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Built to Bite: Cranial Design and Function in the Wrinkle-Faced Bat

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ABSTRACT

The scientific discipline of evolutionary biology looks at the boundaries of phenotypic diversity. Centuriosenex The skull of Centuriosenex is shaped in an unusual way. The relevance of its relatively small size in comparison to the width of its skull has been suggested by a number of qualified individuals in the field of morphological study. According to the findings of study, the peculiar form of Centurio's skull is linked to high bite forces and/or wide-gape bites that combine significant biting forces. Throughout the course of our investigation, we will put this hypothesis to the test. Comparisons are made between the biting force measurements taken in the field and the gape limits that were calculated based on museum specimens. We are interested in discovering whether or whether Centurio eats in a way that exposes it to a certain pattern of stress. It is possible that the Centurio's small head prevents it from exerting substantial biting pressures across a larger range of gape angles, despite the fact that it is one of the fruit-eating phyllostomid bats with the most powerful attacks that have ever been documented. As there were no other resources available, its ability to chew tough food may have been subjected to strong selection pressure, as shown by a violent bite. This may have led to dramatic changes in the shape of its skull. The peculiar dependence on unilateral biting shown in Centurio's diet is revealed by his eating habits (loading). According to this theory, Centurio's relatively small and wide skull may have developed as an adaptation to the extreme biting forces and the repeated unidirectional loading of the facial bones that Centurio experiences when it feeds. This theory was developed to explain how Centurio's skull came to be so small and wide.

KEYWORDS: *the formation and structure of chiroptera, the feeding behaviors of chiroptera, and the severity of their bites*

INTRODUCTION

Both biology and philosophy have spent a significant amount of time trying to unravel the mysteries surrounding the genesis of nature's many fascinating phenotypes. In recent years, phenotypic diversity has emerged as a primary research interest in a broad variety of academic disciplines. According to the findings of these researchers, the most essential variables in determining the overall success of an organism are not the organism's shape but rather its physiological and behavioral characteristics. [Citation needed] These innate

characteristics put a person at a disadvantage when it comes to their mobility, as well as their capacity for strength and speed. It is possible that selection for performance under ecological constraints would lead to fast anatomical phenotypic changes in populations, which will ultimately result in phenotypic variation (e.g.Losos, Schoener&Spiller, 2004; Phillips & Shine, 2006; Herrel et al., 2008b). Even though extreme phenotypes have a tendency to mirror the extremes of organismal design, when paired with performance constraints, they can help reveal design principles that may be buried in more generic forms. This is the case even though extreme phenotypes tend to mirror the extremes of organismal design (Adriaens&Herrel, 2008).

We examine the animal's eating habits, as well as its biting abilities and skull architecture, in order to get a deeper understanding of the ecological ramifications and likely origins of this characteristic. Gray (1842) identifies Centuriosenex as having one of the most superior skull morphologies. [Citation needed] This particular species of bat has a very tiny skull in comparison to others, yet its facial bones are rather large (Freeman, 1988; Swartz, Freeman & Stockwell, 2003; Stevens, 2005). In appearance terms, a considerable quantity of flesh can be seen protruding from Centurio's nose and mouth. (Fig. 1). Because the underlying skull does not exhibit gender-specific heterogeneity in terms of size and form, specialists believe that sexual selection is to thank for these peculiar face traits (Paradiso, 1967). The unusual shape of Centurio's head is most likely the result of functional changes that allow him to better digest food of varying sizes and textures. Journal of Zoology of the United States of America

Figure 1. Adult male (left) and female (right) Centuriosenex (photo by A. H.)

