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Abstract

Fallback foods are defined as resources of relatively poor nutritional quality that become particularly important dietary components in times where preferred foods are unavailable. Consumption of these foods is correlated with times of great stress and mortality within a species, indicating their potential to act as a selective pressure on the feeding adaptations of organisms. The focus of this study was on the individual adaptations that have evolved in the family Hominidae (the Great Apes) as a response to the fallback foods particular to each species. Three members of Hominidae were selected for examination; Pongo pygmaeus (the Bornean Orangutan), Pan troglodytes (the Common Chimpanzee), and Gorilla gorilla (the Lowland Gorilla) based on the significant variation between their known fallback food selections. P. pygmaeus is known for consumption of unripe fruits, seeds, and barks, G. gorilla is notorious for consumption of low quality terrestrial herbaceous vegetation (THV), bark and woody pith, and P. troglodytes frequently expand their territory in search of preferred foods, rather than defaulting to lower quality food sources. Sample images of each organism were obtained from the Field Museum of Natural History (Chicago, IL). Measurements were then made of several relevant cranial-morphological indices using the image analysis software ImageJ. Mean values, standard deviation, and

analysis of variance were calculated using the statistics software SYSTAT. Significant differences were found among the three species examined in moment arm of both the temporalis muscle and masseter muscle, the height of the dentary, and the mechanical advantage of the temporalis muscle at M1, suggesting the potential evolutionary impact of fallback foods on some of these features.

Introduction

As human beings, our fascination with our own evolutionary history leads us almost categorically on a path of discovery to our closest living relatives, the Great Apes. Throughout our antiquity, and even before we understood the process of evolution, we have searched for answers in the remains of our forebears and those species similar to us. As a result, in the modern era of scientific discovery, many studies have examined the Great Apes as an answer to our developmental questions, particularly the question of how we evolved to consume the foods we do in the way that we do. One such study of Hominidae examined the effects of "fallback foods" and their importance in primate evolution in terms of tooth enamel morphology (Constantino *et al.*, 2009).

The term "fallback foods" is one without a truly standardized definition. In general, it is accepted that fallback foods are foods of relatively low nutritional quality that become highly important in the primate diet when preferred sources of food are scarce or altogether unavailable (Marshall *et al.*, 2008, Constantino *et al*., 2009, Watts *et al*., 2012). Their use is generally inversely proportional to the consumption of those foods that classify as preferred or high quality. In this case, "quality" refers to the ease of energy extraction from the source of food, such that those foods with low processing needs and high output may be considered preferred (Watts *et al.*, 2011). Fallback foods can be any number of edibles, and have been shown in certain instances to play an important role in shaping both the behavioral and physiological adaptations among many animals, including all members of the family *Hominidae* (Strait *et al.*, 2013, Constantino *et al.,* 2009).

The ability to gather and store energy cannot be overstated for its adaptive importance. Food, second perhaps only to water, is of obvious and fundamental importance to all life on our planet, primates included. For many species it is a key determinant of fitness and it may determine a species geographic range and population size (Marshall *et al.*, 2008). More specific to organisms however is the ability to process food effectively; including the morphological, biochemical, and mechanical adaptations that make the consumption of food easier (Anapol and Lee, 1994, Taylor, 2002, Terhune, 2013). This is especially true of fallback foods, which serve as the last resort in numerous instances, making the ability to consume fallback foods efficiently a selective pressure throughout thousands of years of primate evolution to shape anatomical traits (Marshall *et al.*, 2008).

