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Developmental stress in wild Nigerian olive baboons (*Papio anubis*)

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Background. Developmental instability in archaeological populations can be detected through analysis of human skeletal and dental remains. During life, disruptions to biological internal homeostasis that occur during growth and development redirect bodily resources to returning to homeostasis and away from normal processes such as symmetrical development. Because dental enamel does not remodel in life, any deviations from normal development are left behind. Even subtle disturbances to developmental trajectory may be detected in asymmetrical development of traits, specifically a random variation in sides termed fluctuating asymmetry. We investigate the permanent dentition of wild olive baboons, *Papio anubis*, for potential fluctuating asymmetry relative to sex, weaning, and reproductive maturity. **Methods.** The skulls of adult baboons were collected after their natural death in Gashaka Gumti National Park, Nigeria. The permanent dentition of antimeric teeth (paired) were measured for maximum length and breadth using standard methods. The metrics were analyzed to assess the presence of fluctuating asymmetry in adult permanent mandibular and maxillary dentition. Measurement error and other forms of asymmetry (antisymmetry, directional asymmetry) were considered and dental measures expressing true fluctuating asymmetry were used to address three research questions. **Results.** Males exhibit greater fluctuating asymmetry than females, suggesting that males experience greater overall stress during the developmental period. While weaning is not more stressful than other life history stages for males and females (using the first molar fluctuating asymmetry index as a proxy compared to other teeth), it is more stressful for females than males. Reproduction is also not more stressful than other life history stages for males and females (using the third molar fluctuating asymmetry index as a proxy compared to other teeth), but it is more stressful for males

than females.

MANUSCRIPT TITLE

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ABSTRACT

Background. Developmental instability in archaeological populations can be detected through analysis of human skeletal and dental remains. During life, disruptions to biological internal homeostasis that occur during growth and development redirect bodily resources to returning to homeostasis and away from normal processes such as symmetrical development. Because dental enamel does not remodel in life, any deviations from normal development are left behind. Even subtle disturbances to developmental trajectory may be detected in asymmetrical development of traits, specifically a random variation in sides termed fluctuating asymmetry. We investigate the permanent dentition of wild olive baboons, *Papio anubis*, for potential fluctuating asymmetry relative to sex, weaning, and reproductive maturity.

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Results. Males exhibit greater fluctuating asymmetry than females, suggesting that males experience greater overall stress during the developmental period. While weaning is not more stressful than other life history stages for males and females (using the first molar fluctuating asymmetry index as a proxy compared to other teeth), it is more stressful for females than males. Reproduction is also not more stressful than other life history stages for males and females (using the third molar fluctuating asymmetry index as a proxy compared to other teeth), but it is more stressful for males than females.

INTRODUCTION

Papio (baboons), one of the most intensively studied primate taxa, inhabit a wide range of habitats across Africa. Most troops inhabit dry, open savanna in East and South Africa, while habitats that include forests are rare. Our study focuses on the population of olive baboons in Gashaka Gumti National Park in North-eastern Nigeria. These monkeys are outliers in terms of geography, climate and local environment, inhabiting the wettest and most humid habitat of any studied population (Sommer & Ross 2011). Compared to savanna-dwelling baboons, their troop sizes are significantly smaller (Higham et al. 2009), possibly because forest fruits occur in clumped patches that may be difficult for larger groups to exploit. Additionally, many troops across the park raid maize and other agricultural crops to varying extents (Warren et al. 2011). These combined factors have implications for reproduction, life history and survival. For example, inter-birth intervals are longer here than elsewhere (Ross et al. 2011), and crop-raiding troops have both higher energy intake and reproductive success rates (Lodge et al. 2013).

