing, and measuring bats have been approved by the University of California, San Diego's Institutional Animal Care and Use Committee. **Bite forcefully:**

With a piezoelectric force transducer (Kistler type 9203, range 500 N; Amherst, New York, USA), we measured biting force from *Centurio* individuals (Kistler, type 5995). According to Herrel et al. (1999) and Aguirre et al. (2001), the transducer was placed between two bite plates (2002). Cloth medical tape was applied to the tips of both upper and lower bite plates to prevent the bats' teeth from coming into direct contact with the metal plates. Bilateral molar biting produced the strongest bite forces, which were measured at this posterior bite posture (Dumont & Herrel, 2003). At least three trials were conducted at each site, and each animal was given a 20-minute break in between sessions. To arrive at a mean maximum biting force value for the species, we utilized the maximum bite force of each individual participant. Our normal field data (body mass and

forearm length) and measurements of the head length, head breadth, and height were recorded after the collection of biting force readings. All bats were released the same night, with the exception of a few *Centurio* that were kept to conduct behavioral studies. We took biting force and head measurements from 26 adult *Centurio* (means standard deviations; maximal 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 see if *Centurio*'s bite forces are out of line with its size, we gathered previously published data on maximum bite force from 21 additional phyllostomid species (Aguirre et al., 2002; Dumont & Herrel, 2003, Santana & Dumont, in press) and used least squares regression to see if head length, head width, or head height was the best predictor of maximum bite force. In order to assess *Centurio*'s biting ability, we examined the regressive residuals with the greatest r^2 and lowest AIC values. In order to do the analysis, all variables were first converted using natural logarithms.

Muscle stretch factors

Live, unanesthetized animals in the wild cannot be used to assess the link between muscular stretch and force output because of their lack of anesthesia. Therefore, we used measurements of dry skulls from museum collections to assess the capacity of animals to produce biting force at vast gaps. The origin–insertion ratio of the muscle and the angle formed between the origin and insertion points, as well as the temporomandibular joint, are all taken into consideration when determining the extent to which opening the jaw stretches the superficial masseter and reduces its ability to generate force (Fig. 2; Her ring & Herring, 1974). This model predicts that as the origin–insertion ratio and angle rise, so does the maximum opening of the jaws before the superficial masseter is stretched. It may, however, compensate for low values in one of these variables by calculating a "stretch factor," which expresses the overall balance between them (Herring & Herring, 1974). The temporalis muscle provides more to masticatory force than the mass eter muscle in bats, according to data summarizing physiological crosssectional areas of masticatory muscles (Herrel et al., 2008a). In order to account for the temporalis muscle, we modified the masseter stretch factor calculations From the joint to the tip of the coronoid process, we determined that the muscle's origin was the distance from the joint's posteriormost position in lateral view to its insertion (Fig. 2). Calculations for the superficial masseter were based on the lengths of these line segments and their dorsal angles.

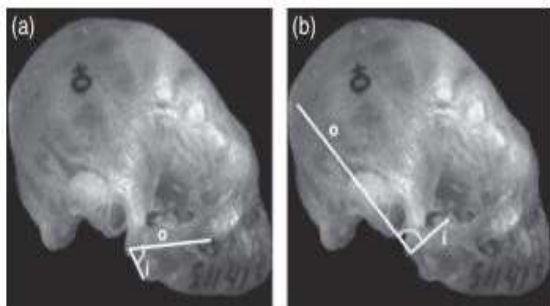


Figure 2 Stretch factors for the superficial masseter (left) and temporalis (right) are calculated using linear distances and angles. An articulated crania and dentary were used for all measurements. created by Herring and Herring is the origin of this term (1974). We measured the masseter and temporalis muscle stretch factors in 16 species of phyllostomid bats using a large gape angle of 601 degrees (Table 1).

