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The Effects of Diet, Size, and Phylogeny on Primate Dental Proportions

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The Effects of Diet, Size, and Phylogeny on Primate Dental Proportions

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Arts in Anthropology

by

Rudolph J. Wilkins
Oklahoma State University
Bachelor of Science in Anthropology, 2021

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This thesis is approved for recommendation to the Graduate Council.

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ABSTRACT

It is generally appreciated that there is a relationship between the relative size of the incisors, mandible length, and diet in primates. More specifically, the differences in relative incisor size among primate species are believed to be evolutionary adaptations to their use during food processing and acquisition. While this satisfactorily explains relatively large incisors, it fails to address the relatively small incisor size seen in many taxa.

One hypothesis is that there is a trade-off between molar size and incisor size in species with relatively short mandibles. The following study uses two-way ANOVA to evaluate the possibility that spatial constraint limits incisor size as a function of mandible length and molar size to better understand the evolutionary pressures that might drive anterior tooth size variation. I hypothesize folivores will demonstrate dental and mandibular proportions consistent with incisor size that is partly impacted by spatial constraint.

Results from the analyses show an association between mandibular length and mesiodistal tooth lengths, which may reflect crowding in the dental arcade. Future research into this topic will contribute to our understanding of the development of megadontia and subsequent anterior tooth reduction seen among early hominins.

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I also want to thank my dearest mother, Vanessa Wilkins, for supporting me when nobody else did. You never doubted me even when I doubted myself. Thank you for always believing in my capabilities as a student, scholar, researcher, and writer.

DEDICATION

This thesis is dedicated to my recently deceased grandfather, Dr. William Arthur Davis Sr. Thank you for inspiring me to pursue a career in education and providing me with positive affirmations the whole way through. Without your gentle words of encouragement, I would not be where I am today. I can only hope I accomplish half as much as you did in your illustrious life. Your motto is forever with me:

“To know nothing of the past, is to know little of the present, with no conception of the future”.

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INTRODUCTION

Among primates, folivores have relatively smaller incisors than frugivores (e.g., Anthony & Kay, 1993; Anapol & Lee, 1994; Eaglen, 1984; Fleagle, 1988; Hylander, 1975; Scott, 2021). Differences in relative incisor size are explained as a product of incisal preparation, whereby species that eat large, fleshy fruits functionally benefit from an expanded anterior cutting surface more so than leaf-eating taxa (Ang et al., 2006; Hylander, 1975; Scott, 2021). While this conclusion is satisfactory in explaining why frugivores have larger incisors, it fails to address possible alternative hypotheses, such as the adaptive benefit of having smaller incisors.

This question is especially interesting with regard to the megadont hominins, who have a package of derived traits, including small incisors, long thought to reflect hard object feeding. All *Paranthropus* species possessed large posterior teeth and small anterior ones by comparison (Wood & Schroer, 2013). The molars of this group were broad and flat, with thick enamel to provide resistance against wear (Constantino et al., 2018). In addition, the molarization of the premolars in *Paranthropus*, particularly the P₄, suggest a level of morphological divergence from sympatric early *Homo* taxa (Schroer & Wood, 2015). The total occlusal area of the posterior teeth in combination with the large muscles of mastication would have given this group the ability to process a much larger amount of food per chewing cycle than other hominins (Grine, 1986). By contrast, the incisors were small and narrow, being more comparable in size to modern humans (Grine, 1986; Ungar & Grine, 1991; Wood & Constantino, 2007). Many authors have suggested the small incisors of this group indicate they would have had a diet that required only minimal incisal preparation (e.g., Eaglen, 1984; Hylander, 1975; Kay, 1985; Ungar & Grine, 1991; Wood & Constantino, 2007). Ungar (1991), in a study of incisor microwear, found that the wear dimensions, scratch orientation, and pitting indices of *Paranthropus robustus* and

Australopithecus africanus were all comparable but that the taxa differed in mean feature density. This suggests *A. africanus* potentially processed more abrasive foods with their incisors and may have used them more often during feeding. More recent evidence using stable isotope analysis has found that *P. boisei*, specifically, had a diet that consisted primarily of C₄ resources, while the South African *P. robustus* had a varied diet more like that of other early hominins (Cerling et al., 2011). Even so, both taxa show varying degrees of wear on the anterior dentition, which suggests the incisors of *P. robustus* were used extensively during feeding despite their smaller relative size. This is problematic if we are to assume incisor size is dependent on use during food preparation since those of *Paranthropus* are simultaneously worn and relatively small (Hylander, 1975). Since *Paranthropus* incisors demonstrate a similar wear pattern to other hominins, a small object diet as suggested by Hylander (1975) may not entirely explain the degree of anterior reduction seen in this group.

Similarly, many extant species traditionally viewed as being more folivorous also utilize their incisors quite frequently despite their smaller relative size. Fruits, seeds, nuts, and bark all represent supplementary food sources harvested by monogastric folivores (Anthony & Kay, 1993; Bouvier, 1986; Hylander, 1979). Even among folivorous species, incisors remain important in food gathering and processing.

While the dietary model is commonly accepted, it has not been the object of much research. Alternative models to explain variation in incisor size have not received a lot of attention. Outside of Scott (2021), few researchers have examined how mandible length may be used to compare relative incisor size. As such, it is possible incisor size is constrained by space rather than diet specifically. The following thesis proposes the idea (called here the Spatial Constraint Hypothesis) that small incisors are a product of limited space within the dental arcade.

The implications of spatial constraint as a product of face length and dental crowding are analyzed to better understand what evolutionary pressures may have resulted in anterior tooth reduction among folivores species.

BACKGROUND

The Spatial Constraint Hypothesis

Many studies have demonstrated variation in the dental proportions of primates (e.g., Anapol & Lee, 1994; Anthony & Kay, 1993; Eaglen, 1984; Fleagle, 1988; Hylander, 1975; Scott, 2021). However, the interdependence between tooth and jaw size is not well understood. Theoretically, the absolute size of the teeth may be limited by the space provided for them within the mandible and maxilla. Tooth dimensions that exceed the normal range of variation may disturb mastication by interrupting occlusion (Bishara et al., 1996; Zere et al., 2018). In this analysis, spatial constraint is the idea that constraints on jaw size create limit(s) on the available space for the dentition, and that in folivorous species selection to maintain molar size results in pressure to trade off incisor size. There are a few ways the incisors may be restricted and have pressure to reduce in size: first, if the posterior dentition increases in size relative to total mandible length (i.e., tooth crowding), second, if the total mandible length decreases in size relative to the posterior dentition (i.e., mandibular shrinkage), or third, some combination of these two factors (Figure 1).