The New World leaf-nosed bats that belong to the Centuriosenex branch are among the most frugivorous of the members of the New World bat family. This is because the New World leaf-nosed bats are a monotypic species of Centuriosenex (Phyllostomidae: Stenodermatinae). A handful of the various areas it calls home include Mexico, northern parts of South America, and Trinidad and Tobago (Snow, Jones & Webster, 1980). According to the records of the bird's catches, it seems that it travels quite a bit and that it favors living in natural forest surroundings (Handley & Leigh, 1991; Fenton et al., 1992; Estrada, Coates-Estrada & Meritt, 1993; Kalko, Handley & Handley, 1996; Medellin, Equihua & Amin, 2000; Schulze, Seavy & Whitacre, 2000; Stoner, 2001). In spite of the vastness of its habitat, very little is known about the natural history of this bat. On the basis of the little dietary information that has been uncovered, Centurio seems to be a fruit-eating specialist (Goodwin & Greenhall, 1961; Gardner, 1977; Herrera, Fleming & Sternberg, 1998). There is also the possibility that Centurio consumed a fruit that has not yet been identified. It is fairly uncommon for a food item to experience two conflicting forces as it is being given to a creature. These bats eat large fruits, which need their jaws to open wider than usual in order for them to be able to hold and chew the food. This helps the bats avoid being eaten by predators (Kalko, Herre & Handley, 1996).

Because of this, frugivory is an undertaking that is fraught with difficulty. To puncture some of them, all you need to do is use your teeth, but to puncture others, you'll need more effort and more determination (Dumont, 1999; Aguirre et al., 2002; Dumont, 2003). Fungivorous fungi, such as bats, have reported having difficulty digesting fungus, and this issue has also been seen in insects (Aguirre et al., 2002, 2003). Given the great variety of fruit sizes and textures, the ability of frugivorous bats to consume their food is likely to be affected by the size of their mouths and the power with which they bite. According to the length–tension curve, muscles that are at the point on the curve when they are at their optimal length create the highest force (Rome & Lindstedt, 1997; Burkholder & Lieber, 2001). Depending on the length and direction of the muscle fibers, as well as the spatial connection between the muscle attachments and the joints they impact, it is possible to stretch muscles while still retaining the maximum force they are capable of producing. There is no information available on the length of the muscle fibers in a bat's mastica tory. Researchers found that the muscle fiber orientation in the jaw adductors of all 24 species of bats that they examined and dissected was virtually identical to one another. On the other hand, there is little evidence to suggest that the bat jaw adductors have a particularly distinctive architecture in terms of the fiber lengths and orientations that they exhibit. Bats with jaw adductors that have large gaps in their length–tension curves while they are at rest have less muscle power than bats with smaller gaps. It is quite probable that a change in the muscles in connection to the temporomandibular joint will be able to compensate for this drop in biting strength. In order to compensate for variances in the thickness of the superficial masseter muscle, the structure of the masseter muscle has been subjected to modification (Herring & Herring, 1974). Because of the enormous distances that exist between its origin and insertion places in reference to the joint, it is possible that this muscle will have the greatest capacity for biting when stretched to significant gape angles. Estimates of the stretch factors of the superficial masseter muscle are made and compared with those of the temporalis muscle using a model for the latter.