Feeding behavior

We analyzed Centurio's eating behavior to discover if it varies considerably from that of other stenodermatines. First, we evaluated if Centurio, like other stenodermatines (Dumont, 1999), exhibits distinct feeding patterns while consuming soft and hard fruits. Second, we studied the eating behavior of Centurio and other stenodermatines while they were feeding on hard things. We focused on hard object eating because it poses a physical challenge that generates larger bite forces (loads on the facial skeleton) and sometimes different biting behaviors (loading regimes) than those utilized during soft object feeding. Seven individuals were maintained after netting in order to monitor their eating habits. Bats were videotaped at night using a digital video camera (Sony TRV-900, New York, NY, USA) and low-level, white spotlight lighting. Bats were kept separately or in groups of up to three individuals in portable (40 cm³) cages. The rear wall and roof of each cage was fashioned from shade cloth (a loosely woven, screen like plastic fabric), which enabled the bats to roam about the cage freely and prevented them from hurting their claws. Varnished plywood was utilized for cage floor for simplicity of daily cleaning. Two fixed side walls and a movable front wall were constructed of plexiglass. These guaranteed that the bats were seen from a broad variety of vantages and that the insides of the cages were readily accessible. Similar procedures were employed to gather the previously reported behavioral data for the other stenodermatines included in this research (Dumont, 1999; Santana & Dumont, in press) (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), $P < 0.001$]. *Maclura tinctoria* is a moderately soft fruit that may be pierced with 0.4 0.10 N mm² (n= 10), whereas apple is tougher (1.1 0.19 N mm², n= 25). All individuals happily ate both *M. tinctoria* and apple, despite the fact that apple is not an usual component of Centurio's diet and is missing from the field site and other ecosystems within its range. A total of around 16 hours of camera footage was evaluated at both regular and slow speeds to capture any biting activity. It was only during the early phases of feeding that observations could be made, when the fruits had shrunk to half their original size. After previous research (Dumont, 1999; Dumont and O'Neal, 2004), each biting event was classified into one of four descriptive categories based on the teeth used to bite into the fruit. These are shallow unilateral bites, shallow bilateral bites, deep unilateral bites, and deep bilateral bites. Deep unilateral bites were the most common type of bite. Canines were the focus of shallow bites, while postcanine teeth were the focus of deep bites in these studies. Centurio's feedings were videotaped, and this allowed us to see whether he utilized pulling or ripping gestures, dissimilar from those found in other phyllostomids, during feeding (Dumont, 1999). Three-way ANOVA was performed to explore if 'fruit kind' (soft or firm) had any significant effect on a bat's 'bite type' for each of the bat species in our sample (proportions of shallow unilateral, shallow bilateral, deep unilateral and deep bilateral bites). It was decided to accommodate variance across people in the formulation of error terms by designating 'fruit type' and 'bite type,' respectively, as fixed variables in the ANOVA model. Only those individuals for whom we obtained eating data for both kinds of fruit were included in the study for each species. The percentages of each of the four 'bite kinds' for each person and fruit were shown. The relevance of 'fruit kind' could not be tested, and, more significantly, no correct error terms could be generated as a result. As a result, before doing our research, we omitted the shallow unilateral bite type. To be clear, this had no impact on the ANOVA findings, since information regarding bite type was included in the data for the three remaining groups. Before the percentages for each bite type were analyzed, an arcsine transformation was conducted (Sokal & Rohlf, 1995)

Results

The greatest predictor of biting force was found to be head height (rhead height 2 = 0.59, b= 2.46, Po0.00, AIC= 29.69; rhead length 2 = 0.29, b= 1.87, P= 0.009, AIC= 17.48; rhead width 2 = 0.38, b= 1.87, P= 0.005, AIC= 19.72) in this sample. Among fruit-eating bat species, Centurio had the largest positive residuals (Fig. 3). Centurio has high values on both axes in the scatter plot of the computed masseter and temporalis stretch factors (Fig. 4). As a general rule, frugivores have the largest temporalis stretch factors while nectarivores have the lowest. These findings show that the general structure of the masticatory system promotes high force output at low gape angles in frugivores. These findings, on the other hand, show that insectivores and nectar feeders can maintain biting power at broader gape angles than frugivores do. However, this does not imply that nectar and insect feeders have the strongest biting power at larger openings, but it is projected that it would decline more slowly in these species as the gape widens. In terms of food and superficial masseter stretch variables, there is no apparent pattern of connection to be seen. For generalist mammals, the masseter stretch factor ranges from (1.2) to (1.7) for devoted herbivores (Herring & Herring, 1974). These bats did not demonstrate the low stretch factors that are typical of predators that are specialized for producing strong biting forces at wide gapes. To remove a mouthful of food from the mouth, Centurio took many bite-sized pieces and chewed the bolus for a long amount of time before spitting out a dry fiber wad and repeating the procedure. After analyzing biting sequences it was shown that Centurio preferred deep unilateral bites on both soft and hard foods.

