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Scaling of Anatomically Derived Maximal Bite Force in Primates

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SCALING OF ANATOMICALLY DERIVED MAXIMAL BITE FORCE IN PRIMATES

By

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THESIS SUMMARY

Because the masticatory apparatus plays a role in processing food, its morphology has been evolutionarily shaped by the mechanical properties of diet. The masticatory apparatus consists of several muscles that act together to produce force along the tooth row. These jaw adductors, which are muscles that act in closing the jaw, are the temporalis, the masseter, and the medial pterygoid. The highly variable diets of species in the primate order make them particularly intriguing for studying signals of dietary adaptation. Because of this dietary diversity, we decided to categorize primate diets for analysis. We have chosen to divide our sample into two categories: (1) species that consume pliant and mechanically unchallenging diets, which include those who primarily eat fruits and (2) species that consume hard diets requiring forceful or repetitive mastication, which include species that are primarily leaf-eating. Bite force is an important variable of the masticatory apparatus that can be examined for signals of dietary adaptation. In the primate order, empirically measured bite force, which involves forcing a living specimen to bite down on a transducer, is not available because many species are rare or endangered and therefore unavailable for the invasive procedure. We have instead chosen to anatomically estimate bite force (BF) in our sample. Our sample consists of 31 specimen representing 23 different species. Eight of these species are platyrhines, new world monkeys, and 15 are catarrhines, old world monkeys and apes. 14 of the species fell into dietary category 1, while 9 species fell into dietary category 2.

For this study, we have chosen to estimate BF by combining physiological cross-sectional area (PCSA) data with skull dimensions that approximate the moment arms of the muscles and bite points to model the action of the jaw. PCSA is a function of muscle mass, fascicle length, and the specific density of muscle. It represents the area of the muscle in cross

section perpendicular to the muscle fascicle direction. This accounts for the force generated along the muscle's line of action in pennate muscles, which produce an angled force due to angular fiber orientation. Pennation is the angulation of muscle fibers.

In order to estimate BF, we modeled the jaw as a third-class lever, such that the fulcrum was the point of rotation on the mandibular condyle, the force was applied by each of the masticatory muscles, and the load was at a specific bite point along the tooth row. We measured the moment arm of the muscle and the moment arm of the bite at each point to scale PCSA and produce a BF estimate. We chose three realistic bite points along the tooth row: first upper incisor, the upper canine, and the front cusp of the first upper molar. We used muscle attachments as a guide for modeling the orientation of a muscle's force. The muscle's action was modeled between the centroid of the origin and insertion of each muscle. PCSA was scaled by the mechanical advantage of each muscle in order to estimate BF.

We examined the scaling of bite force variables with body size proxies for the sample as a whole and for each suborder and dietary category. We found no statistically significant deviation from isometry (symmetric scaling) in our bite force variables, although bite force approached positive allometry in our sample at all bite points in the catarrhine suborder. We also analyzed the residuals of bite force grouped by diet category and suborder. We found no statistically significant differences in scaling between these variables.

The discrepancy between these findings and those in Hartstone-Rose and colleagues (2017) demonstrate the role of leverage in force production. These results suggest that PCSA, which represents force production capability, scales allometrically to counteract muscle or bite point leverages that are inadequate for sufficient force production rather than dietary signals. The

lack of clear signals of dietary adaptation in our sample are likely due to the large variation within primate diets and the generalized dentition of all primates.

ABSTRACT

Bite force analysis is important the examination of the evolutionary factors that have shaped the masticatory apparatus. Unfortunately, in primates, empirically measured bite force is largely unavailable because of the invasive nature of the procedure. Because of this, we have estimated bite force in a large sample across the primate order at three different realistic bite points along the tooth row: the first maxillary incisor, the maxillary canine, and the paracone of the first maxillary molar. Here, we model bite force by combining measured physiological cross-sectional area of the jaw adductors from Hartstone-Rose and colleagues (2017) with osteological measurements from the same specimen. We did this by treating the jaw as a third-class lever as has been done by Hartstone-Rose and colleagues (2012). Our findings at all bite points suggest that there is no statistically significant difference in scaling of bite force based on diet or suborder. These findings contrast the findings of positive allometry in the Catarrhine suborder for the bite force proxies of muscle mass and muscle PCSA by Hartstone-Rose and colleagues (2017). This difference is likely due to the role of leverage in bite force production. PCSA has been evolutionarily driven up to account of inadequacies in bite point or muscle leverages in order to produce forces necessary for food consumption. The lack of dietary signals seen in the sample is likely due to the generalized dentition of primate species and the variation within species' diets.

INTRODUCTION

Due to the role that the musculoskeletal masticatory apparatus plays in chewing, its morphology has been evolutionarily shaped by the mechanical properties of the diet. The masticatory apparatus consists of several jaw muscles, which produce forces with different magnitudes and orientations, that act cooperatively in a system to produce force along the tooth row, thereby mechanically processing food. Modeling muscle force production is essential for understanding muscle function, because of its functional correlates and the current unavailability of empirically measured bite force data.