The jaw muscles of bats are very necessary for the animal to be able to consume food (Storch, 1968; Herrel et al., 2008a). It is feasible for this to happen if Centurio's skull is constructed in such a way that it can withstand both a wide gape and a violent bite. Freeman (1988), who conducted a morphological study of bats' preferences for fruit consumption, found that fruit-eating bats had developed specific jaw adaptations. In order to penetrate fruits with an expanded labial rim that is equipped with sharp shearing crests, Centurio's jaws are exceptionally tiny, wide, and furnished with postcanine teeth that, for all intents and purposes, occlude at the same time. In this sense, Centurio's broad and thin cheeks may aid in balancing the lever-to-load arm ratios of the masticatory muscles, which is necessary in order to allow for relatively large jaw adductors to be present. Through the use of class III levers and limited bite force models, Centurio seems to be capable of producing larger biting forces than bat species that have less severe facial morphology (Greaves, 1998; Spencer, 1999). Because there is so little of it, centurio cannot be explored in great detail. We were taken aback when we arrived at a remote field location in the southern region of Mexico and discovered that Centurio was the predominate species there. We seize this once-in-a-lifetime opportunity in order to test the notion that Centurio's highly developed skull is capable of delivering significant biting pressures at high gape angles. This is an opportunity that will never come around again. The feasibility of reaching this result was made possible by the process of measuring the biting force of Centurio bats and other phyllostomid bats in conjunction with calculations of muscle stretch parameters. It has been decided to investigate Centurio's feeding patterns to see whether they are distinctive from those of other stenodermatines. The facial bones of Centuriosenex have been put through a variety of loading regimens in accordance with the findings of previous research on eating behavior in phyllostomids (Dumont, 1999, 2007; Dumont, Piccirillo & Grosse, 2005). AH provided these images for use. It is believed that feeding the early stenodermatines led to the development of skulls that are lopsided and lopsidedly lopsided (Santana & Dumont, in press). If the structure of the skull reflects adaptations to the stressors that are placed on it on a daily basis, then abnormal eating habits may be connected to abnormal cranial morphologies.

MATERIALS AND METHODS

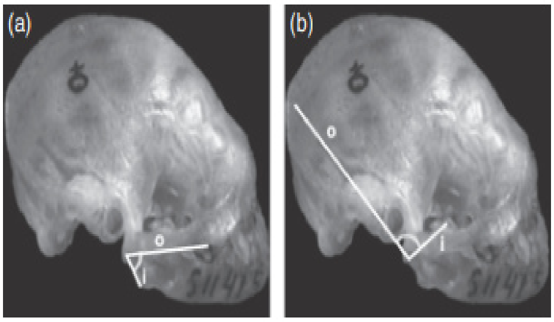
A field examination was carried out by the Centurio research team in September 2005 at Laguna Silvituc, which is located in the southern part of Campeche, Mexico. A area that was known to have Macluratinctoria fruiting was surrounded by ground-level mist nets for a duration of one week (Rosales: Moraceae). The majority of the higher limbs of the tree were covered with what looked like green mulberries hanging from its branches. Each day, there were as many as a thousand ripe fruits gathered, and the total quantity of fruit collected did not fluctuate. During the first two or three hours after darkness set, they opened their nets regularly at intervals of 10 minutes each. Any bats discovered in the nets that were not breeding or pregnant were released from a base camp located around 300 meters away from the location where the netting was placed. Any method that has been given the go-ahead by the Institutional Animal Care and Use Committee at the University of California, San Diego may be used to capture bats and take their measurements.

BITE FORCEFULLY

A piezoelectric force transducer (Kistler type 9203, range 500 N; Amherst, New York, USA) was used in order to determine the amount of biting force possessed by Centurio people (Kistler, type 5995). According to the findings that Herrel et al. presented, the transducer was positioned in the middle of two bite plates (2001). (2002). It was decided to take the precaution of applying cloth medical tape to both of the bite plate tips in order to prevent the teeth of the bats from coming into direct contact with the metal plate surfaces. The biting forces that were exerted at this posterior bite position were the greatest when molars were bitten on both sides (Dumont & Herrel, 2003). At least three times at each location, a twenty-minute respite was provided for each animal between sets of testing. We obtained the species' average maximum biting force by taking each participant's highest reported value for biting force and averaging them together. Before collecting measurements of the length, width, and height of the head, the researchers measured the body weight and the length of the forearms. After all of these operations were finished, statistics on the biting force were gathered. With the exception of a few Centurio bats that were retained for behavioral investigations, all of the bats were let free on the same night. Research was conducted on the biting force and head measurements of 26 mature Centurios, yielding a mean standard deviation of 10.9 0.85 N for the biting force (maximum bite force, head length, head breadth, head height). We utilized previously published data on the maximum bite force from 21 other species of phyllostomid to determine whether or not the biting forces of Centurio were out of proportion to its size (Aguirre et al., 2002; Dumont & Herrel, 2003, Santana & Dumont, in press). Because it was possible to make a prediction about the maximum biting force by utilizing least squares regression, that's what we performed. The effectiveness of Centurio's bite was determined by analyzing the residual regressive data that exhibited the highest r 2 value and the lowest AIC value. Before beginning any kind of analysis, all of the variables were first transformed into natural logarithms.