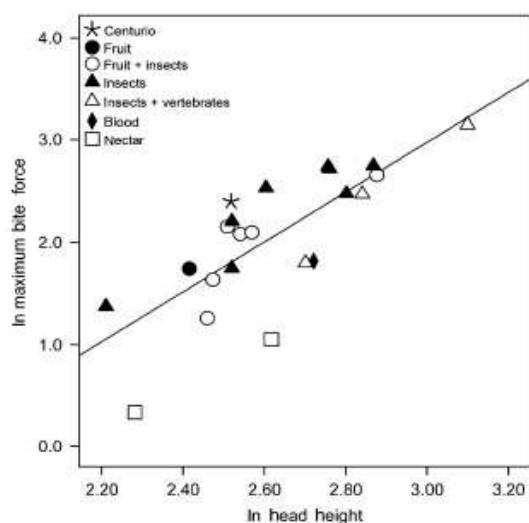


Figure 3 Maximum unilateral molar biting force on head height ($b=2.46$, $r^2=0.59$, $P<0.001$; p -value 0.0001). The species means are represented by symbols. Following Wetterer et al., we may classify foods according to their nutritional value (2000). Evidence of a blood-sucker in the form of bite force a fruit-eating decomposer known as *Desmodus Artibeusphaeotis*, fruit and insect feeders (*Artibeusjamaicensis*, *Carollia brevicauda*, *Carollia perspicillata*, *Platyrrhinus helleri*, *Sturnira lilium* and *Urodermabilobatum*), insectivores (*Lophostomabasilense*, *Lophostomasilvicolum*, *Micronycter* (Aguirre et al., 2002; Dumont & Herrel, 2003; Santana & Dumont, in press)

fruits and vegetables (Table 2). There were also a lot of shallow one-sided bites, particularly when the bats ate the soft *M. tinctoria* fruits. Centurio's bites were seldom bilateral. Three-way ANOVA showed that Centurio's bite type proportions changed significantly while eating soft and hard fruits (fruit type bite type interaction term, $F_{2,10}=4.65$, $P=0.037$). Deep unilateral biting replaced the low unilateral canine nibbles as food hardness rose. The eating habits of the majority of other stenodermatines likewise changed significantly when the hardness of the meal was increased (Table 2). Even though just two people were available for examination, this conclusion should be taken with a grain of salt. With his last effort to remove a piece of fruit from his mouth, Centurio would move his head quickly side to side while doing so. There was no significant difference in the frequency of these movements between feeding on soft and hard objects (paired t-test, $t=1.44$, $P=0.20$). *P. helleri* and *Urodermabilobatum* didn't move their heads while eating, according to our observations of the videotapes. Prior to *Sturnira lilium*'s regular usage of head motions when snatching food, no other bat was known to do so (Dumont, 1999). As compared to Centurio, *S. lilium* performs a much greater number of head movements when eating hard fruit. As a result, the specifics of the bats' motions are vastly different. To extract a fruit bolus, Centurio utilizes a combination of its forelimb and thumb claws to get hold of the fruit before biting into it to secure it. Using a combination of tugging and shredding, the *Sturnira lilium* grabs the fruit by the

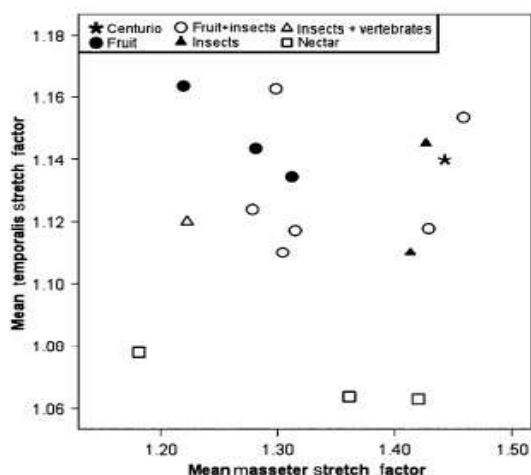


Figure 4 Mean masseter and temporalis stretch factors at a 60° gape angle are shown in this scatterplot. High numbers imply a greater degree of muscular stretching. The species means are represented by symbols.