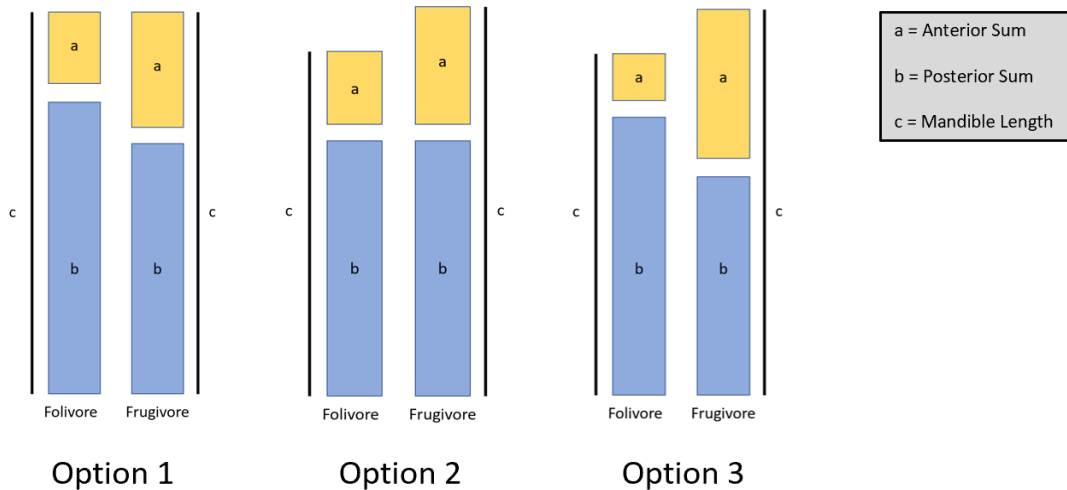


Figure 2: Visualizations of the ways spatial constraint could limit anterior tooth size.

Option 1 – Posterior sum increases in size; mandible length remains constant.

Option 2 – Mandible length decreases in size; posterior sum remains constant.

Option 3 – Mandible length decreases in size; posterior sum increases in size.

Ancestral Incisor Size

For questions pertaining to incisor size, it is important to consider the ancestral condition. Early anthropoid incisors found in the Fayum Depression of Egypt, such as those of *Catopithecus browni* and similarly aged taxa, indicate they would have had subvertically implanted incisors of a moderate to small size with a somewhat spatulate shape (Gunnell & Miller, 2001). These teeth are indicative of a primarily insectivorous diet, likely supplemented by fruits when available. The shape and size of these incisors differ substantially from modern anthropoids, which suggests that all living anthropoids have a derived incisal morphology. This may have occurred due to the increased reliance on large fruiting bodies in anthropoids broadly, regardless of dietary categories (Milton, 1993). However, this interpretation should be approached with caution since tooth use and food item size cannot infer incisor shape when analyzing more distantly related taxa (Ungar, 1996). In addition, factors such as phylogenetic inertia and/or adaptive radiation may also influence the incisor size of anthropoid primates.

Feeding Mechanics

The relationship between tooth size and face length is important to consider when analyzing non-human primates given that the level of prognathism differs quite substantially from species to species. Functionally, the effectiveness of chewing is greatly dependent on the length of the mandible. The masticatory apparatus functions as a class III lever, meaning the load is applied opposite of the fulcrum (Ravosa & Hylander, 1994; Smith, 1978). The key here is the ratio of the bite point lever arm to the muscle lever arm. The closer these two are to one another, the more able you are to convert muscle force to bite force, reducing the inefficiencies of the system (Hylander, 1979; Ravosa & Hylander, 1994). As the span between the anterior teeth and the elevator muscles decreases, bite force exponentially increases. This relationship implies bite force is inversely proportional to overall face length (Hylander, 2013).

Among leaf-eating taxa, compromises are made to increase muscular strength whilst reducing mandible length (Fricano & Perry, 2018). Shorter mandibles resist bending and twisting forces better than long mandibles with a lengthened fulcrum (Bouvier, 1986; Hylander, 1979). A shorter mandible also means less space available for the dentition, with prior evidence in support of this (e.g., Anapol & Lee, 1994; Anthony & Kay, 1993; Eaglen, 1984; Fleagle, 1988; Hylander, 1975; Scott, 2021). The muscles of mastication are also shifted more anteriorly towards the load and away from the fulcrum (jaw joint), increasing the potential strength output further. If the mandible length of folivorous species decreases in size relative to the molars and premolars, this would create a spatial constraint that could limit the maximum length of the anterior dentition.

Dental Adaptations Related to Diet

Folivorous primates possess larger, more complex molars and premolars relative to body size when compared to other dietary groups (Eaglen, 1984; Hylander, 1975; Kay, 1975). Functionally, large cheek teeth with tall, shearing cusps improve the efficiency of the masticatory apparatus when eating resistant foods (Anapol & Lee, 1994; Lucas & Luke, 1984; Thiery, 2017). The anterior teeth of leaf-eating taxa are smaller and simpler by comparison (Hylander, 1975; Scott, 2021). When eating leaves or other small objects, folivores use their incisors as gripping implements or to strip leaves from branches (Ang et al., 2006; Ungar 1994). In addition, they also demonstrate incisal preparation when consuming large fruits (Ungar, 1996).

Even the most folivorous taxa are opportunistic and will feed on a wide variety of food stuffs depending upon availability and seasonality. For example, intensely folivorous species such as *Procolobus verus*, which have a diet consisting primarily of young foliage (59%), also regularly engage in the consumption of unripe fruits, young seeds, flowers, and floral buds (19%) (Oates, 1988). Additionally, sympatric populations of gorillas and chimpanzees living in the forests of Kahuzi have been observed eating fruits at a similar frequency throughout most of the year (Yamagiwa, 2009). However, during periods of prolonged fruit scarcity, gorillas can survive almost exclusively on vegetative foods while chimpanzees must pursue fruiting plants throughout their home range (Yamagiwa, 2009). Even though many folivores use their incisors for food processing and manipulation as often as frugivores, their incisors are smaller (McCollum, 2007). If large incisors are selected in association with processing fruit, this begs the question of why folivores that eat fruit do not also have large incisors. One possible reason is that

the relatively larger posterior teeth present in many folivores may limit the room in the mandible to accommodate broad incisors.

According to the diet model, frugivorous primates have large incisors with an expanded cutting surface to aid in the incisal preparation of soft, fleshy fruits (Eaglen, 1984; Hylander, 1975; Scott, 2021). Conversely, the postcanine dentition of frugivores tends to be relatively smaller (by comparison to mandibular size) with flatter and less pronounced cusps on the molars and premolars (Kay, 1975). It is presumed that there is little selective pressure to shorten the face as processing soft foods require only minimal force on the molars (Bouvier, 1986; Eaglen, 1984; Hylander, 1975; Hylander, 1979; Scott, 2021). In general, fruit-eating taxa lack many of the specialized adaptations seen in folivores since soft foods offer little mechanical resistance when compared to tough foods (Freeman, 1988; Kay, 1975; Lucas & Luke, 1984; Thiery, 2017; Yamashita, 1996).