The highly variable diets of species in the primate order make them particularly intriguing for studying signals of dietary adaptation. Primate muscle architecture has been widely studied for this reason. In particular, cross-sectional area, a variable of muscle architecture, has been found to scale with body size isometrically or with slight positive allometry in primate masticatory muscles across both strepsirrhines and platyrrhines (Anapol et al., 2008; Perry and Wall, 2008; Hartstone-Rose et al., 2017). Previous studies have demonstrated the relationship between masticatory muscle fiber architecture and dietary requirements in primates. A correlation between masticatory muscle architecture and mechanical requirements of diet, including gape and bite force have been demonstrated in Callitrichid monkeys. Some Callitrichids engage in tree gouging to encourage the flow of tree gum or sap. Tree gouging requires a relatively wide jaw gape, which has driven muscle fiber lengths (FL) to be relatively long in relation to muscle mass (Taylor and Vinyard, 2004; Eng et al., 2009; Taylor et al., 2009). Another primate study on capuchins showed that some primates have both large jaw adductor physiological cross-sectional area (PCSA) and long FL, likely as an adaptation to maximize gape and bite force for processing large, resistant foods (Taylor and Vinyard, 2009).

Previously, the masticatory apparatus has been modeled to estimate bite force (BF) (Perry et al., 2010; Taylor et al., 2015). This study builds upon previous literature by examining the correlation of bite force with diet and body size in a large sample across the primate order. We produced bite force estimates at several bite points along the tooth row, which is valuable, because actual bite force data of this kind are not available for many species. Modeling bite force in primates is important for making inferences about diet and feeding behavior in fossil primates and for understanding the masticatory apparatus of primates in the field of primatology.

Empirical bite force data is not readily accessible for primates primarily due to the invasive nature of this research. Therefore, it is essential to be able to effectively model the force generated by the masticatory muscles. The most relevant variables for modeling bite force are electromyography, physiological cross-sectional area (PCSA), and skull dimensions that approximate moment arms of the masticatory muscles and jaw (Hartstone-Rose et al., 2012).

Electromyography (EMG) allows for the analysis of electrical signals during muscle contraction. This is ideal for the analysis of the relationship between diet and masticatory muscle architecture, because it allows for the contraction of different muscle groups to be analyzed individually in-vivo during chewing of foods of various textures. EMG data for primate jaw adductors has been used by Vinyard et al. (2008) and Vinyard and Taylor (2010). A recent study of primate jaw adductor EMG activity and fiber architecture suggests that evolutionary forces acting upon masseter and temporalis fiber architectures may have occurred separately (Vinyard and Taylor, 2010). Despite the useful nature of this data, the collection of EMG data was not feasible for this study, because it was logistically impossible to travel to numerous zoos for data collection. More importantly, the EMG procedure is fairly invasive, and as many primate species are rare or endangered, the EMG procedure was not a viable option for data collection.

Therefore, in this study, we have instead selected to model the forces produced by the masticatory apparatus of primates in our sample by combining data on the PCSA of the mandibular adductors with cranial geometry to model BF.

The contractile force of a muscle, BF in the case of masticatory muscles, is a function of cross-sectional area such that muscle size and the force of contraction are positively correlated (Hartstone-Rose et al., 2017). Cross-sectional area does not adequately represent the force production capabilities, because it models the muscle as though all muscle fibers are parallel to the orientation of the muscle throughout the entire muscle. This is, however, not always the case. Many muscles are divided by fascial planes, which the muscle fibers attach to at an angle rather than parallel to muscle orientation as assumed in cross sectional area. This angulation of muscle fascicles is called pennation, and it impacts the force production capabilities of a muscle (Anapol and Barry, 1996). Because of this, it is important to take the cross-section of of the muscle fibers perpendicular to the fiber orientation rather than the entire muscle. The measurement that takes this into account is the physiological cross-sectional area.

Physiological cross-sectional area is a function of muscle mass, fascicle length, and the specific density of muscle. It represents the area of the muscle in cross section perpendicular to the muscle fascicle direction. This measurement accounts for pennation of muscle fibers within the muscles, by accounting only for force generated along the muscle's line of action, where pennate muscles produce angled force due to their angled fiber orientations. Pennation increases the number of fascicles present within a given volume of muscle, thus increasing PCSA. Since force is produced in a muscle along the muscle fascicle, PCSA is related to maximum muscle force production (Close, 1972; Anapol et al., 2008), making it important for modeling BF.

Force production capabilities are maximized by increasing pennation and shortening fiber length. Shortening fiber length or increasing pennation, however, decreases muscle stretch and contraction speed. Therefore, there is a physiological trade of between BF production and gape that is based on dietary requirements. Both BF and gape can only be simultaneously increased by increasing muscle mass, allowing for a relatively larger number of fascicles to be present within the given muscle.

Hartstone-Rose and colleagues (2017) examined the muscle architecture of the masticatory muscles within a large sample from across the primate order. That same sample has been used in this contribution to further investigate bite force. In that study as well as others, PCSA has been found to scale isometrically or with positive allometry in primates (Perry and Wall, 2008; Anapol et al., 2008; Hartstone-Rose et al., 2017). Although there was little evidence of dietary signals in the masticatory muscle architecture data, Hartstone-Rose and colleagues (2017) found that fiber length scaled with positive allometry in the temporalis in taxa that consume softer foods (i.e., frugivores). This suggests that the temporalis plays an important role in the production of gape in primates. This intriguing relationship was the catalyst needed for us to expand the investigations conducted by Harstone-Rose and colleagues (2017) by combining the previous findings with skeletal measurements from the same specimen in order to produce BF estimations.