A study of fecal glucocorticoid in Gashaka Gumti female baboons suggests they experience unusual amounts of thermoregulatory and nutritional stress throughout their lives, and this stress varies seasonally relative to rainfall and food availability (MacLarnon et al. 2015). No data are yet available on stress in male baboons. Permanent teeth develop *in utero* and record interruptions to growth and development during periods of developmental instability, which may leave permanent marks in the teeth such as fluctuating asymmetry (FA) (Van Valen 1962), dental enamel defects (Sarnat & Schour 1942; Sarnat & Schour 1941), and variation in molar cusp morphology (Corruccini & Potter 1981; Riga et al. 2014). While dental enamel defects are easier to record (presence/absence) and simpler to analyze, there does not appear to be a correlation between them and FA (Corruccini et al. 2005; Hoover et al. 2005)—enamel defects may be better at recording nutritional stress due to their association with famine (Zhou & Corruccini 1998) and weaning (Katzenberg et al. 1996; Ungar et al. 2017). FA, however, is an established proxy for and a broader signal of developmental instability, or childhood stress (see Markow 1994; Polak 2003) (Frederick & Gallup Jr. 2007; Hoover & Hudson 2016; Leamy & Klingenberg 2005). FA is manifest in paired traits as non-directional deviations from perfect symmetry with equal mean development on both sides (Van Valen 1962). The underlying biological theory behind FA as a proxy for developmental instability is allied with concepts of homeostasis and canalization. During growth and development, traits may canalize (reach their final form) in an internal environment where disruptive stochastic processes (developmental noise) and the capacity to resist disruption (developmental stability or homeostasis) become unbalanced (Waddington 1942). The result in non-directional bilateral variation of traits (Van Valen 1962). These minor deviations from normal growth can be measured by variance across the midline of traits (Van Valen 1962). Thus, presence and degree of FA reflect an individual's ability to canalize a trait despite genetic and/or environmental stresses that disrupt the normal phenotypic trajectory.

Because primates have longer developmental stages compared to other mammals in which they can record periods of stress in the hard tissues of the body (Gingerich & Schoeninger 1979) and the development of molars overlaps in time with the life history events of interest (weaning, reproductive maturity) (Fortman et al. 2002; Hlusko & Mahaney 2009; Phillips-Conroy & Jolly 1988), we have an opportunity to identify if there are peaks of stress associated with specific developmental ages. Weaning, for example, occurs during the developmental window of the first molar and is associated with increased dental stress markers in both human and non-human primates (Kelley & Schwartz 2010; Smith et al. 2013). In the case of weaning and, presumably, other stresses differences exist between captive populations and those in the wild, where developmental delay is common due to greater variance in environmental stress (Zihlman et al. 2004). In nonhuman primates, most published data are neither collected on dentition nor used to examine developmental differences based on sex or life history (Atkinson et al. 2016; Boulton & Ross 2013; Hallgrimsson 1993; Leigh & Cheverud 1991; Little et al. 2012; Newell-Morris et al. 1989; Reeves et al. 2016; Sefcek & King 2007; Waitt & Little 2006; Willmore et al. 2005).

There are a few studies that examine FA in dentition in nonhuman primates and they find that traits under sexual selection exhibit greater asymmetry (are more developmental vulnerable to stress) (Manning & Chamberlain 1993; Manning & Chamberlain 1994). While we might form expectations based on human studies of FA—such as, there is no clear signals sex bias in FA (e.g., Garn et al. 1965; Harris & Nweeia 1980; Kieser et al. 1986; Perzigian 1981)—but humans exhibit greater FA than other apes (Frederick & Gallup Jr. 2007) and comparing our patterns to or using them build hypotheses about nonhuman primates may not be accurate. Thus, we need a wider comparative dataset on nonhuman primate FA, in order to understand sex differences in life history stress and instability introduced by habitat and social system variation. We contribute the first data on dental FA in baboons and answer the following life history questions:

1. Is there a difference in developmental stress based on sex? Gashaka Gumti baboons live at the edge of their species' geographic and ecological range (Sommer & Ross 2011) and high levels of stress have been reported in adult and subadult females, as measured by fecal glucocorticoid and (MacLarnon et al. 2015). There are no comparative data ~~are~~ available for males and the limited data in nonhuman primate dental FA suggest that traits under sexual selection in both males and females are more vulnerable to FA~~.~~(Manning & Chamberlain 1993; Manning & Chamberlain 1994) Thus, we are not able to make an expectation of whether there will be sex differences across the entire sample of teeth and, if there are, which sex will have higher FA.
    a. Hypothesis: There is no difference
2. Is weaning a stressful time compared to other developmental stages? In baboons, suckling ceases before the eruption of the first molar (Dirks & Bowman 2007), which suggests that the first molar will be diagnostic in answering this question. The null hypothesis is that there is no difference between the FA index for first molars and the FA index for all remaining teeth. Because weaning stress has been previously reported in baboons (Dirks et al. 2002; Rhine et al. 1985), we expect that first molar indices will exhibit significantly higher than the FA index for all remaining variables.
    a. Hypothesis: FA values for first molars are higher than FA values for other teeth.
3. Are there sex-based differences in reproductive stress? In baboons, menarche and first reproduction occur before the eruption of the third molar (Dirks & Bowman 2007), which suggests the third molars will be diagnostic in answering this question. Given that sexually selected structures may be more susceptible to environmental stress (Manning & Chamberlain 1994)and because reproductive stress is particularly high in females due to extra demand on resources, we expect female third molars will exhibit greater FA than male third molars.
    a. Hypothesis: FA values for female third molars are higher than those for males.

MATERIALS

We analyzed data collected from olive baboons (*Papio anubis*) inhabiting Gashaka Gumti National Park (06°55′ – 08°13′ N and 011°13′ – 012°11′ E) in Northeastern Nigeria. Permits for research at Gashaka Gumti National Park were awarded (VS) by The National Parks Service, Nigeria (NPH/GEN/378/V/504). The reserve extends over 6731 km^2 and represents the northern edge of the Gulf of Guinea forests and the Cameroonian Highlands, with the highest peak rising to 2416 m (Sommer & Ross 2011). The park is surrounded by villages that practice subsistence farming and includes various enclaves inhabited mainly by settled Fulani cattle herders. GGNP baboons live close to the southern edge of the western biogeographical distribution of the species ~~(~~(Zinner et al. 2011). Baboons are replaced by large forest-dwelling monkeys (mainly drills), a short distance from the park to the south.

In GGNP, pronounced annual wet and dry seasons correspond with fluctuations in temperature and humidity (Sommer & Ross 2011). Based on weather station data for two study sites collected from 2000–2014 (Kwano at 583 m above sea level and Gamgam at 320 m above sea level), mean minimum temperature is 20.9°C and mean maximum 32.5°C. Five months with very little or no rainfall are followed by heavy downpours from mid-April to mid-November that constitute 96.3% of all precipitation (annual mean 1945 mm, range 1681–2337 mm). Among baboon field sites, GGNP is an extreme outlier with regards to rainfall, representing the wettest of all baboon study sites to date (Higham et al. 2009).

Our study sample is from baboon skulls that were delivered to the Gashaka Primate Project research station at Kwano by locals and park rangers between 2008 and 2013. The majority were found opportunistically while working in fields or during ranger patrols. Skulls were not accepted if there was evidence (e.g., bullet holes) that the animals had been killed by humans (which is illegal inside the park). Thus, ~~we have~~ a natural death sample. Informal weathering assessments in the field indicate the material was deposited over approximately 6 years as assessed by weathering stages 0-2 (Behrensmeyer 1978)~~).~~ The skulls originated from the vicinity of six localities within GGNP or its buffer zone: Bodel, Mayo Yum, Gashaka, Selbe and Filinga, which are near human habitation, and Yakuba, where baboon ranges do not extend into cultivated areas (Fig. 1). Stretching across a corridor of ca. 50 x 30 km, these 1500 km^2 are colonized by a single baboon population, which inhabits the park's Southern Gashaka sector (Higham et al. 2009; Ross et al. 2011; Warren et al. 2011), where the vegetation is a mosaic of montane, submontane, lowland and riverine gallery forest with some proportions of Guinea woodland-savannah and grassland (Adanu et al. 2011). Troop sizes average 21 individuals, with 5 females and males and offspring (Higham et al. 2009). Most crania were found in the vicinity of human dwellings where they are more likely to be recovered but their locations suggest that all skulls stem from troops that engaged in crop-raiding to some extent. The single exception one female skull, assumed to have been philopatric, which was found many kilometres away from the nearest cultivated fields and is not likely a crop-raider.