Studies comparing the tooth dimensions of the highly prognathic cercopithecines and flatter faced colobines found the former possessed larger molars, incisors, and canines on average when size-adjusting dental measurements onto body mass (Hylander, 1975; Lucas, 1981; Lucas, 1982; Scott, 2011). Given that cercopithecines are primarily frugivorous, it is within reason to assume they would possess more broad and lengthened incisors (Hylander, 1975; Scott, 2011; Scott, 2021). However, the fact that they have a larger posterior dentition is a notable exception to the rule that folivorous species, like colobines, would possess larger molars and premolars when scaled upon an independent size measurement.

However, after size-adjusting the posterior dentition onto face length, the conclusion that frugivores have large molars was found to be a consequence of the elongated faces possessed by cercopithecines (Scott, 2011). This is to say, frugivorous cercopithecines have larger molars than

colobines when compared to overall body size, but relatively smaller molars when compared to jaw length specifically. These results seem to suggest that comparing tooth size to facial dimensions, such as mandible length or face length, may provide a more optimal way to assess questions about dental proportions and tooth size, than body size (Scott, 2011; Scott 2021). This is important to consider since the spatial constraint hypothesis refers to the packing of the teeth within the jaw. Therefore, any test of the spatial constraint model should compare tooth size to mandible length, and not body mass (Scott, 2011; Scott 2021).

HYPOTHESES

The primary aim of this thesis is to establish whether a spatial constraint limits the size of the anterior dentition in folivores primates. While many studies have focused on the relationship between diet and incisal preparation as related to incisor size, few have attempted to address possible alternative explanations for the difference between dental ratios (Corruccini & Beecher, 1982; Lucas, 2006; Mills, 1963). Although diet is potentially the single most important parameter to consider when evaluating the differences between masticatory adaptations, other factors, such as jaw length, may prove to be equally, if not more, impactful on tooth size. In addition, primate diets are complex, varied, and notoriously difficult to categorize (Harding, 1981). Ungar (1996) found no correlation between incisor size and number of fruits eaten by sympatric primates at Ketambe. Species that are classified as more folivorous regularly provision resources other than foliage and employ incisal preparation at a similar regularity to other dietary groups (Ungar, 1996).

Naturally, questions about the functional significance of large incisors in certain primates should also be considered. When space is not a confounding factor, large incisors are more

efficient than small incisors for the ingestion of soft fruits. However, there exists a negligible advantage to having large incisors when the space within the dental arches is limited (Bishara et al., 1996; Scott, 2021). In many cases, the relatively small incisors found in folivores are nearly as capable as those of frugivores (Bishara et al., 1996; Scott, 2021). The large molars and premolars of certain species would further impact incisor size since they occupy the most space within the dental arch (Anapol & Lee, 1994; Anthony & Kay, 1993; Eaglen, 1984; Fleagle, 1988; Hylander, 1975; Scott, 2021). As such, it would seem the dimensions of the anterior teeth can only be expanded so far before the physiology of the mandible and muscles of mastication must change in accordance (Anapol & Lee, 1994).

Based on the background and research on primate dental ratios, mandible length, and diet, this thesis proposes several hypotheses:

1. I predict folivorous primates demonstrate various dental signatures indicative of a spatial constraint. Hypotheses about this relationship are as follows.
 - a. Since folivores process a greater volume of lower quality food material, larger cheek teeth should provide greater surface area and be advantageous towards survivability. Therefore, they should possess the largest relative posterior tooth sum regardless of evolutionary history. In addition, using mandible length instead of body size as a relative size measurement could push the lower boundary of how small molars can be and still be functional (Scott, 2011; Scott 2021). Considering this, it is also possible folivores have an even smaller relative incisor size to mandible length than body mass. In addition, diet and mandible length are at least partially a product of phylogenetic relations since more closely related species often

provision the same food types at a similar regularity. As such, controlling for a suspected phylogenetic signal is essential in this analysis.

- b. Prior research has already established that frugivores possess larger incisors compared to folivores when scaled to body mass (Hylander, 1975; Lucas, 1981; Lucas, 1982). However, few analyses have been conducted using jaw length as the relative size measurement (Scott, 2011; Scott 2021). Here, I predict frugivores to have the largest relative anterior tooth sum and potentially show a greater variation in tooth size since fruit-eating taxa are not limited by either space in the jaw or large posterior teeth. Conversely, since it is presumed that mandibular shrinkage and/or posterior tooth enlargement is driving much of the reduction in relative incisors size seen in folivores, I hypothesize they will have the smallest anterior tooth sum relative to jaw length and less variation in tooth size regardless of evolutionary history when compared to frugivores.
- c. Frugivorous primates should have the largest anterior to posterior summed-tooth-size ratio regardless of evolutionary history. This assumes the length of the posterior dentition proportionally occupies a greater space within the mandible of folivores than the incisors. As such, the anterior dentition would be constrained by either a shrinking dental arcade, an expanding posterior dental battery, or some combination of these factors (Figure 1). It is also possible that folivores and frugivores could have approximately equal ratios of dental ratios. This outcome

would imply the dentition of folivores is decreasing in size proportionally to mandible length.

2. When assessing the absolute differences between males and females within this sample, I expect the relationships between variables to be comparable even though the former should have significantly larger dental measurements on average. For example, the anterior dental battery should encompass proportionately the same space within the mandible regardless of sex. Any variation seen would therefore be insignificant. However, male primates who experience a high degree of intrasexual sexual selection often possess large canines to aid in competition over mates. If the effects of canine dimorphism ultimately prove to be impactful the relationship between variables may differ quite drastically between the sexes. These enlarged teeth would then provide yet another spatial limitation on the males of highly dimorphic species.

MATERIALS AND METHODS

Primate Sample

Mesiodistal lengths for the mandibular dentition (i1, i2, c1, p2*, p3, p4, m1, m2, m3) and representative mandible lengths from condyle to infradentale inferior (idi) were sourced from Plavcan (1990, 2002, 2003). Dental measurements from only one side of the mandible were used in this study. The combined dental/mandibular sample totals over 2,500 specimens across 79 species/subspecies of haplorrhines (62 catarrhines and 17 platyrrhines) (Table 1). Dental wear was ranked from 1 to 3, with 3 representing the most extreme occlusal wear. Since this analysis focuses on tooth length rather than topographic features or functional use, light abrasion and

erosion present on specimens is not of great concern. Specimens which exhibit excessive wear were removed from the data set prior to the analysis. Given the totality of the data set, sample sizes range from 1 to 57 individuals per sex depending on the species. Males and females were analyzed separately.

Dental ratios were calculated by adding up the mean mesiodistal lengths of the corresponding teeth for each species (Figure 2). Four dental sum measurements were used in this analysis, which include the anterior sum length (i1, i2, and c1), posterior sum length (p2*, p3, p4, m1, m2, m3), posterior sum w/ canine length (c1, p2*, p3, p4, m1, m2, m3), and incisor sum length (i1, i2). Dimensionless shape ratios were created by dividing each dental sum by mandible length or the opposing dental measurement (e.g., anterior sum/mandible length: anterior sum/posterior sum). Spatial constraint as a function of mandibular shrinkage was assessed using ratios consisting of a dental sum measurement and mean mandible length representing each species (i.e., anterior sum / mandible length). Spatial constraint as a function of dental crowding was assessed using ratios consisting of two opposing dental sum measurements (i.e., anterior sum / posterior sum).