The measurements of the skull used in BF estimation allow for the masticatory apparatus to be modeled as a third-class lever. This model has been suggested by many authors (e.g., Turnbull, 1970; Hartstone-Rose et al., 2012). The orientation of the force produced by the each of the jaw adductors (the masseter, temporalis, and medial pterygoid) can be approximated using each muscle's respective origin and insertion. The orientation of each individual muscle's force

is important for modeling this complex system in which the jaw adductors perform a single action together. The moment arm of each muscle can then be modeled as a vector perpendicular to the orientation of the force that spans the force line to the rotational axis on the mandibular condyle. The moment arm can be used to scale PCSA in order to find the mechanical advantage of the muscle. This can then be multiplied by the force constant of muscle cross-section as defined by Close (1972) to calculate the force production capabilities of each muscle. This force acts as the in-lever for the system.

BF estimation must account for the force produced on the working side, side of the jaw that contains the load, and balancing side, side that has no load but contracts to allow for symmetrical closure. Bite force is therefore the result of working side bite force (WBF) and balancing side bite force (BBF). Both WBF and BBF are estimated using the same in-lever, the force produced by the masticatory muscles; however, they have different out-levers based on their action. The out-lever of WBF is from the point of rotation on the mandibular condyle to the point on the same side of the skull where the load is applied, which is a bite point. BBF is the contraction of the muscles on the side opposite to that of the bite point. Because of this, the out-lever must wrap around the skull. It is measured from the point of rotation on the mandibular condyle to interdentale and then to the bite point on the other side. Because we made these measurements on two dimensional images of the specimen taken from only one side, we assume bilateral symmetry in our measurements. We have modeled BF in this way at three different realistic bite points along the tooth row: the first maxillary incisor, the canine, and the paracone of the first molar. This method of modeling assumes that muscles are firing constantly, uniformly, and maximally. It also assumes that all fascicles within a muscle fire simultaneously. These conditions are unrealistic for any normal consumption; however, these assumptions are

necessary for the purpose of modeling bite force. This kind of modeling has been used to represent bite force when muscles contract maximally (e.g., Perry et al., 2011; Hartstone-Rose et al., 2012).

The primate order is particularly interesting for the examination of dietary signals on bite force because of the varied nature of primate diets. We applied the dietary categorization used by Hartstone-Rose and colleagues (2017), which categorizes primate diets as either primarily frugivorous or primarily folivorous. For these categorizations, dietary data was taken from dietary descriptions in the Handbook of the Mammals of the World (Mittermeier et al., 2012). We assess the way in which the functional demands of diet impact masticatory muscle architecture because of the functional relationships of muscle architecture with bite force and gape. This relationship of functional adaptation to physical morphology has been demonstrated in several primate studies. In Callitrichid monkeys, tree gouging, which requires a relatively wide jaw gape, has driven muscle fiber lengths (FL) to be relatively long in relation to muscle mass (Taylor and Vinyard, 2004; Eng et al., 2009; Taylor et al., 2009). Another primate study on capuchins showed that some primates have both large jaw adductor physiological cross-sectional area (PCSA) and long FL, likely as an adaptation to maximize gape and bite force for processing large, resistant foods (Taylor and Vinyard, 2009). Hartstone-Rose and colleagues (2017) found little impact of diet on PCSA in the sample used in this study; however, we attempted to determine whether BF is impacted differently than PCSA by functional requirements of diet.

This contribution evaluates the effect of leverage on scaling by examining the functionally significant differences in scaling of BF from the simpler PCSA. We assess the scaling of estimated maximum bite force production with the geometric means of the skull, jaw length, and body mass, which we use as proxies for body size, and determine whether

mechanical properties of food can account for some of the deviation. We have modeled bite force by scaling the jaw adductor PCSA data from Hartstone-Rose and colleagues (2017) using cranial geometry data from the same specimen to approximate moment arms of the masticatory apparatus. This procedure is similar to that used in Hartstone-Rose et al. (2012); however, this study differs in that species within the primate order have more variable diets than species of the felid order. For instance, species of the Aotus genus are primarily frugivorous, whereas species of the genus Mandrillus eat a fairly obdurate diet including crabs and small mammals (Mittermeier et al., 2012). A similar study has been performed in a small sample of primates (Perry et al., 2011); however, the sampling of this study only included primates within the strepsirrhines suborder, which is less diverse than the order as a whole. The order is more extensively sampled in this study and represents a larger diversity of diets. Additionally, this study attempts to model bite force at three realistic bite points along the tooth row, which has not previously been done in such a large and diverse sample of primates.

HYPOTHESES

We hypothesize that estimated BF scales isometrically with body mass (BM), geometric mean (GM), and jaw length (JL), which act as proxies for body size, across this primate sample based on the scaling observed in strepsirrhines (Perry et al., 2011).

Previous studies have suggested that bite volume relative to body size is larger in frugivorous Strepsirrhines than in folivorous Strepsirrhines (Perry and Hartstone-Rose, 2010). Species that consume relatively large bites of food, such as ripe fruits, will require a relatively larger gape than species who consume diets that do not require wide gape, such as foliage. Because of the physiological trade-off that exists between gape and bite force, we can expect that

these two capabilities will have an inverse relationship. Therefore, we can expect that frugivorous primates (Category 1) will have lower maximum bite force capabilities than folivorous primates (Category 2).

We expect that species that exploit relatively obdurate (hard or tough) foods, such as hard nuts and seeds (Category 2), will exhibit relatively larger maximal bite force when compared with species who consume more malleable diets, such as ripe fruits or flowers (Category 1).

Primarily folivorous species, which consume a rough diet requiring a relatively large amount of masticatory manipulation prior to exploitation (Category 2) will have a relatively higher estimated bite force than those that consume more malleable, primarily frugivorous diets (Category 1), because of the greater need for force production during consumption.