<Figure 1. Collection locations in Gashaka Gumti National Park, Nigeria>

Each cranium was soaked for one day in a denture-cleansing powder solution to remove debris, given a field accession number, and stored in a plastic or metal box. As of April 2013, the collection comprised 111 skulls, but weight specimens displayed extensive damage or lack of antimeric teeth and were unsuitable for our analysis. Of the remaining 103 specimens, we excluded three females and one subadult of unknown provenance, but we retained two males of unknown provenance. Our starting analytical sample of adult specimens consisted of 81 individuals with antimeric pairs including 43 adult males and 38 adult females.

METHODS

Age and sex estimation. Age was assessed using the developmental stage of each tooth (e.g. unerupted, emerging or in occlusion) and the development of the basilar suture (Kahumbu & Eley 1991; Reed 1973). Adults are defined by full occlusion including the third molar—subadults demonstrate variable eruption but may have a full complement of permanent dentition in occlusion, with the exception of third molars. Sex was assessed visually in adults on the basis of overall skull size, robusticity, size of canines or canine orifice, and other known dimorphic features that are easily observed (Leigh & Cheverud 1991; Singleton 2002; Singleton et al. 2017).

Data collection. Standard maximum length and breadth measurements for bilophodont primates (Swindler 2002) were taken 10 times (EG) on the permanent dentition of adult mandibular and maxillary premolar and molar teeth using Mitutoyo digital calipers. The final dataset consisted of a maximum of nine variables per individual (we did not collect data on the maxillary third premolar due canine honing). Because some individuals were missing teeth or exhibited traits that precluded measurement. (e.g., cracked crowns, wear, poor preservation), data collection on all nine variables was not always possible for each individual.

Data Sharing. Data, scripts, and preliminary analysis outputs (e.g., distribution testing, outlier tests, scatterplots) are available at Github: https://github.com/kchoover14/Baboon-Stress.

Choosing Replicates. Because measurement error (ME) is a component of any metric value, an analysis of FA must consider the contribution of ME to FA. We had the luxury and burden of ten replicates for each trait—luxury because most studies take 2-3 replicates and burden because ten is an unwieldy number for analysis. Replicate measures were taken over a period of time with breaks between each data collection trial. Early trials of data collection may contain more ME due to a lack of familiarity with the teeth but later trials may contain more ME due to data collection fatigue. Thus, we assessed ME across sets of replicates (Table 1) to determine the minimum number of replicates with the lowest ME. ME, as a percentage of between-sides difference attributable to ME (Palmer 1994), was calculated in the FA worksheet (Palmer 1994; Palmer & Strobeck 1986; Palmer & Strobeck 2003a). The full set of 10 replicates had the lowest mean ME3 (8%) but with a wide range (18%). These ME values are high for FA but can be reduced after excluding individual datum that fail the data inspection tests for outliers.

Table 1: ME summary by replicate set>

Statistical Methods—Data Visualization. Data distributions for all ten replicates and plots of FA10a were visualized using ggplot2 (Wickham 2016).