Ranking Diet

Diet is defined as the food group most often eaten by any given species within their natural environment. For wild primates, diet is based on observed feeding time dedicated to each food category (e.g., most time eating fruit = frugivore, most time eating leaves = folivore). Feeding habits were sourced from secondary literature and have been categorically ranked based on the majority food type consumed (Bowler & Bodmer, 2011; Chapman & Fedigan, 1990; Clutton-Brock & Harvey, 1980; Cunningham & Janson, 2006; de Carvalho Jr. et al., 2004;

DeCasien, 2017; Dunbar, 1974; Elder, 2009; Galetti & Pedroni, 1994; Gittins, 1982; Guillotin, 1994; Jaffe & Isbell, 2007; Jones et al., 2009; Kaplin & Moermond, 2007; Kappeler & Heyman, 1996; McGraw, 2017; Oates, 1985; Oates, 1988; Olaleru et al. 2020; Olupot et al. 1998; Palombit, 1997; Pinheiro & Pontes, 2015; Smith & Jungers, 1997; Stevenson et al., 1994; Van Roosmalen et al. 1988; Viela & Del-Claro, 2011). After grouping, the sample consists of 24 folivores and 55 frugivores (Supplemental Data). Careful consideration has been taken to ensure species were not egregiously misclassified by cross comparing the primary literature within each of the secondary sources referenced.

Canine Integration

New research into size/shape covariation suggests the mandibular canine area may be uncoupled from either the posterior or incisor areas within the alveolar bone (Delezene, 2015; Lawrence & Kimbel, 2021; Steltzer et al., 2017). The independence of variation in the canines is important to the spatial model since integration would imply that a genetic mechanism might constrain variation in size. The difference in canine area is described as a response to species-specific sexual dimorphism, size correlation, and shape covariation (Lawrence & Kimbel, 2021; Steltzer et al., 2017).

Several analyses were run multiple times to address the question of canine integration. For the first series of tests, the mandibular incisor and canine measurements were added together to create a single variable, called anterior sum length (Figure 2). The assumption here is that the canines are either functionally or genetically integrated with the incisors. Therefore, both units would potentially face a spatial constraint from mandible length and/or posterior sum length.

For the second series of tests, the mesiodistal lengths of the canine, molars, and premolars were added together to create a new variable called posterior sum w/ canines (Figure 2). The assumption here is that the canines are either functionally or genetically integrated with the posterior dentition. Therefore, posterior sum w/canine length and/or mandible length may create a spatial constraint with regard to incisor size.

For the last series of tests, the canine measurements were excluded from the analyses all together. The assumption made here is that the canines are morphologically independent. Therefore, incisor size faces a spatial constraint from mandible length and/or posterior sum length, but not from the canines.

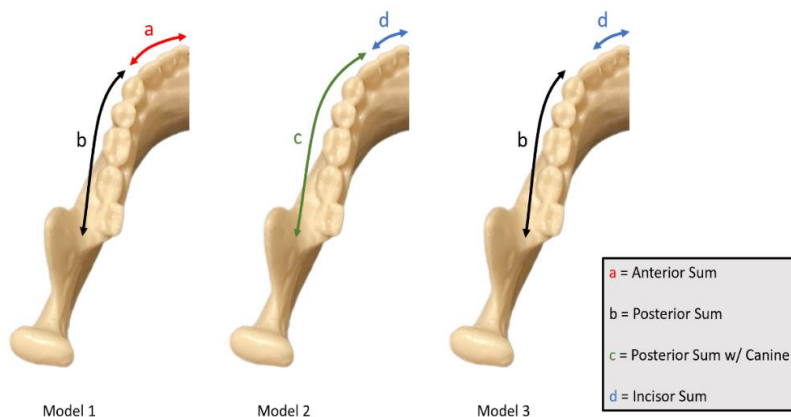


Figure 2: Three dental models for testing spatial constraint. (a) Anterior sum is the total mesiodistal length of $i1$, $i2$, $c1$. (b) Posterior sum is the total mesiodistal length of $p2^$, $p3$, $p4$, $m1$, $m2$, $m3$. (c) Posterior sum w/ canine is the total mesiodistal length of $c1$, $p2^*$, $p3$, $p4$, $m1$, $m2$, $m3$. (d) Incisor sum is the total mesiodistal length of $i1$, $i2$.*

Testing Parameters

All statistical analyses were carried out in RStudio Ver. 4.2.3 (Posit Software, Boston, MA). The packages used include ape, nlme, geiger, lme4, caper, picante, phytools, smart,

ggplot2, and ggpubr. The phylogenetic tree used to represent evolutionary history was sourced from the 10KTree website (Anderson et al. 2010). The critical alpha value was 0.05 for all analyses.

Experimental Design

The data failed to meet the assumptions of a parametric test (linearity, independence, normality, equal variance) prior to the necessary transformations. Generally, ANOVA and its derivatives are robust to asymmetry when the sample sizes are roughly equal. However, the taxa representing frugivores in this data set is nearly double the sample size of that of folivores (Table 2). To combat asymmetry, the shape ratios were transformed using natural log to normalize the non-linear distribution of data prior to analysis. Natural log was chosen over log 10 since it is the most used method of transformation for biological data and provides an approximate representation of difference that is easily diametrically interpretable.

Next, a series of two-way ANOVAs (Analysis of Variance) were run to see whether diet or sex influence the proportionality of the dimensionless tooth ratios. In total, seven tests were performed in conjunction with the three dental models previously described (Figure 2). Considering the experimental design, a potential interaction between the effect variables is not expected since they are independent of one another. In addition, a post-hoc analysis will not be necessary since each of the effect variables only has two levels. Box and whisker plots are used to help visualize the results of the two-way ANOVA, illustrate the difference between groups, and make inferences about potential canine integration.

To control the effects of phylogenetic proximity, multiple phylogenetic ANOVAs were used to see if diet still influences relative tooth ratios after accounting for non-independence

(Adams & Collyer, 2018; Garland et al., 1993; Rohlf & Nielsen, 2015). Controlling for a suspected phylogenetic signal works to identify whether ancestor-descendent relations influence gene expression in accordance with Brownian motion (Kamilar & Cooper, 2013). With regards to the following analysis, it is important to assess each sum length individually to determine the weight of each tested variable. Brownian motion is assumed to minimize the effects of biological relatedness on dental sum measurements of different dietary groups. Also known as “random walk,” Brownian motion describes the complete independence of direction and magnitude within trait evolution (Kamilar & Cooper, 2013). Here, any changes to a trait in direction and distance occur at random intervals across space and time. The parameter used to assess the phylogenetic signal is the p-value of the f-ratio. If this value falls below the alpha threshold, then we would reject the null hypothesis.

RESULTS

Descriptive statistics of are presented in Tables 1 and 2.