The Muscles are Loosened up by Stretching

It is not possible to conduct research on the link between muscular stretch and the creation of force using animals that are found in their natural environments since these animals are not sedated. The biting capacity of different animals required an analysis of dried skulls from different museum collections. When trying to estimate how much the temporomandibular joint and the muscle's origin–insertion angle impact the ability of the muscle to contract, it is necessary to take into account both the muscle's capacity to generate force and the ratio of its origin to its insertion (Fig. 2; Her ring & Herring, 1974). According to this model, the maximum opening of the jaws before the superficial masseter is stretched will grow as the origin–insertion ratio and angle increase. Additionally, this model predicts that this increase will take place in a clockwise direction. When there are low values for one or more variables, it is possible to use something called a "stretch factor" to represent the overall equilibrium of those variables (Herring & Herring, 1974). When it comes to the masticatory power that is generated by a bat's mastica, research conducted by scientists has shown that the temporalis muscle exceeds the mass eter muscle (Herrel et al., 2008a). The masseter stretch factor has been updated to take into account the temporalis muscle, which required the adjustment. It was discovered that the space between the joint's posteriormost point in lateral view and the tip of the coronoid process was the place where the muscle originated (Fig. 2). The thickness of a superficial masseter was determined by taking measurements along these line segments.



both (left) of them (right) When stretching the superficial masseter and temporalis muscles, linear lengths and angles, respectively, are used for the stretches (right). All of the measurements were performed on a moveable craniodental mannequin, which is a term that was first used by the legal firm of Herring & Herring (1974). In order to evaluate the masseter and temporalis stretch properties of sixteen different phyllostomid bat species, a gape angle of 601 degrees was utilized (Table 1).