Statistical Methods—Confounding Factors Affecting FA. Estimates of FA may be confounded by a variety of factors including bad raw measurements, high ME, aberrant individuals, DA, antisymmetry, and trait size dependency (Palmer & Strobeck 2003a). The data repository contains a step-by-step analysis of all factors affecting FA in this dataset and the results of various tests (Palmer & Strobeck 2003b). Due to high DA, four variables were eliminated (female mandibular first and second molar lengths, male mandibular first and second molar lengths). Due to trait size dependency, one variable was eliminated (male maxillary third premolar length). Because ME was high and varied considerable across tooth, metric (i.e., length, breadth), and sex, we used the FA10a index. The FA10a index is a measure of the magnitude of FA *after* parsing ME (Table 2). The total dataset for analysis consisted of nine variables for female breadths, 7 variables for female lengths, nine variables for male breadths, and six variables for male lengths. Table 2 displays the sample size per each variable's FA10a index to provide perspective on statistical power underlying the index.

<Table 2: FA10a Index Values for Hypothesis Testing>

Statistical Methods—Hypothesis Testing of Research Questions. Analysis was conducted by KCH in R v3.6.2 (R Development Core Team, 2008) using R Studio v.1.2.1335 (RStudio Team, 2015). Because FA is a measure of variance about the mean, Levene's test for equality of variance was used to test hypotheses in R via the leveneTest function in the car package (Fox & Weisberg 2011). The eruption of upper and lower teeth varies by a few months in baboon species, which allowed us to pool mandibular and maxillary molars for analysis (Fortman et al. 2002; Hlusko & Mahaney 2009; Phillips-Conroy & Jolly 1988; Reed 1973).

RESULTS AND DISCUSSION

Data Exploration. In humans, FA varies by dimension (e.g., length, breadth), arcade (e.g., mandible, maxilla), and tooth class (e.g., incisor, canine, premolar, molar) (Bailit et al. 1970; Harris & Nweeia 1980). We explored the data to identify similar trends in our baboon sample (Table 3). There were significant differences in dimensions, with breaths exhibiting lower FA (0.02) and lengths exhibiting higher FA (0.06)—same as in humans (Harris & Nweeia 1980). There were no significant differences by tooth class or arcade.

<Table 3: FA10A Trends>

Sex Differences. The first research question is whether there is a sex-based difference in developmental stress. We tested the null hypothesis of no difference Results indicate there are significant sex-differences in this population (Table 4), suggesting that males experience greater developmental stress across the period of growth and development. Figure 2 shows the spread of FA10a index values for males and females. Both sexes exhibit greater FA in lengths compared to breadths and males have overall greater variance (FA is a measure of variance), even if some values overlap with females. Mandibular P4 is the greater FA value for males and females, but female values are almost half that of males.

<Figure 2: FA10a by Sex>

Weaning Stress. ~~The second research question~~ is whether weaning is a more stressful time compared to other developmental stages. Due to its developmental timing, the first molar is diagnostic for weaning stress and was expected to have greater variance than the other teeth. FA10a is lower in M1 than other teeth, suggesting weaning is not more stressful compared to other stages of life history (Table 4). There are significant differences between male and female FA10a values, however (Table 4, Figure 3). Both sexes exhibit greater FA in lengths compared to breadths and values for fourth premolars are again the highest (Figure 3)

<Figure 3: FA10a comparing first molar to other teeth by sex>

Reproductive Stress. The third research question is whether reproduction is more stressful for females compared to males. We expected female third molars to have greater FA10a values than males and for FA10a to be higher in third molars compared to other teeth. FA10a is lower in M3 than other teeth when sexes are pooled, suggesting that weaning is not more stressful compared to other stages of life history (Table 4). There are significant differences between male and female FA10a values (Table 4, Figure 4). With males have higher FA10a values during reproductive years (based on the third molar developing during this life history stage). Both sexes exhibit greater FA in lengths compared to breadths (Figure 4).

<Figure 4: FA10a comparing third molar to other teeth by sex>

<Table 4: Results of Hypothesis Testing>

CONCLUSION

We used the FA10a index because it eliminates measurement error from the final index used for hypothesis testing. We then examined FA across variables (length and breadth measures for individual teeth) to identify any trends in FA. The only one we found was that lengths exhibit more FA than breadths—a trend identified in humans as well (Harris & Nweeia 1980). Lengths are the preferential target of data collection for FA analysis, in humans and baboons.