We expect that primates who consume relatively obdurate or folivorous (Category 2) diets will be capable of producing relatively higher BF at the paracone bite point than other species, due to the requirement of large force in grinding foods. We also expect that species that consume diets that require tearing (Category 2) have relatively higher estimated BF at the canine bite force compared to other species.

MATERIALS AND METHODS

Sample

Our sample consisted of 31 specimens representing 23 species from 14 different genera (Table 1). The muscle architecture for these same specimens was examined by Hartstone-Rose and colleagues (2017). We have combined the PCSA values from that contribution with cranial

morphology data from in order to calculate BF. As stated in Hartstone-Rose and colleagues (2017), these specimens were all captive-raised adults, which, with the exception of one specimen (*C. jacchus,* which was dissected in the USA), were from zoos in Spain and were dissected at the Universidad de Valladolid in Valladolid, Spain. These specimens were preserved and dissected according to the methodology described in Hartstone-Rose and colleagues (2017). In this contribution, we examined two-dimensional images of the cleaned skull of each specimen to assess cranial morphology. We produced well-lit lateral and superior photographs of each specimen's skull at dental occlusion with a bar shown for scale.

Force Production Variables

For our sample, PCSA for each muscle group (masseter, temporalis, and medial pterygoid) was calculated in Hartstone-Rose and colleagues (2017) according to a formula modified from Schumacher (1961):

$$q = m/lp$$

Where, q is PCSA, m is muscle mass, l is fascicle length, and p is a constant representing the specific density of muscle (1.0564 g/cm^3) (Murphy and Beardsley, 1974). We have combined this data with leverage measurements from the skull in order to estimate BF.

To calculate maximum force production capabilities of each muscle, we have scaled each muscle's PCSA by the muscle's mechanical advantage found using measurements from the lateral images of the skulls. We used the muscle attachments as a guide for modeling the orientation and location of the muscle's force. We utilized the bony prominences viewed in the lateral photographs as markers to identify the origin and insertion of each muscle in each specimen (Figure 1). The program, imageJ, was used to identify the centroid for each of these

muscle attachments and insertions. The centroid of the origin and insertion of each muscle were connected to model the line of action of the muscle (Figure 1). We have modeled each muscle's mechanical advantage as the line perpendicular to the muscle's line of action from the line of action to the point of rotation on the mandibular condyle (Figure 1). We scaled the PCSA of each muscle with its mechanical advantage and combined it with the constant of skeletal muscle force production (3 k/cm^2; Close, 1972) to calculate the in-lever of the masticatory system.

FIGURE 1. Mandibular adductor, temporalis (red), masseter (blue) and medial pterygoid (green), origins (solid outlines) and insertions (dashed outlines). The line of action of each muscle is represented by the solid line connecting the centroid of its origin and insertion. Male *C. cephus* from study.
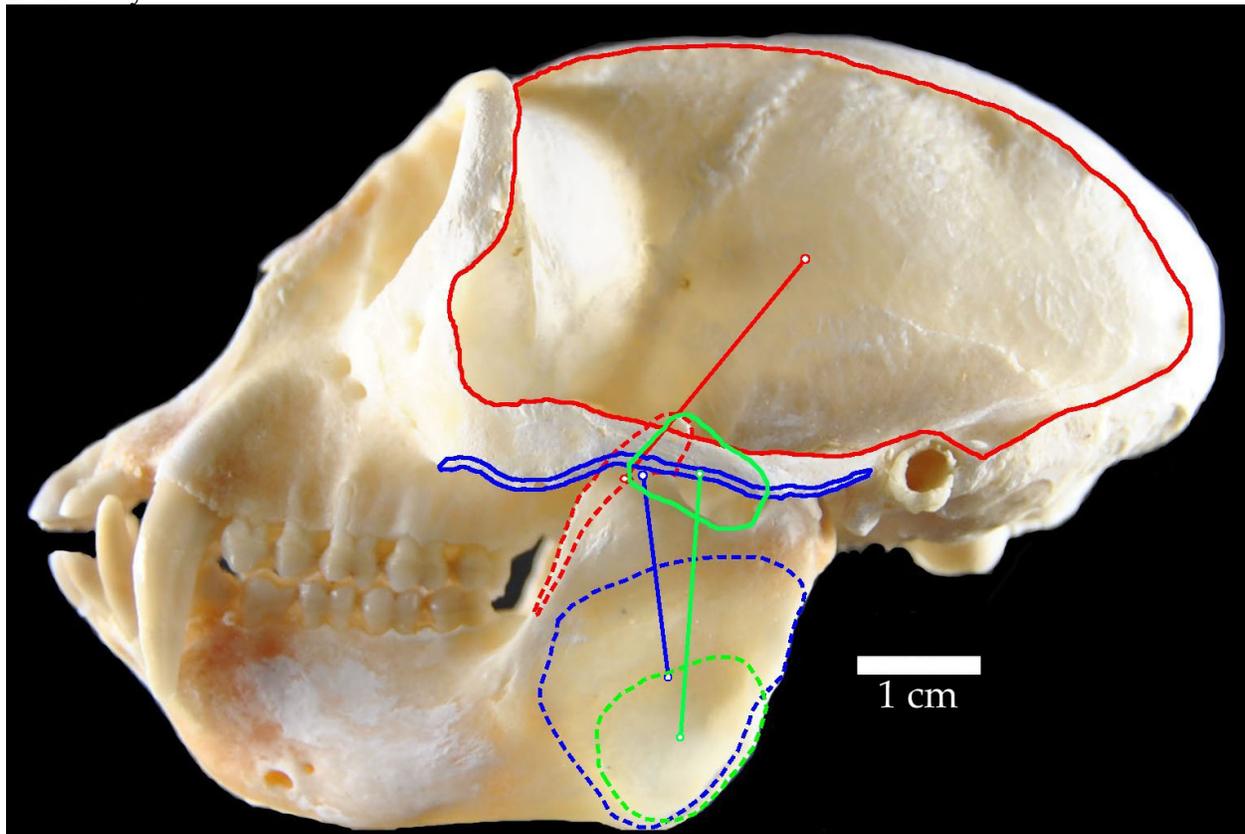
We calculated the out-lever of the masticatory system at three different realistic bite points along the tooth row (the tip of the first maxillary incisor, the maxillary canine, and the paracone of the first maxillary molar. The bite moment arm for each bite point on both the