Table 2

Biting while eating on both soft and hard objects

Species	Fruit texture	n	Site	Shallow		Deep		P
				bilateral	unilateral	bilateral	unilateral	
<i>Artibeus jamaicensis</i> ^a	Hard	7	204	1.01 ± 0.56	11.13 ± 2.53	11.27 ± 3.96	76.57 ± 4.04	< 0.001
	Soft	9	202	14.33 ± 4.09	18.89 ± 7.48	40.21 ± 10.69	20.37 ± 6.17	
<i>Artibeus praecox</i> ^a	Hard	3	190	7.53 ± 2.36	19.76 ± 6.27	8.37 ± 3.42	64.23 ± 5.51	0.023
	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 ± 0.89	12.57 ± 4.73	7.70 ± 2.55	77.64 ± 5.08	0.008
	Soft	7	185	5.54 ± 2.30	37.11 ± 7.75	4.89 ± 1.26	52.64 ± 6.96	
<i>Platyrrhinus helleri</i>	Hard	2	35	0.00-30.5	0.00-1.00	14.00-14.30	51.60-65.70	0.657
	Soft	2	18	0.00-50.00	0.00-0.00	16.70-50.00	0.00-40.30	
<i>Stenomys illardi</i> ^a	Hard	3	75	14.00 ± 5.25	6.00 ± 3.05	62.67 ± 5.33	17.23 ± 4.81	0.028
	Soft	3	81	14.07 ± 6.12	16.67 ± 12.74	39.27 ± 18.41	0.00 ± 0.00	
<i>Uroderma bilobatum</i>	Hard	4	102	14.63 ± 9.17	2.50 ± 2.50	1.80 ± 0.82	80.60 ± 9.26	0.074
	Soft	3	22	26.50 ± 13.76	10.70 ± 5.36	27.37 ± 20.16	35.47 ± 7.94	

Our claim that *Centurio* produces strong biting forces but not at high gape angles is consistent with what we know about its diet. The few extant studies assume that *Centurio* feeds on soft, mushy fruits or ripe, juicy fruits from which these bats suck the fluids (Goodwin & Greenhall, 1961; Snow, Jones & Webster, 1980; Emmons & Freer, 1997; Reid, 1997; Nowak, 1999). (Goodwin & Greenhall, 1961; Snow, Jones & Webster, 1980; Emmons & Freer, 1997; Reid, 1997; Nowak, 1999). Azullo (Ramirez-Pulido & Lopez-Forment, 1979) and Guettardafoliacea (Gianini & Kalko, 2004) are the only plants that have been linked to *Centurio*'s diet. These fruits are unknown in terms of their size and texture. *Centurio* and other stenodermatines were seen feeding on soft (Vargas Contreras et al., 2009) and juicy fruits from a big *M. tinctoria*, further supporting the hypothesis that it is predominantly a soft-fruit eater. In order to hold fruits securely in the mouth, *Centurio*'s large jaws and strong postcanine teeth with sharp labial shearing

crests occlude almost immediately (Freeman, 1988). A modest biting force and a broad gape angle may be adequate if the fruits are tender. Because of *Centurio*'s powerful bite, we expect it to only eat hard food at certain times of the year or in a certain area of its habitat range. The development of *Centurio*'s unusual craniofacial morphology may have been influenced by the availability of these meals during resource 'bottlenecks'.

Chiroderomediora and *Chirodermavillosum*, two stenodermatine bats, have lately been found as seed eaters (Nogueira & Peracchi, 2003; Nogueira et al., 2005). It is possible that *Centurio* may break apart the tiny 1–2mm seeds of *M. tinctoria* during our feeding experiments, however we were unable to find any evidence of this. We expect that *Centurio*'s diet will consist mostly of seasonal fruits and seeds, with a few exceptions throughout its migratory route. When challenged with a hard food item, *Centurio*'s biting behavior changes significantly, as it does with the majority of stenodermatines (Table 2). *Centurio*, *U. bilobatum*, and *P. helleri*, on the other hand, lack this behavioral flexibility (Santana & Dumont, in press). *Centurio* is the only one of these three species that depends extensively on unilateral biting for both hard and soft-object eating, making it the most peculiar of the three. When it comes to the upper molars, premolars, and canines, there are well-developed shearing surfaces along the labial edge that are diagnostic of derived stenodermatines (Freeman, 1988; Freeman, 1992). This research shows that *Centurio*'s unusual morphology is linked to a higher than predicted biting force and unique eating habits. Comparatively speaking, *Centurio* has a powerful bite for its small head size, prioritizes one-handed biting, and utilizes its head in an unusual way to snatch up a mouthful of food. *Centurio*'s face is also anticipated to be subjected to far higher unilateral loading than other bats' faces. The extraordinarily small and broad skull of *Centurio*, we propose, represents adaptations for withstanding such a stress regime. Across order to test this idea, more investigation into the mechanical relationship between loading and skull shape in a wide variety of species with known loading behaviors and biting forces would be necessary.

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