Table 1: Summary of the sample

<u>Parvorder</u>	<u>Genus</u>	<u>Species/subspecies</u>	<u>Sex</u>	<u><i>n</i></u>	
Platyrrhini	<i>Callicebus</i>	<i>C. moloch</i>	M	12	
			F	7	
		<i>C. torquatus</i>	M	10	
			F	10	
		<i>Aotus</i>	<i>A. lemurinus</i>	M	13
				F	13
	<i>A. trivirgatus</i>		M	7	
	<i>Cebus</i>	<i>C. apella</i>	F	18	
			M	18	
		<i>C. capucinus</i>	F	21	
			M	27	
			F	26	

Table 1 Cont.

	<i>Saguinus</i>	<i>S. fuscicollis</i>	M	19
			F	15
	<i>Alouatta</i>	<i>A. belzebul</i>	M	10
			F	10
		<i>A. caraya</i>	M	10
			F	10
		<i>A. guariba</i>	M	8
			F	10
		<i>A. palliata</i>	M	14
			F	21
		<i>A. pigra</i>	M	7
			F	9
		<i>A. seniculus</i>	M	22
			F	19
	<i>Ateles</i>	<i>A. geoffroyi</i>	M	22
			F	20
		<i>A. paniscus</i>	M	10
			F	15
	<i>Brachyteles</i>	<i>B. arachnoides</i>	M	4
			F	4
	<i>Lagothrix</i>	<i>L. lagotricha</i>	M	14
			F	9
Catarrhini	<i>Allenopithecus</i>	<i>A. nigroviridis</i>	M	11
			F	5
	<i>Cercopithecus</i>	<i>C. ascanius</i>	M	23
			F	21
		<i>C. cephus cephus</i>	M	24
			F	16
		<i>C. diana</i>	M	9
			F	18
		<i>C. erythrogaster</i>	M	3
			F	3
		<i>C. erythrotis</i>	M	4
			F	5
		<i>C. lhoesti</i>	M	15
			F	11
		<i>C. mitis</i>	M	25
			F	14
		<i>C. mona</i>	M	20
			F	10
		<i>C. neglectus</i>	M	24
			F	15

Table 1 Cont.

	<i>C. nictitans</i>	M	24
		F	21
	<i>C. petaurista</i>	M	13
		F	4
	<i>C. pogonias</i>	M	30
		F	23
	<i>C. preussi</i>	M	7
		F	7
	<i>C. wolfi</i>	M	12
		F	11
<i>Chlorocebus</i>	<i>C. pygerythrus</i>	M	60
		F	47
	<i>C. sabaesus</i>	M	7
		F	9
<i>Cercocebus</i>	<i>C. agilis</i>	M	11
		F	6
	<i>C. torquatus atys</i>	M	19
		F	20
<i>Lophocebus</i>	<i>L. albigena</i>	M	8
		F	4
	<i>L. aterrimus</i>	M	21
		F	17
<i>Macaca</i>	<i>M. sinica</i>	M	26
		F	15
	<i>M. fascicularis</i>	M	11
		F	16
	<i>M. fuscata</i>	M	11
		F	25
	<i>M. hecki</i>	M	12
		F	13
	<i>M. mulatta</i>	M	31
		F	32
	<i>M. nemestrina</i>	M	20
		F	14
	<i>M. nemestrina leonina</i>	M	4
		F	5
	<i>M. nigra</i>	M	21
		F	16
	<i>M. silenus</i>	M	3
		F	1
	<i>M. tonkeana</i>	M	12
		F	12
<i>Mandrillus</i>	<i>M. leucophaeus</i>	M	25

Table 1 Cont.

		F	18
	<i>M. sphinx</i>	M	8
		F	3
<i>Theropithecus</i>	<i>T. gelada</i>	M	24
		F	6
<i>Colobus</i>	<i>C. guereza</i>	M	28
		F	35
	<i>C. polykomos</i>	M	25
		F	25
<i>Nasalis</i>	<i>N. larvatus</i>	M	7
		F	8
<i>Piliocolobus</i>	<i>P. badius</i>	M	26
		F	18
	<i>P. kirkii</i>	M	2
		F	9
<i>Presbytis</i>	<i>P. comata</i>	M	8
		F	7
<i>Procolobus</i>	<i>P. verus</i>	M	24
		F	22
<i>Pygathrix</i>	<i>P. nemaeus</i>	M	15
		F	9
<i>Rhinopithecus</i>	<i>R. roxellana</i>	M	3
		F	3
<i>Semnopithecus</i>	<i>S. entellus</i>	M	57
		F	52
<i>Trachypithecus</i>	<i>T. cristatus</i>	M	20
		F	20
	<i>T. francoisi</i>	M	4
		F	5
	<i>T. johnii</i>	M	3
		F	3
	<i>T. obscurus</i>	M	18
		F	27
	<i>T. vetulus</i>	M	22
		F	23
<i>Brunopithecus</i>	<i>B. hoolock</i>	M	34
		F	15
<i>Gorilla</i>	<i>G. gorilla gorilla</i>	M	20
		F	20
<i>Hylobates</i>	<i>H. agilis</i>	M	16
		F	9
	<i>H. klossii</i>	M	14
		F	7

Table 1 Cont.

	<i>H. lar</i>	M	20
		F	20
	<i>H. pileatus</i>	M	3
		F	2
<i>Nomascus</i>	<i>N. concolor</i>	M	7
		F	9
<i>Pan</i>	<i>P. paniscus</i>	M	17
		F	14
	<i>P. troglodytes schweinfurthii</i>	M	9
		F	6
	<i>P. troglodytes troglodytes</i>	M	14
		F	25
<i>Pongo</i>	<i>P. abelii</i>	M	3
		F	4
	<i>P. pygmaeus</i>	M	20
		F	20
<i>Symphalangus</i>	<i>S. syndactylus</i>	M	28
		F	25

Table 2: Averages for species within dietary categories

<u>Dental Sum</u>	<u>Diet</u>	<u>Sex</u>	<u>N</u>	<u>Mean</u>	<u>SD</u>
Anterior Sum	Folivore	Female	24	12.8mm	3.9mm
		Male	24	14.3mm	5.3mm
	Frugivore	Female	55	13.3mm	5.2mm
		Male	55	15.2mm	6.4mm
Posterior Sum	Folivore	Female	24	37.8mm	9.2mm
		Male	24	41.1mm	11.1mm
	Frugivore	Female	55	32.3mm	11.1mm
		Male	55	35.5mm	14.1mm
Incisor Sum	Folivore	Female	24	6.8mm	2.3mm
		Male	24	6.8mm	2.6mm
	Frugivore	Female	55	7.5mm	3.2mm

Table 2 Cont.

		Male	55	7.7mm	3.4mm
Posterior Sum w/Canine	Folivore	Female	24	43.9mm	10.8mm
		Male	24	48.6mm	26.1mm
	Frugivore	Female	55	40.3mm	13.0mm
		Male	55	45.9mm	13.6mm
Mandible Length	Folivore	Female	24	78.0mm	18.8mm
		Male	24	87.9mm	13.6mm
	Frugivore	Female	55	71.6mm	24.6mm
		Male	55	86.2mm	17.1mm

Non-Phylogenetic Results

Table 3: Analytical statistics comparing relative dental ratios to different dietary groups and sex prior to controlling phylogeny.