Although fallback foods vary by region and species, the preferred foods among the Great Apes appear to have a certain degree of consistency to them. Common as the preferred food among *Pan troglodytes* (common Chimpanzee), *Pongo pygmaeus* (Bornean Orangutan), and *Gorilla gorilla* (lowland Gorilla) appears in almost all cases to be soft ripe fruits (Constantino *et al.*, 2009, Watts *et al.*, 2012). The case of fallback foods however sees a significant divergence among these closely related species. For the common chimpanzee in cases of preferred food unavailability, the species has a unique behavioral response; they will break off into smaller foraging parties and begin to search more extensively for their preferred soft, ripe fruits (Constantino *et al.*, 2009, Watts *et al.*, 2011). In the case of the Bornean orangutan, the scenario is different. Because of their natural habitat location, *P. pygmaeus* must go through much of the year without any possibility of finding ripe fruits. Thus they are often driven to consume harder fallback foods such as, unripe fruits, bark, nuts, and seeds (Constantino *et al.*, 2009). Finally, in the case of the lowland gorilla, the species exhibits the consumption of some of the most low-quality and toughest foods of all. Common fallback foods for *G. gorilla* include; terrestrial herbaceous vegetation (THV), bark, woody pith, and tough fibrous fruits. Thus in summary, it is generally agreed upon that members of *G.gorilla* consume the most mechanically demanding fallback foods, while Chimpanzees consume the softest with Orangutans representing a relative intermediate.

Based on this previous research, a study was conducted in order to ascertain the potential effects that differences in fallback food consumption between species of Hominidae could have on the evolution of Great Ape skull morphology, particularly as it relates to the development of chewing muscles (Taylor, 2002, Schmittbuhl *et al.*, 2007, Armfield and Vineyard, 2010). To do this, variables indicative of morphological masticatory characteristics were measured (e.g. mechanical advantage at both temporalis and masseter muscles, dentary height, and muscle attachment points). It is hypothesized that because of the distinct differences in fallback food toughness between *P.troglodytes, P. pygmaeus, G. Gorilla*; there will be a corresponding difference in the relative adaptations in skull morphology to better consume these foods, lending support to the theory that fallback foods do indeed act as a selective pressure. It is expected that Gorillas will exhibit greater indicators of enhanced masticatory morphology because of the high mechanical demands of their fallback diet. It then follows that Chimpanzees should show the least amount of adaptation and Orangutans should represent the intermediary between the two.

Materials and Methods

For the purpose of this study, pertinent images of specimens were obtained from the Field Museum of Natural History, Chicago, IL. The organisms chosen for this study were readily available extant members of the family Hominidae. The sample included specimens of *G. gorilla* (Western Gorilla, n=5), *P. pygmaeus* (Bornean Orangutan, n=8), and *P. troglodytes* (Common Chimpanzee, n=5). Using ImageJ, an Image Processing and Analysis software program (NIH), linear measurements of the cranium and mandible were taken from the digital images. From these cranial and mandibular measurements, indices were computed and standardized (by dividing by skull length or jaw length, respectively). The indices were then used to calculate mechanical advantage of both the temporalis and masseter muscles at the lower first molar. These indices were next analyzed using the statistical package SYSTAT 10.2 to generate means and standard deviations of each variable. An analysis of variance was performed on

the variables to determine if there were any significant differences between species.

Table 1: Definitions of variables and indices used in the study.