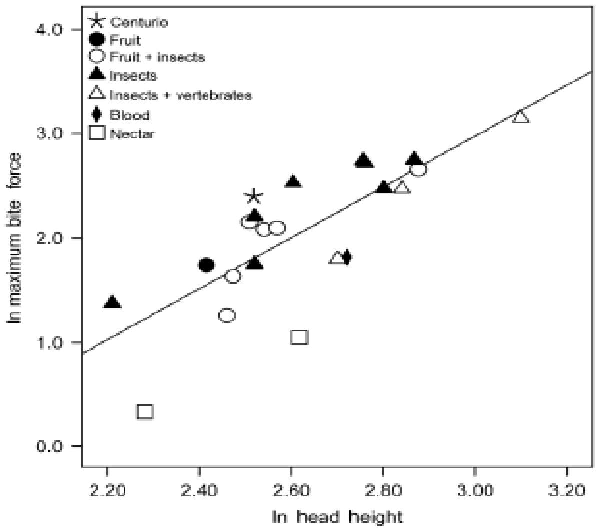
Behavioral Aspects of Eating

We compared Centurio to other stenodermatines so that we could determine whether or not his feeding habits were significantly different from those of other stenodermatines. When it came to Centurio, one of our goals was to determine whether or not it exhibited any peculiar patterns of eating when it was given both soft and hard fruits, as is the case with other stenodermatines (Dumont, 1999). To get started, we started by observing and recording the eating activities of Centurio and some of the other stenodermatines. Physically, chewing on hard objects results in greater bite pressures (loads on the facial bones) and occasionally different biting behaviors than the more typical practice of chewing on soft objects. This is because hard objects need more force to bite into. Following the netting, there were seven people who were detained so that we could observe their eating patterns. The nighttime footage of bats was captured using a digital camera (a Sony TRV-900 from New York, New York) and a white floodlight that had a rather dim setting. Portable cages with a volume of forty centimeters cubed were used to house the bats, either alone or in groups of up to three. The rear and ceiling of each cage were covered with shade cloth so that the bats could fly freely without injuring their claws. This also prevented the bats from becoming dirty (a loosely woven, screen-like plastic fabric). The floor of the cage is made of varnished plywood so that it can be cleaned very quickly and efficiently. Plexiglass was used in the construction of three walls: a front wall that can be moved, two side walls that are fixed. The spectators were able to get an excellent look at the bats from a number of positions, as well as the inside of the cages themselves, thanks to these. In previous research, such as Dumont (1999) and Santana and Dumont (now under review), stenodermatines used methods that were comparable to this one to obtain behavioral data (Dumont, 1999; Santana & Dumont, in press). Centurio were provided with M. tinctoria fruits (n=10) and apple pieces that had been chopped to mimic the size and shape of the native fruit. The purpose of this study was to determine whether or not the hardness of food impacted their eating behavior. However, there was a significant amount of variation in the apple's resistance to being punctured [one-way analysis of variance (ANOVA), p=0.001]. The force of 0.4 0.10 N mm 2 (n=10) is sufficient to penetrate the soft fruit of Macluratinctoria (n=10), but the force of 1.1 0.19 N mm 2 is required to puncture the hard fruit of Apple (n=25). Even though apples aren't a typical part of Centurio's diet and they aren't found at the field site or any of the other sites where the species is found, M. tinctoria and apples were enjoyed by everyone.

This was done at regular and slow speeds during the length of the 16 hours of footage in order to identify any biting action that may have occurred. Before any measurements could be done, the fruits needed to be reduced by one half before any results could be drawn. In this study, the different types of teeth that were utilized to bite into the fruit were taken into account while classifying each individual biting event (Dumont, 1999; Dumont and O'Neal, 2004). On one side, the bites are shallow, but on the other side, there are shallow bites in addition to deep ones. The most typical presentation was a severe bite on one side alone. In a number of experiments, researchers found that shallow bites targeted the canines, while deep bites targeted the postcanine teeth. When Centurio was being fed, we were able to see whether or not he pulled or ripped at the food. in contrast to the majority of other species of phyllosotmids (Dumont, 1999). An analysis of variance with three factors was carried out to see if the "fruit kind" (whether soft or firm) had any bearing on the "bite type" of the bats in our sample (proportions of shallow unilateral, shallow bilateral, deep unilateral and deep bilateral bites). Because of this, the ANOVA model accounted for individual variations in error terms by including fixed factors such as "bite type" and "fruit type." Only those participants were included for the research who provided information on the amount of both types of fruit they consumed. We calculated the proportion of each of the four different kinds of bites present in each sample, and we did this for each individual and each fruit. In the process of determining whether or not the 'fruit sort' function is beneficial, there was no generation of error-free words. As a direct consequence of this, the shallow unilateral bite was omitted from the parameters of our investigation. Because the data for the other three groups already had the bite type, this had no impact whatsoever on the results of the ANOVA. A modification using the arcsine function was carried out before the percentages for each sort of bite were calculated (Sokal & Rohlf, 1995)