Two-Way ANOVA ResultsLn (Anterior Sum/Mandible Length) ~ Diet * Sex

Source	df	Mean Squares	F-ratio	p-value
Diet	1	0.575	37.52	<0.001
Sex	1	<.001	0.006	0.941
Diet:Sex	1	0.001	0.066	0.797

Ln (Posterior Sum/Mandible Length) ~ Diet * Sex

Source	df	Mean Squares	F-ratio	p-value
Diet	1	0.172	30.73	<0.001
Sex	1	0.044	7.875	0.006
Diet:Sex	1	<.001	0.038	0.846

Ln (Anterior Sum/Posterior Sum) ~ Diet * Sex

Source	df	Mean Squares	F-ratio	p-value
Diet	1	1.375	64.182	<0.001
Sex	1	0.04	1.876	0.173
Diet:Sex	1	<.001	0.014	0.905

Ln (Incisor Sum/Mandible Length) ~ Diet * Sex

Source	df	Mean Squares	F-ratio	p-value
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Table 3 Cont.

Diet	1	1.144	43.184	<0.001
Sex	1	0.413	15.595	<0.001
Diet:Sex	1	0.003	0.102	0.75

Ln (Posterior Sum w. Canine/Mandible Length) ~ Diet * Sex

Source	df	Mean Squares	F-ratio	p-value
Diet	1	0.085	19.283	<0.001
Sex	1	0.004	0.991	0.321
Diet:Sex	1	<.001	0.108	0.743

Ln (Incisor Sum/Posterior Sum) ~ Diet * Sex

Source	df	Mean Squares	F-ratio	p-value
Diet	1	2.202	66.627	<0.001
Sex	1	0.188	5.675	0.01
Diet:Sex	1	0.001	0.043	0.837

Ln (Incisor Sum/Posterior Sum w. Canine) ~ Diet * Sex

Source	df	Mean Squares	F-ratio	p-value
Diet	1	1.854	62.559	<0.001
Sex	1	0.333	11.223	<0.001
Diet:Sex	1	0.001	0.031	0.861

Model 1

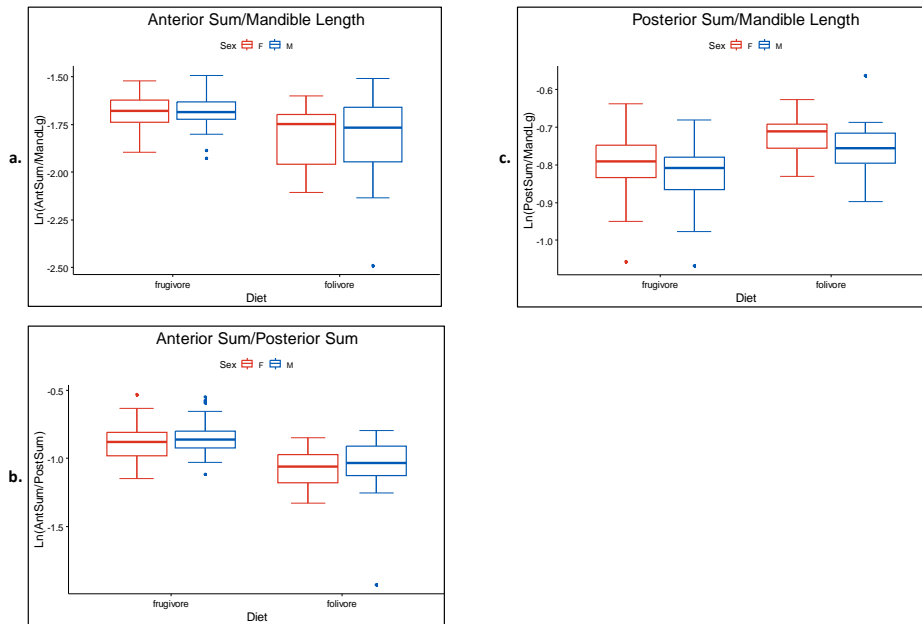
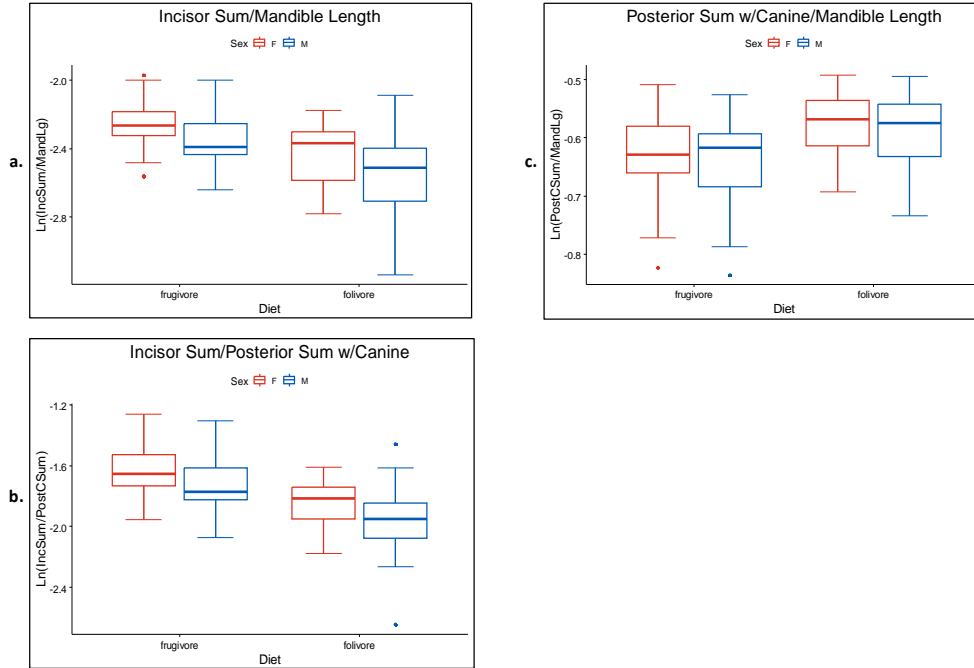


Figure 3 Cont.