working and balancing side were calculated using imageJ on the lateral photograph for each specimen. The moment arm of the working-side (Figure 2) was modeled as the distance from the point of rotation on the mandibular condyle to each of the bite points. The moment arm of the balancing side of the system was modeled as the distance from the point of rotation on the mandibular condyle to interdentale, the point on the maxilla between the central incisors, and back to one of the bite points. This measurement assumes bilateral symmetry.

FIGURE 2. Yellow lines represent working-side bite point leverages at the central incisor (A), paracone (B) and canine (C) bite points. The lever arm for each mandibular adductor, temporalis (red), masseter (blue), and medial pterygoid (green), is represented by the line perpendicular to the muscle's line of action that connects with the mandibular condyle.
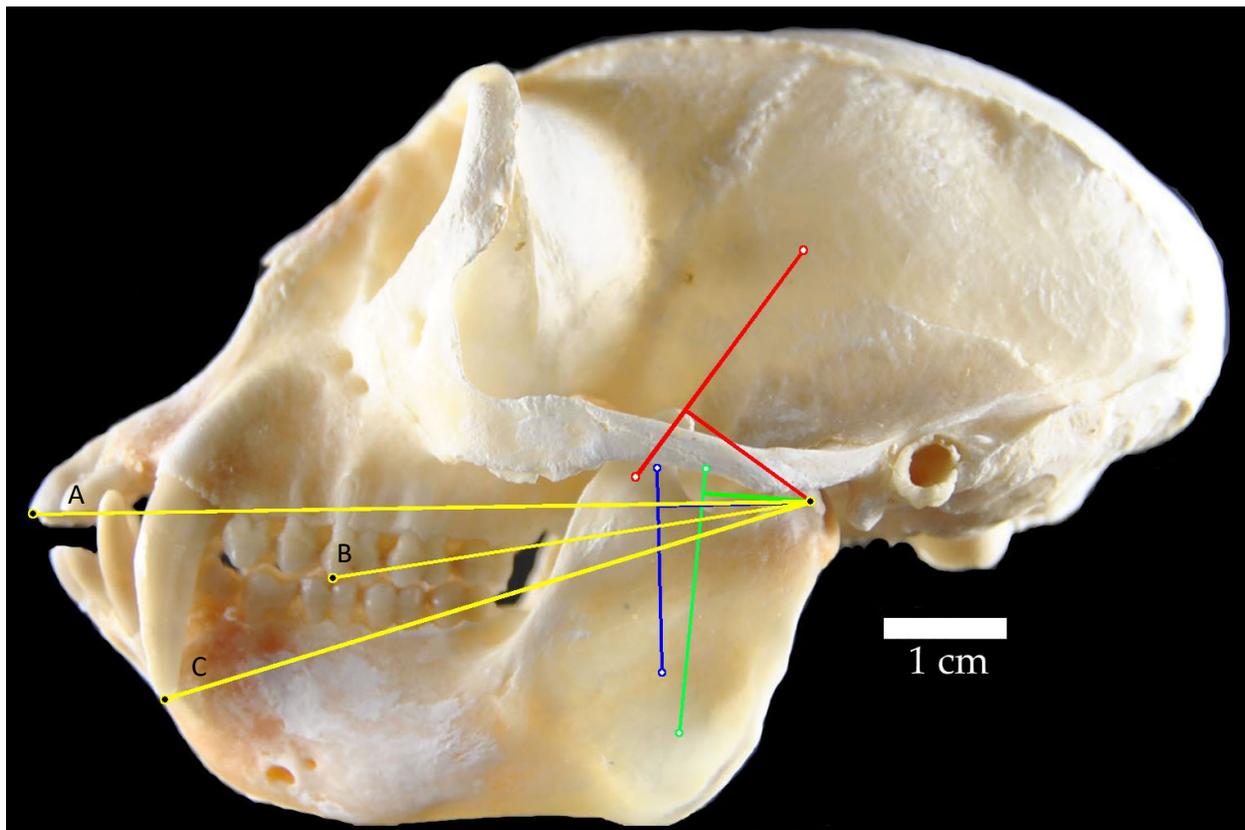
The measurements of the load arms that applied the force to the specific bite points and the moment arm of muscle force production were combined to calculate the working-side bite force at each bite point (Hartstone-Rose et al., 2012):

$$WBF_{IC} = c\left(\frac{(q_{MS}L_{MS}) + (q_{TMP}L_{TMP}) + (q_{MP}L_{MP})}{(L_{IC})}\right)$$

$$WBF_{CA} = c\left(\frac{(q_{MS}L_{MS}) + (q_{TMP}L_{TMP}) + (q_{MP}L_{MP})}{(L_{CA})}\right)$$

$$WBF_{PC} = c\left(\frac{(q_{MS}L_{MS}) + (q_{TMP}L_{TMP}) + (q_{PM}L_{MP})}{(L_{FM})}\right)$$

where WBF_{IC}, WBF_{CA}, and WBF_{PC} are the BF on the working side at the central incisor, canine, and paracone bite points respectively. The moment arms for the masseter, temporalis, and medial pterygoid are represented by L_{TMP}, L_{MS}, and L_{MP}, respectively. q_{TMP}, q_{MS}, and q_{PT} represent the PCSA values (Hartstone-Rose et al., 2017) for the temporalis, masseter, and medial pterygoid, respectively. The load arms for the incisor, canine, and molar bite points from the working-side are indicated by L_{IC}, L_{CA}, and L_{FM} in the equations above, respectively. The force constant that is generated by the muscle cross-section is indicated by c in the equations above (3 kg/cm^2; Close, 1972).