Index	Definition
MAM	Moment Arm of Masseter m.- distance from approximate midpoint of mandibular condyle to ventral border of masseteric fossa
MFL	Masseteric Fossa Length-taken at widest point
HOD	Height of Dentary-distance from height of mandibular condyle to ventral border of mandible
LTRL	Lower Tooth Row Length-distance from front of canine to back of M3
JL	Jaw Length
MAT	Moment Arm of Temporalis m.-distance from midpoint of mandibular condyle to midpoint of coronoid process
MAMo	Lever Arm at Molar 1-line at HOD to front of M1
TFL	Temporal Fossa Length
SL	Skull Length-distance from anterior point of maxilla to opisthocranion
UTRL	Upper Tooth Row Length-distance from front of canine to back of M3
MAM1T	Mechanical advantage at M1 by temporalis m. (MAT/MAMo)
MAM1M	Mechanical advantage at M1 by masseter m. (MAT/MAMo)
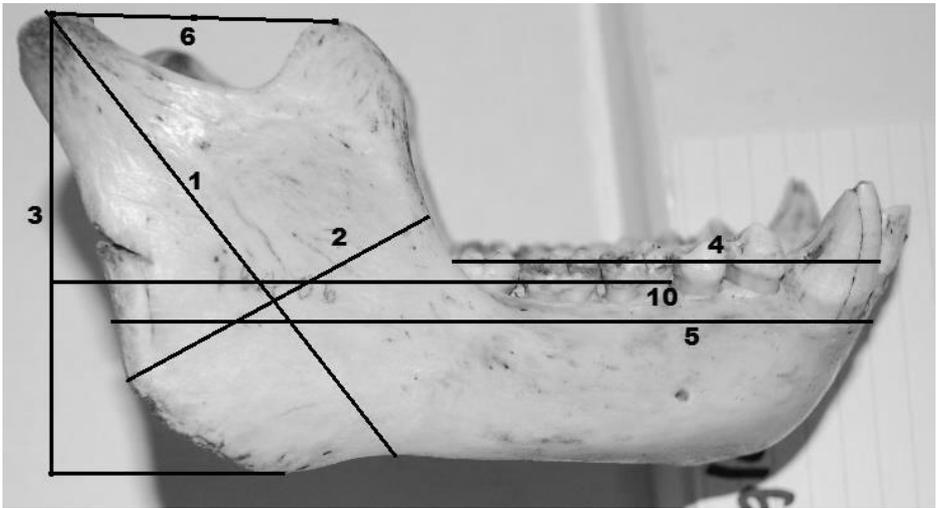
Figure 1: Mandible of P. troglodytes showing the variables measured in the experiment. 1 (MAM), 2 (MFL), 3 (HOD), 4 (LTRL), 5 (JL), 6 (MAT), 10 (MAMo).

The definitions of all measurements taken and indices calculated are shown above in Table 1. The diagrams in Figure 1 and Figure 2 illustrate these measurements on the Chimpanzee, *P. troglodytes*.
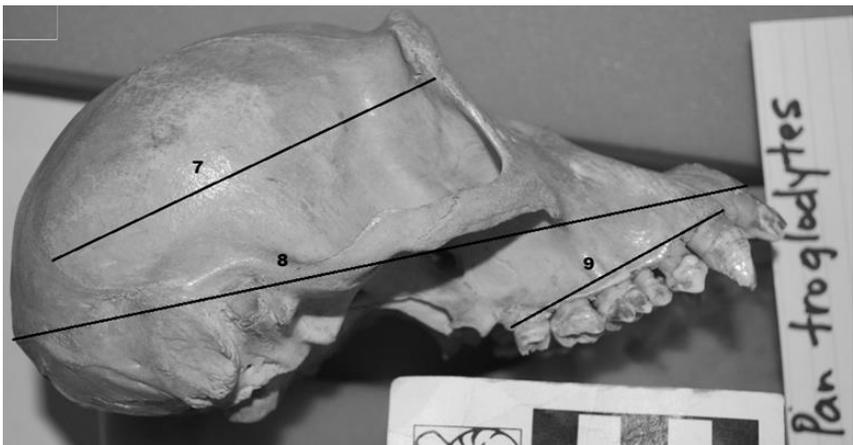
Figure 2: Cranium of P. troglodytes showing the variables measured in the experiment. 7 (TFL), 8 (SL), 9 (UTRL).

Results

The linear measurements and calculations by indices were subject to statistical analysis. From this it was found that the Orangutan exhibited a significantly longer MAM (moment arm of the masseter) than either the Gorilla or the Chimpanzee ($p<0.005$) and a significantly longer MAT (moment arm of the temporalis than the Gorilla ($p<0.05$), (Table 2). The Orangutan and Gorilla exhibited significantly larger HOD (height of the dentary) than that of the Chimpanzee ($p<0.05$). The Mechanical Advantage of the Temporalis muscle at the first lower molar (as calculated above, Table 1) was found to be significantly greater in the Chimpanzee and the Orangutan than the Gorilla ($p<0.05$). There were no significant differences observed among the rest of variables and indices.