Model 2



Model 3

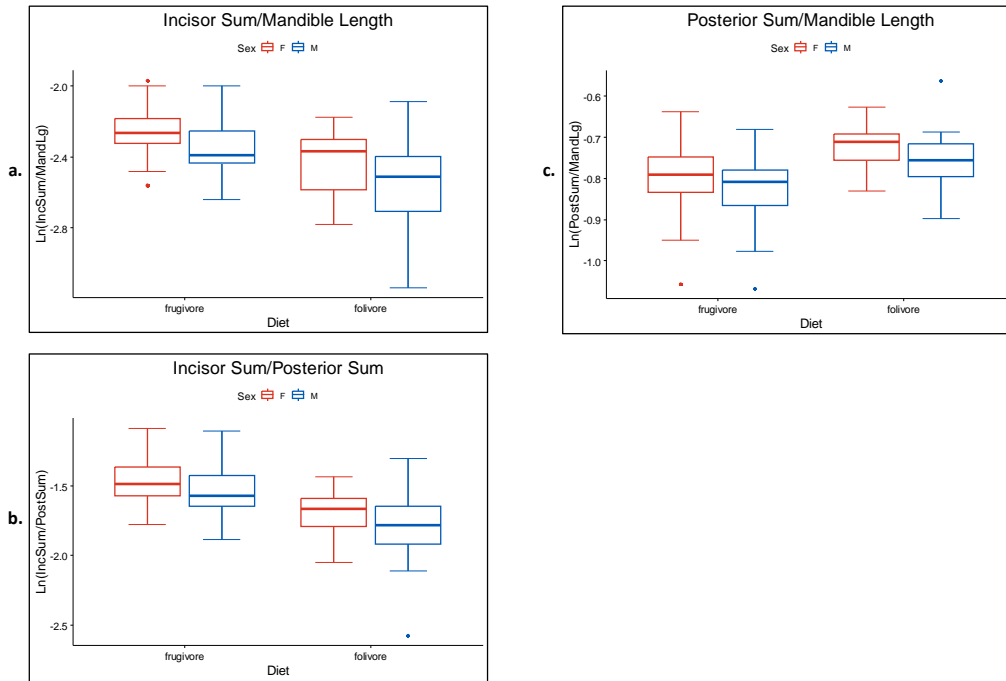


Figure 3: Box and Whisker plots for dental sum analysis. Boxes indicate the interquartile ranges (middle 50% of data). Whiskers indicate the upper and lower extreme ranges (25th and 75th

percentile). The median is represented by the middle quartile line. Females are represented in red. Males are represented in blue.

Two-Way ANOVA

The results for the two-way ANOVAs differed depending on the shape ratio (Table 3). Diet was found to be statistically significant in all tests regardless of the response variable ($p < 0.05$). Comparatively, sex resulted in a significant p -value in only four of the seven tests. These include the log-transformed ratios of posterior sum / mandible length ($p = 0.006$), incisor sum / mandible length ($p < 0.001$), incisor sum / posterior sum ($p = 0.01$), and incisor sum / posterior sum w. canine ($p < 0.001$). A significant interaction was not detected between the effect variables in any of the tests ($p > 0.05$). The supplementary box and whisker plots are used to help visualize the range of data (Figure 3).

Box and Whisker Plots

Box and whisker plots help visualize the range of data (Figure 3). Corresponding to the first dental model, frugivores have a larger anterior sum ratio, while folivores have a larger posterior sum ratio (Figure 3). According to the two-way ANOVA performed on the anterior sum ratio, sex is not a statistically significant effect factor ($p = 0.941$). These plots demonstrate males have a greater upper extreme range but a slightly lower median value when observing the effect of sex on this measurement. By comparison, sex was found to be statistically significant on the posterior sum ($p = 0.006$). Females have a greater upper extreme range and median value when compared to males.

Corresponding to the second dental model, frugivores have a larger incisor sum ratio, while the posterior sum with canine ratio was found to be larger in folivores (Figure 3).

According to the two-way ANOVA, sex is a significant effect variable for the incisor sum ($p = 0.001$), but not for the posterior sum with canine ($p = 0.321$). With the incisor sum, the plots demonstrate males present a greater upper extreme range, while females present a much higher median value by comparison. With the posterior sum w/canine, the results differ depending on diet. Frugivorous males have a higher median value but a lower upper extreme range, while folivorous males have a lower median value and upper extreme range than females.

Corresponding to the third dental model, both diet and sex were found to be significant. The box and whisker plots indicate frugivores have a larger incisor sum, while the posterior sum was found to be larger in folivores (Figure 3). Unlike the previous models, females present a higher median value and upper extreme range in both dental sum measurements.

Phylogenetic Results

Table 4: Analytical statistics comparing the relative dental ratios of different dietary groups after controlling phylogeny.

A. Phylogenetic ANOVA Comparisons

Females			Males		
<u>Ln (Ant. Sum/Mand. Length) ~ Diet</u>			<u>Ln (Ant. Sum/Mand. Length) ~ Diet</u>		
Mean			Mean		
Sq.	<i>F</i> -ratio	<i>p</i> -value	Sq.	<i>F</i> -ratio	<i>p</i> -value
0.264	23.166	0.052	0.312	16.209	0.091
<u>Ln (Post. Sum/Mand. Length) ~ Diet</u>			<u>Ln (Post. Sum/Mand. Length) ~ Diet</u>		
Mean			Mean		
Sq.	<i>F</i> -ratio	<i>p</i> -value	Sq.	<i>F</i> -ratio	<i>p</i> -value
0.092	17.250	0.115	0.080	13.681	0.148
<u>Ln (Ant. Sum/Post. Sum) ~ Diet</u>			<u>Ln (Ant. Sum/Post. Sum) ~ Diet</u>		

Table 4 Cont.

Mean	Sq.	<i>F</i> -ratio	<i>p</i> -value
	0.668	39.050	0.015

Mean	Sq.	<i>F</i> -ratio	<i>p</i> -value
	0.708	27.487	0.038

Ln (Inc. Sum/Mand. Length) ~ Diet

Mean	Sq.	<i>F</i> -ratio	<i>p</i> -value
	0.518	25.498	0.038

Ln (Inc. Sum/Mand. Length) ~ Diet

Mean	Sq.	<i>F</i> -ratio	<i>p</i> -value
	0.708	19.248	0.087

Ln (Post. Sum w. Canine/Mand. Length) ~ Diet

Mean	Sq.	<i>F</i> -ratio	<i>p</i> -value
	0.049	12.153	0.157

Ln (Post. Sum w. Canine/Mand. Length) ~ Diet

Mean	Sq.	<i>F</i> -ratio	<i>p</i> -value
	0.036	7.616	0.255

Ln (Inc. Sum/Post. Sum) ~ Diet

Mean	Sq.	<i>F</i> -ratio	<i>p</i> -value
	1.046	40.905	0.017

Ln (Inc. Sum/Post. Sum) ~ Diet

Mean	Sq.	<i>F</i> -ratio	<i>p</i> -value
	1.158	28.558	0.044

Ln (Inc. Sum/Post. Sum w. Canine) ~ Diet

Mean	Sq.	<i>F</i> -ratio	<i>p</i> -value
	0.886	38.276	0.021

Ln (Inc. Sum/Post. Sum w. Canine) ~ Diet

Mean	Sq.	<i>F</i> -ratio	<i>p</i> -value
	0.968	26.819	0.043

Phylogenetic ANOVA

After using Phylogenetic ANOVA to control evolutionary relatedness, four of the seven comparisons maintained significance when regressed on diet (Table 4). These include the log transformed ratios of anterior sum / posterior sum (Male: $p = 0.038$, Female $p = 0.015$), incisor sum / mandible length (Male: $p = 0.038$, Female $p = 0.038$), incisor sum / posterior sum (Male: $p = 0.044$, Female $p = 0.017$), and incisor sum / posterior sum with canine (Male: $p = 0.021$, Female $p = 0.043$). These tests produced comparable results for both males and females.