Estimated BF on the balancing-side of the was calculated using the same formula. The moment arm for the muscles on the balancing-side were modeled as being equivalent to that of the working-side; however, the load arms of the bite points were different (as described above). These measurements were used in the following equations with slight modifications from Hartstone-Rose and colleagues (2012) to calculate balancing-side BF:

$$BBF_{IC} = c\left(\frac{(q_{MS}L_{MS}) + (q_{TMP}L_{TMP}) + (q_{MP}L_{MP})}{(L'_{IC})}\right)$$

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$$BBF_{CA} = c\left(\frac{(q_{MS}L_{MS}) + (q_{TMP}L_{TMP}) + (q_{MP}L_{MP})}{(L'_{CA})}\right)$$

$$BBF_{PC} = c\left(\frac{(q_{MS}L_{MS}) + (q_{TMP}L_{TMP}) + (q_{PM}L_{MP})}{(L'_{FM})}\right)$$

where BBF_{IC}, BBF_{CA}, and BBF_{PC} are the BF on the balancing side at the central incisor, canine,

and paracone bite points respectively. L_{TMP}, L_{MS}, L_{MP}, q_{TMP}, q_{MS}, q_{PT}, and c are defined as in the

working-side equations and represent equivalent values. The load arms for the incisor, canine,

and molar bite points from the working-side are indicated by L'_{IC}, L'_{CA}, and L'_{FM} in the

equations above, respectively.

Because the working-side and balancing-side BF act simultaneously to produce a BF at a

specific bite point, the BF for the working-side and balancing-side were summed to calculate

total BF estimates for each bite point as follows:

$$BF_{IC} = WBF_{IC} + BBF_{IC}$$

$$BF_{CA} = WBF_{CA} + BBF_{CA}$$

$$BF_{PC} = WBF_{PC} + BBF_{PC}$$

Where BF_{IC}, BF_{CA}, and BF_{PC} represent the estimated total BF at the first maxillary incisor,

maxillary canine, and paracone bite points, respectively.

Dietary Categorization

In order to assess the adaptation of bite force to the mechanical properties of diet, we

have categorized the species in our sample into two groups based on mechanical properties of

diet (Table 1). The species were sorted as in Hartstone-Rose and colleagues (2017) based on published accounts of species diets (Mittermeier et al., 2012). The first category consists of species that consume diets made up of pliant and mechanically unchallenging foods, such as ripe fruits (score of 1). The second category is made up of species that consume obdurate (hard or tough) diets requiring a great deal of forceful or repetitive manipulation prior to digestion (score of 2). We have categorized gummivorous members of the genus *Callithrix* into category one despite their engagement in tree gouging. Tree gouging requires a relatively wide jaw gape, which has driven muscle fiber lengths (FL) to be relatively long in relation to muscle mass (Taylor and Vinyard, 2004; Eng et al., 2009; Taylor et al., 2009), rather than a large BF. Two dietary categories were chosen despite the subtle differences that can be observed amongst the diversity of primate diets, because morphology tends to largely fall along the lines of broad dietary divisions. This functional split between primarily frugivorous and primarily folivorous groups is a classical observation in primate adaptation literature (notably Kay, 1975).

Body Mass Proxies

Last living body weight was not available for the specimens in this sample. In order to assess scaling of the bite force with body size in our sample without actual individual body mass measurements, we selected three different proxies for body size: 1) average species body mass (BM) from literature, 2) the geometric mean (GM) of a series of cranial measurements (Hartstone-Rose et al., 2017) (Table 2), and 3) mandibular length for each individual specimen (JL). Body mass measurements were taken from Fleagle (2013) based on the average weight by sex for each species. For specimens of unknown sex, the overall species average was used. All of the craniometric measurements included in GM and JL (mandibular length being a component of

GM and the proxy JL) were measured from the lateral and superior photographs of the specimens' skulls.

Data Analysis

For analysis, the BF variables were analyzed by species. In this sample, several of the species had multiple specimen. Because of this, the data for all variables from specimen of the same species were averaged prior to analysis.

The BF variable for each bite point were regressed against the body mass proxies to assess scaling. Before regression, the BF and BM variables were reduced to linear variables in order to simplify the analysis of scaling, so that their predicted slopes were standardized to 1. The cube root of the BM and square root of BF variables were taken before the variables were logged. Pairwise comparisons were applied according to phylogenetic and dietary groups. Residuals were calculated from these RMA regressions as the distance from the line in log space. All analyses were done in JMP13 (SAS), using a significance criterion of alpha < 0.05.