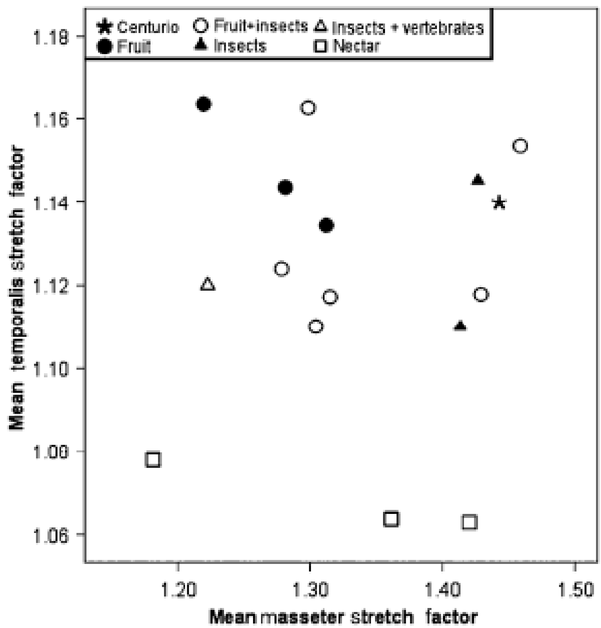
RESULTS

There is a statistically significant correlation between the amount of biting force and the rhead height 2 (rhead height 2 = 0.59, b = 2.46; Po0.00, AIC= 29.69). Centurio stood out from the other fruit-eating bats with the strongest positive residuals, setting him apart from the others (Fig. 3). Both of Centurio's masseter and temporalis show significant values on both axes of the scatterplot that represent their respective stretch factors (Fig. 4). When it comes to the temporalis stretch factors, fungivores have the greatest value, whereas nectarivores have the lowest value. Fungivores have the highest value. As was just said, research has shown that the masticatory system in herbivores has been discovered to increase high force production. Insectivores and nectar feeders, on the other hand, are able to sustain their biting force at a larger angle than frugivores, according to the data that was collected by the researchers. As the holes become bigger, the animals that feed on nectar and insects are likely to lose their ability to bite. It has been shown that diet has no influence on the flexibility of the superficial masseter muscles. [Citation needed] [Citation needed] Herbivores' masseters have stretch factors that vary anywhere from 1.2 to 1.7, while generalist mammals' stretch factors are in the same ballpark (Herring & Herring, 1974). It is typical for large-gaping predators such as these bats to have low stretch factors, however these individuals did not have such characteristics. After spitting out a wad of dry fiber, Centurio cleaned his mouth by chewing on a bolus of food for a significant amount of time. It didn't matter to him if the meal was chewy or crunchy; he preferred to consume it all in a single mouthful.



(b=2.46, r 2=0.59, Po0.001; p-value =0.0001), the maximal unilaterally molar biting force on head height (Fig. 3). The value of a specific species is conveyed via the use of symbols. Yes, it makes logical to classify foods according to their nutritional value (2000). If the fruit-eating decomposer Desmodus bites hard, it might be a bloodsucker. Carollia species that devour fruit and insects include Artibeusphaeotis, Lophostomabrasiliense, Lophostomasilvicolum, Micronycter, and Sturniralilium, as well as Carolliaperspicillata and Urodermabilobatum (Aguirre et al., 2002; Dumont & Herrel, 2003; Santana & Dumont, in press)

a large selection of dishes that have been freshly made (Table 2). Many fruits of M. tinctoria were consumed by the bats, each of which only bit into the fruit on one side. At least as far as I can tell, Centurio usually attacked in pairs whenever they could. Centurio's proportions of bite-types increased significantly when he consumed both soft and hard fruits (fruit-type bite-type interaction term, F2,10 =4.65, P=0.037). When the food became more solid, the canine nibbles were gradually replaced by more substantial, unilateral bites. When the meal's hardness was increased, almost all of the other stenodermatines exhibited a substantial shift in their eating behavior (Table 2). The results of the research should be interpreted with some degree of care due to the limited size of the sample. Centurio made an attempt to remove the remaining piece of fruit from his mouth by jerking his head back and forth as he tried to do so. A paired t-test was used in this research, and the results showed that there was no significant difference in the number of feedings required between soft and hard meals (t=1.44; P=0.20). Researchers were able to see on film that both P. helleri and Urodermabilobatum ate with their heads held in the same position during the whole meal. Only the Sturniralilium bat has been seen seizing food using head motions, and no other species has been observed doing so (Dumont, 1999). When it comes to eating a tough apple, S. lilium's head moves around substantially more than Centurio's does. As a direct result of this, bats' behavior will undergo significant shifts. The fruit is cut in half by the Sturniralilium's teeth, making it possible for Centurio to bite into it and store it in a bolus for later consumption.