Index	*Pongo pygmaeus*	*Pan troglodytes*	*Gorilla gorilla*
MAM	0.850 (0.054) [C,G]	0.713 (0.047) [O]	0.756 (0.071) [O]
MFL	0.468 (0.015)	0.422 (0.040)	0.444 (0.034)
HOD	0.800 (0.041) [C]	0.591 (0.053) [O,G]	0.777 (0.100) [C]
LTRL	0.541 (0.019)	0.549 (0.024)	0.550 (0.055)
MAT	0.357 (0.047) [G]	0.359 (0.041)	0.280 (0.050) [O]
MAMo	0.786 (0.048)	0.766 (0.016)	0.779 (0.076)
TFL	0.479 (0.041)	0.535 (0.038)	0.514 (0.061)
UTRL	0.332 (0.035)	0.314 (0.017)	0.309 (0.031)
MAM1T	0.456 (0.063) [G]	0.468 (0.045) [G]	0.358 (0.042) [O,C]
MAM1M	1.087 (0.117)	0.931 (0.042)	0.979 (0.141)

Table 2: Mean values and standard deviations of the standardized measurements and indices for each species. Superscript letters indicate that the denoted species differs significantly from the listed species. Superscripts are defined as follows: G- Gorilla, O- Orangutan, C- Chimpanzee

Discussion

In agreement with the hypothesis, the Gorilla and the Orangutan were observed to have relatively larger dentaries (HOD) when compared to the chimpanzee. This is significant because HOD has previously been shown to correlate with the robustness of the Temporal Mandibular Joint (TMJ) and size of the masseter muscle (Durmont, 1997; Terhune, 2013). These morphological features (TMJ robustness and masseter size) are important indicators of enhanced masticatory morphology, and as such may indicate an adaptation for consumption of more mechanically demanding foods in both Gorillas and Orangutans.

Overall however, the results indicate that the data collected from this study did not support the hypothesis. Direct calculation of mechanical advantage indicated a higher mechanical advantage of the temporalis in the Orangutan and the Chimpanzee suggesting that these two species have evolved more robust jaws and jaw-closing musculature. Additionally, the Orangutan, which appeared to have the most intermediate mechanically demanding fallback foods, exhibited significantly larger MAM and MAT values. These values are important for estimating the mechanical advantage given by leverage in chewing, which is calculated as $MA = \frac{L_i}{L_O}$ (where L_i is the in-lever, and L_o is the out-lever). Thus the increased length of moment arm (or in-lever) measured indicates greater mechanical advantage of both the masseter and temporalis muscles at the lower first molar in the Orangutan as compared with the other species in the study.

One possible explanation behind this peculiar find may deal with the masticatory method responsible for the processing of fallback foods, and not just the mechanical demand of the food itself. Previous studies conducted relating in particular to fallback foods have shown that adaptations in the Gorilla include features such as larger relative tooth size and thicker occlusional enamel (Constantino *et al.*, 2009). These particular adaptations are useful advantages in the Gorilla fallback diet, which is highly folivorous in nature (comprised of mostly leaves, pith, bark, and THV) and therefore requires more daily

chewing cycles and greater protection against surface wear (Constantino *et al.*, 2009; Taylor, 2002). In contrast, this study focused in particular on morphological indicators of bite force and muscle size, and has revealed evidence that in these categories, members of *P. pygmaeus* are more adapted for a mechanically demanding fallback diet than are members of *G. gorilla*. The answer to this puzzle may lie in the particular chewing methods involved for the respective fallback diet of each species. Because Orangutans are known to chew on foods of relatively high hardness (i.e. nuts, seeds) with their post-canine teeth, they may require a greater bite force than other members of Hominidae to cope with the cracking process of mastication. Consequently it follows that measurements indicative of a higher mechanical advantage for chewing via both temporalis and masseter muscles (MAT and MAM respectively) at the lower first molar would be significantly larger in *P. pygmaeus*.

In conclusion, on the basis of the variables measured, members of *P. pygmaeus* were shown to have the greatest degree of adaptation in their chewing morphology. This can be observed as the combination of their significantly larger HOD, MAM, and MAT measurements. In theory, this could be due to the unique hardness of Orangutan fallback foods, which would require a larger one time bite force to process as compared to organisms whose diets are more folivorous or frugivorous. This data is limited by the number of images available, thus a future study with a greater cohort may prove useful. Additionally, certain indices (particularly dental features) were not measured in this study. It may be worthwhile in future studies to examine these in conjunction with the morphological characteristics examined here.

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