DISCUSSION

Overall, the results of this analysis corroborate the spatial constraint hypothesis. Summary statistics for the two-way ANOVA tests confirm there is a difference between the dental proportions of frugivores and folivores (Table 3). The results described here do not disprove the diet model necessarily. Rather, they suggest face length is yet another limiting factor on tooth size.

The variability of primate feeding habits can sometimes mask results if diet is not considered as a gradient. However, this does not seem to be the case in this analysis. In all tests, the p -value for diet falls well below the alpha threshold ($\alpha = 0.05$) and the F -values are comparatively large ($F > 15$). In addition, the box plots suggest folivorous primates exhibit the various dental signatures hypothesized in this analysis (e.g., largest relative posterior tooth sum; the smallest relative anterior tooth sum).

Sex was significant in four of the seven tests. This effect is likely a response to the large canines found in the males of highly dimorphic primates. These teeth would potentially limit maximum incisor size within the tooth row. Regarding canine integration, three of these tests did not incorporate the canines into the dental sum at all. In all cases where significance was identified, females had the higher median value and consistently presented significantly larger relative dental size on average. The most intriguing set of outcomes were between the incisor / posterior and anterior / posterior ratios. As seen in the corresponding box plots, females have a larger incisor / posterior ratio than males in both dietary groups. This indicates they have larger incisors when scaled onto the posterior sum. However, after incorporating the canines into the incisor sum, the effect was neutralized. In fact, males now presented a slightly larger anterior / posterior ratio. Without factoring canines into the incisor sum, females have larger measurement

since males are constrained by not just the previously established factors (i.e., mandible length, spatial crowding by posterior expansion, etc.) but also by canine size. Evolutionarily, it is not that the incisors of female primates have gotten any larger, only that they have maintained relative size within the tooth row. These results were a product of sexual size dimorphism, particularly with canines, that ultimately proved to be impactful on the results. Even still, the relationships between variables (tooth sum ~ diet) were comparable between males and females throughout this analysis.

Results from the Phylogenetic ANOVA suggest that phylogeny drives at least some of the variation seen previously in the two-way ANOVA model (Table 4). After controlling phylogeny, diet was found to be significant in four of the tests for females and three of the tests for males. The comparative sum tests, namely anterior sum / posterior sum, incisor sum / posterior sum, and incisor sum / posterior sum w. canine all maintained significance. These results suggest frugivores still have comparatively large incisors when compared to folivores even after the phylogenetic correction. Interestingly, both posterior sum / mandible length and posterior sum with canine / mandible length were no longer significant (Table 4). This is potentially a product of the sample and experimental design. Folivores make up roughly 33% of the species used in this analysis while frugivores make up the remaining percentage. When assuming Brownian motion, variance seen in a trait is a function of branch length, or time since divergence (Kamilar & Cooper, 2013). Since folivores in this sample come from just a few families (i.e., Atelidae and Colobinae), the phylogenetic adjustment masks nearly all variation that may potentially exist. Hansen (2017) describes how using phylogenetic corrections in comparative analysis is inherently limited since they do not consider selective history.

Phylogenetic correlations and stabilizing selection are both products of ancestor/descendent relations and thus disappear at a similar rate in this analysis (Hansen, 2017).

Implications for Hominin Evolution

Previous models have been proposed to explain the reduction in incisor size seen among hominins. For example, the “Lamarckian” notion, which advocates for selection to get rid of expensive tissue that might impede other functions, implies tool use gradually replaced incisal preparation dating as far back as genus *Australopithecus* (Holloway, 1967; Jolly, 1970).

However, all extant great apes demonstrate various levels of tool use without the same sort of dental reduction seen in even the most basal members of our clade. Another early theory was that an upright posture caused facial shortening which would have secondarily reduced the size of the anterior dentition (Jolly, 1970). The issue here is that there is no evolutionary pressure for this to occur. Face length does not decrease in response to a more upright posture. Chimpanzees and gorillas are facultatively bipedal and do not show any reduction in face length or anterior tooth size when compared to other primates. Perhaps the most influential of the early theories was the seed-eater hypothesis proposed by Jolly (1970) who hypothesized that basal hominins would have subsisted off seeds and grain before shifting to a more calorie-rich meat and marrow diet by virtue of hunting and tool use. His basis of claim is that the shifting environmental and climactic conditions sweeping over East Africa in the middle Pliocene would have limited more typical food stuffs (i.e., fruits and leaves) (Jolly, 1970).

Of the early hominins, isotope analysis has shown that only *P. boisei* had a strong C4 signal (Cerling et al., 2011). Foods such as grasses and grass seeds would have provided a high degree of toughness and strongly resisted crack propagation (Lucas & Luke, 1984; Thiery,

2017). Only primates with an exceptionally robust series of masticatory adaptations subsist on these foods. *Paranthropus boisei* is undoubtedly the most specialized taxon within *Paranthropus*. It has all the traits present in other megadont hominins (i.e., large molars, small incisors, dished face, short jaw, large chewing muscles), only much more pronounced (Cerling et al., 2011; Lucas & Luke, 1984; Thiery, 2017). Unlike *Australopithecus*, which demonstrates strict molar enlargement when compared to the ancestral condition, *Paranthropus* had expansion of the entire posterior tooth row (McCollum & Sharpe, 2001). In addition, the canines are shunted forwards to be in line with the incisor and the entire anterior dental battery is highly reduced. McCollum and Sharpe (2001) describe how the enlargement seen in the molars and premolars may have been a developmental correlation with canine reduction. Specifically, an “...anterior relocation of the boundary between posterior and anterior tooth fields might (have) resulted in the correlated development of large postcanine teeth and small canines and incisors” (McCollum & Sharpe, 2001: 487).

The results presented in this analysis suggest *Paranthropus* tooth size is a response not only to diet, but jaw length as well. Overall, it seems a combination of a highly specialized diet, enlarged molars, and shorter toothrow all would have contributed to the distinct craniodental morphology seen in this taxon.

CONCLUSION

In conclusion, the results of this study corroborate the hypothesis that folivores have small incisors and large molars and premolars when compared to frugivores as a function of mandible length. A shorter, deeper mandible benefits folivores during feeding since it can generate more power and concentrate more force onto resistant foods. The association seen here

between mandibular length and mesiodistal ratios therefore may reflect crowding in the dental arcade. The broader implications of the spatial constraint hypothesis cannot be overstated, particularly with regards to the human fossil record. Traditionally, the small incisors of *Paranthropus* are said to indicate they would have had a diet that required only minimal incisal preparation. However, the wear on the anterior dentition of many *P. boisei* and *P. robustus* specimens suggest this is not the case. Instead, it seems more likely the reduction occurred due to a multitude of interrelated factors, one of which being facial shortening and another being posterior tooth enlargement. Future research in this topic may elucidate what factors directly contributed to the reduction in anterior tooth size seen within the hominin clade.

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