RESULTS

We have estimated BF by combining PCSA data from Hartstone-Rose and colleagues (2017) with leverage data from the same specimen for both working- and balancing-side masticatory muscles. Therefore, differences in scaling between PCSA and BF are due to the role of leverage in force production. PCSA and muscle mass, both variables correlated with BF, have been found to scale with slight positive allometry in the Catarrhine suborder (Hartstone-Rose et al., 2017). We examine deviation from this pattern of scaling in bite force (see discussion).

This study examined the scaling of bite force with three different body size proxies. In most allometric regressions (Table 3), all bite force variables scale isometrically. None of the

variables deviated from isometry with statistical significance. Scaling approaches positive allometry in the Catarrhine suborder consistently across all bite points (central incisor, canine, and paracone) when the cranial GM body size proxy was used. At the canine bite point, BF regressed on GM was driven toward positive allometry across the whole sample. None of the correlations between the BF variables and GM or JL approached significance beyond isometry.

The analyses of the residuals (Table 4) do not reveal any statistically significant differences between the two dietary groups; however, all BF variables that approach significance are higher for category 2 species, those who consume obdurate diets. There were no differences approaching statistical significance in the comparison of residuals between catarrhines and platyrrhines.

DISCUSSION

No bite force variables scaled with allometry with statistical significance. Although this data does not demonstrate statistically significant allometric scaling of any bite force variables, BF variables at all bite points do approach statistically significant positive allometry in cattarrhines with the geometric mean body size proxy. These results differ from the finding of statistically significant positive allometric scaling of PCSA and muscle mass in the Catarrhine suborder in this sample (Hartstone-Rose et al., 2017). The difference in scaling between these muscle force production variables, PCSA, muscle mass, and bite force at each of the three chosen bite points, is due to the role of the osteological components of leverage in bite force production. The difference in scaling between these variables is due to the variation of cranial shape, which is obviously correlated with leverage, within the primate order. These results indicate that leverage only acts to counteract or make up for differences in muscle force

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production capabilities (PCSA). Potentially PCSA has been driven up in Catarrhines in order to increase BF due to inadequate muscle or leverage moment arms, such that the bite point is too far from the point of rotation or the muscles too close to produce adequate force.

We have used JL as one proxy for body size. Because of the importance of leverage in muscle force production as demonstrated by these results, jaw length is not an appropriate body size proxy for the purpose of analyzing scaling in the masticatory system. It has impacted and been impacted by the same evolutionary factors as masticatory muscle architecture, because it is a part of the same system.

The analysis of residuals in our sample did not reveal any more statistically significant dietary signals. Although statistically significant differences were not present in our sample, there is consistent evidence that bite strength is higher, although not significantly so, in species who consume obdurate diets. The lack of clear dietary signals for the bite force variables demonstrates the absence of significant evolutionary forces related to diet. This lack of morphological adaptation to dietary requirements is likely due to the varied diets of primate species and their generalized dentition and adaptability.

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TABLE 1. Sample

Species	Suborder	N (M, F, Unknown)	Body Mass (g)[a]	Dietary Description[b]	Dietary Categorization
Aotus nancymaae	Platyrrhine	2 (1,0,1)	790.5	Insectivore/Carnivore	1
Callithrix jacchus	Platyrrhine	1 (1,0,0)	317	Gummivore/Frugivore	1
Cercocebus atys	Catarrhine	1 (1,0,0)	11000	Frugivore/Granivore	2
Cercocebus torquatus	Catarrhine	1 (0,1,0)	6230	Frugivore/Granivore	2
Cercopithecus campbelli	Catarrhine	1 (0,1,0)	2699	Frugivore/Insectivore	1
Cercopithecus cephus	Catarrhine	1 (1,0,0)	4289	Frugivore	1
Cercopithecus hamlyni	Catarrhine	1 (0,1,0)	3360	Omnivore/Generalist	2
Cercopithecus mona	Catarrhine	1 (0,1,0)	5100	Frugivore	1
Cercopithecus neglectus	Catarrhine	1 (1,0,0)	7350	Frugivore	1
Cercopithecus petaurista	Catarrhine	1 (0,1,0)	2900	Frugivore/Folivore	2
Chlorocebus aethiops	Catarrhine	2 (1,1,0)	3563	Omnivore/Generalist	2
Colobus guereza	Catarrhine	1 (0,1,0)	9200	Folivore	2
Hylobates lar	Catarrhine	1 (0,1,0)	5340	Frugivore	1
Macaca silenus	Catarrhine	1 (1,0,0)	8900	Frugivore	1
Macaca sylvanus	Catarrhine	2 (1,1,0)	13266.5	Omnivore/Generalist	2
Mandrillus sphynx	Catarrhine	1 (0,1,0)	12900	Omnivore/Generalist	2
Mico argentatus	Platyrrhine	1 (0,1,0)	360	Gummivore	1
Miopithecus talapoin	Catarrhine	3 (3,0,0)	1380	Frugivore/Insectivore	1
Saguinus imperator	Platyrrhine	1 (0,1,0)	475	Frugivore/Nectarivore	1

Saguinus labiatus	Platyrrhine	1 (0,1,0)	539	Frugivore	1
Saguinus oedipus	Platyrrhine	1 (0,1,0)	404	Frugivore	1
Saimiri sciureus	Platyrrhine	2 (1,1,0)	721.4	Frugivore/Insectivore	1
Sapajus apella	Platyrrhine	3 (0,2,1)	2695.8	Frugivore/Granivore	2

[a]Body mass from species average for each sex listed in Fleagle (2013). The species average was used for individuals of unknown sex.

[b]Based on Mittermeier et al. (2012).

TABLE 2. Craniometric Measurements used in geometric mean calculation from Hartstone-Rose and colleagues (2017).