The fourth time. With a 601 gape angle, this scatterplot depicts the masseter and temporalis stretch components. The more you stretch your muscles, the more you get. The species' symbolic meanings are communicated via their symbols..

Table 2. Biting while eating on both soft and hard objects

Species	Fruit texture	*n*	Bite sequences	Shallow bilateral	Shallow unilateral	Deep bilateral	Deep unilateral	*P*
Artibeus jamaicensis[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	
Artibeus phaeotis[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	
Centurio senex	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	
Platyrrhinus helleri	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	
Sturnira lilium[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	
Uroderma bilobatum	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	

It is possible to extrapolate from Centurio's diet that he has massive biting forces, however this is only the case when his mouth is fully opened. It is believed that Centurio's preferred method of nourishment is to consume the mushes and fluids found in fruits, and it is also said that fruits themselves are his preferred kind of food (Goodwin & Greenhall, 1961; Snow, Jones & Webster, 1980; Emmons & Freer, 1997; Reid, 1997; Nowak, 1999). (1999) Reimer and Nowak (both 1997s), Freer and Emmons (1997) In Reid (1997), as well as Snow, Jones, and Webster (1997), Emmons and Freer (1997), and others. Reimer and Nowak (both 1997s) (1980). There has been speculation that Azullo and Guettardafoliacea had a role in Centurio's diet. There is no information available on the size or consistency of these fruits. It has been seen that Centurio consumes the delicious and supple fruits of a massive M. tinctoria, which is evidence that it, too, is a consumer of soft fruits (Vargas, Contreras, et al, 2009). Centurio's enormous jaws and powerful postcanine teeth with strong labial shearing crests prevent fruits from slipping out of its mouth (Freeman, 1988). When eating delicate fruits, it's best to take easy bites with a wide gape angle and put in as little effort as possible. Because of the violent nature of its bite, we believe that Centurio will only ingest hard food during particular times of the year or in certain parts of the natural area it calls home. It's possible that Centurio's nutrition at a time when resources were few had an effect on the peculiar craniofacial morphology he had. Chirodromedoriae and Chirodermavillosum are two species of stenodermatine bats, and researchers found that both of these bats feed on seeds (Nogueira&Peracchi, 2003; Nogueira et al., 2005). In the course of our feeding studies, we observed that Centurio did not seem to be capable of destroying the 1–2 millimeter seeds of M. tinctoria. As it migrates, Centurio's diet is likely to consist mostly of the fruits and seeds that are available at that time of year. The majority of stenodermatines, including Centurio, exhibit a noticeable reaction to chewing on hard food (Table 2). There is no evidence that Centurio, U. bilobatum, or P. helleri are capable of exhibiting behavioral plasticity (Santana & Dumont, in press). Only one of these three species, Centurio, depends extensively on unilateral biting for the consumption of both hard and soft substances, making it unique among the three. Shearing surfaces that are derived from stenodermatine are located on the labial borders of the upper molars (premolars), canines, and premolars (Freeman, 1988; Freeman, 1992). According to the findings of this research, the conclusion of this study is that the strange form of Centurio is associated with its more intense biting force and its distinctive eating habits. The creature known as Centurio consumes an astonishing quantity of food for having such a little head, and it does so in a peculiar manner. The faces of bats are more vulnerable to one-sided loading, in comparison to the faces of other species. Centurio is no exception. It's possible that Centurio's small and broad head is an adaptation to the harsh environment in which it lives. The mechanical relationship between skull shape and loading has to be investigated in a wide variety of species that have well-established biting forces and behaviors.

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