Mandible length from the posterior edge of the condyle to infradentale
Cranial length from prosthion to inion
Height of the mandibular corpus inferior to m2 protoconid
Maximum cranial height from inferior mandible to vertex
Maximum orbital height
Maximum bizygomatic breadth
Maximum cranial breadth posterior to the zygomatic arches
Postorbital constriction (minimum cranial breadth posterior to the orbits)
Biorbital width (maximum width measured on the lateral margins of the orbital walls)

TABLE 3. Descriptive statistics for RMA regressions of BF variables against BM, cranial GM and JL across the whole sample and by dietary category and suborder. As described in the methods, all slopes are expected to be 1. Significance is assessed at an alpha <0.05 and values that approach significance (~) are noted solely for discussion purposes.

Body Size Proxy Y-variable	Sample	Y-intercept	Slope $(\beta)^b$	Lower β CL	Upper β CL	r
			Log Incisor BF^1/2			
Log Body Mass (g) ^ 1/3	All Primates	-0.53	1.01	0.81	1.25	0.91
	Soft Diet	-0.4	0.87	0.6	1.24	0.89
	Obdurate Diet	-0.48	0.99	0.52	1.87	0.85
	Catarrhines	-0.98	1.36	0.79	2.32	0.77
	Platyrrhines	-0.59	1.1	0.47	2.59	0.86
Log Cranial Geometric Mean	All Primates	-0.07	1.14	0.92	1.42	0.91
	Soft Diet	-0.01	0.99	0.68	1.44	0.88
	Obdurate Diet	-0.04	1.14	0.59	2.22	0.84
	Catarrhines	-0.33	1.51~	0.94~	2.42	0.81
	Platyrrhines	-0.01	1.06	0.16	6.83	0.77
Log Jaw Length (mm)	All Primates	-0.09	0.95	0.78	1.16	0.92
	Soft Diet	-0.06	0.89	0.64	1.23	0.91
	Obdurate Diet	0.07	0.79	0.3	2.12	0.76
	Catarrhines	-0.16	1.02	0.63	1.66	0.8
	Platyrrhines	-0.21	1.22	0.56	2.68	0.87
			Log Canine BF^1/2			
Log Body Mass (g) ^ 1/3	All Primates	-0.51	1.01	0.83	2.15	0.8
	Soft Diet	-0.41	0.9	0.65	1.26	0.9
	Obdurate Diet	-0.51	1.03	0.56	1.88	0.86
	Catarrhines	-0.93	1.33	0.83	2.15	0.8
	Platyrrhines	-0.5	1.02	0.44	2.39	0.86
Log Cranial Geometric Mean	All Primates	-0.05	1.14~	0.94~	1.4	0.92
	Soft Diet	0	1.03	0.73	1.46	0.89
	Obdurate Diet	-0.06	1.18	0.62	2.27	0.84
	Catarrhines	-0.28	1.48~	0.98~	2.23	0.84
	Platyrrhines	0.04	0.98	0.09	10.38	0.76
Log Jaw Length (mm)	All Primates	-0.06	0.95	0.79	1.14	0.93
	Soft Diet	-0.06	0.93	0.7	1.23	0.92
	Obdurate Diet	0.06	0.82	0.35	1.96	0.79
	Catarrhines	-0.11	1	0.65	1.54	0.83
	Platyrrhines	-0.15	1.14	0.5	2.59	0.86
			Log Protoconid BF^1/2			
Log Body Mass (g) ^ 1/3	All Primates	-0.37	0.94	0.77	1.15	0.92
	Soft Diet	-0.25	0.82	0.58	1.15	0.89
	Obdurate Diet	-0.38	0.97	0.55	1.71	0.87
	Catarrhines	-0.82	1.29	0.79	2.11	0.8

	Platyrrhines	-0.38	0.98	0.47	2.03	0.88
Log Cranial Geometric Mean	All Primates	0.06	1.07	0.88	1.31	0.92
	Soft Diet	0.12	0.93	0.66	1.32	0.89
	Obdurate Diet	0.05	1.12	0.65	1.93	0.88
	Catarrhines	-0.19	1.43~	0.97~	2.12	0.85
	Platyrrhines	0.14	0.94	0.22	4.08	0.79
Log Jaw Length (mm)	All Primates	0.05	0.89	0.74	1.06	0.94
	Soft Diet	0.07	0.84	0.63	1.11	0.93
	Obdurate Diet	0.16	0.78	0.37	1.65	0.82
	Catarrhines	-0.03	0.97	0.65	1.45	0.84
	Platyrrhines	-0.04	1.08	0.53	2.21	0.88

TABLE 4. Descriptive statistics for one-way analyses of residuals of BF variables grouped by dietary score. P-values annotated by "~" approach significance. Significance is defined as an alpha of 0.05.

Deutsch: Scaling of Anatomically Derived Maximal Bite Force in Primates

Architecture Variable	p-value	Statistically higher dietary group
Body Mass (BM)		
Incisor Bite Force ^1/2	0.1599~	~Obdurate
Canine Bite Force ^1/2	0.2788	
Paracone Bite Force ^1/2	0.1853~	~Obdurate
Cranial Geometric Mean (GM)		
Incisor Bite Force ^1/2	0.1970~	~Obdurate
Canine Bite Force ^1/2	0.3369	
Paracone Bite Force ^1/2	0.2124	
Mandible Length (JL)		
Incisor Bite Force ^1/2	0.3667	
Canine Bite Force ^1/2	0.5866	
Paracone Bite Force ^1/2	0.3869	