We also tested hypotheses about developmental stress in different life history phases (i.e., weaning, reproduction). Females in our baboon population have elevated glucocorticoid levels that measure physiological stress (MacLarnon et al. 2015). Our data suggest females only exhibit greater stress than males during weaning. Further, when comparing our data for males to females across all variables, we find that males exhibit ~~have~~ greater stress during growth and development than females and stress is highest during early reproductive years. Demonstration of FA and the supposition that a population appears under stress can be relatively straightforward (Leary & Allendorf 1989), but the identification of a specific stressor remains conjectural. Habitat quality (Manning & Chamberlain 1994), psychosocial factors (Newell-Morris et al. 1989) and diet (Swaddle & Witter 1994) have all been implicated.

Sex Differences. Males had greater overall FA values than females, suggesting greater levels of developmental stress. The stability of male developmental pathways may be compromised by several factors. The male fetus stimulates additional maternal antigen production (Lalumière et al. 1999), which may cause male-biased prenatal mortality and other developmental complications (Gualtieri & Hicks 1985). In addition, hormones may influence male development (Folstad & Karter 1992). Elevated testosterone profiles have been associated with immunosuppression (Bradley 1987; Muehlenbein & Watts 2010; Roberts et al. 2012), the costs of which range from parasite susceptibility to developmental instability. Given these ontogenetic challenges, males may be more susceptible to external environmental conditions, such as the extremely wet climate and high pathogen exposure during the rainy season that baboons experience at GGNP (Higham et al. 2009). Others have also demonstrated increased FA in marginal or less favorable environments (Bailit et al. 1970; Parsons 1992) and males may be at a disadvantage in these circumstances.

Weaning. FA values were lower in first molars than other teeth, suggesting that weaning is not more stressful compared to other life history stages. Compared to males, however, females had greater overall FA values for the first molar, suggesting a comparatively more stressful time than males during weaning. Mother-infant contact reduces steadily with growth. Mothers reject suckling attempts as early as six months of age but most vigorously when the infant approaches a year (Nash 1978; Rhine et al. 1985). This schedule corresponds with first molar development. For yearling baboons, developmental instability may be linked to weaning stressors which include (a) nutritional stress from decreasing energy availability (Altmann 1998), (b) psychosocial stress from increased separation from the mother (Levine 2005), and (c) physiological stress in the form of decreased pathogen resistance (Katzenberg et al. 1996).

Reproduction. FA values were lower in third molars than other teeth, suggesting that reproduction is not comparatively more stressful than other life history stages. Males, however, had higher third molar FA values than females, suggesting they have a comparatively more stressful time during reproductive years then females. In olive baboons—and a wide range of other primate species—female philopatry and male dispersal is the rule. Multiple factors may compromise the fitness of emigrating individuals. A lone male is more vulnerable to predation (Dunbar 1987) and, as such, spends less time foraging (Slatkin & Hausfater 1976). Elongated solitary periods of recently matured males also impede their mating prospects. Organisms under such dietary and reproductive stresses expend more energy to counter these challenges (Parsons 1990). The stress associated with male dispersal, both nutritional and psychosocial, may be greater than that of females despite the clear biological burdens of reproduction on the female body. The third molar is the last tooth to develop and has been noted to exhibit greater morphological variation perhaps due to relaxed selective pressure—this might make it more susceptible to the ontogenetic effects of sexual dimorphism (Butler 1939; Gingerich 1974; Mayhall & Saunders 1986). Third molar length exhibits greater variation than other teeth (Gingerich & Schoeninger 1979) and the hypoconulid on the distal surface of cercopithecoid mandibular third molars (Swindler 2002) may act to increase variance and asymmetry. Finally, given the negative association (in gorillas) of crown height and FA, we might expect that lower ranked males, who capture a larger share of any sample, would have higher FA from developmental stress, particularly when secondary sexual traits are developing (Manning & Chamberlain 1994).

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Figure 1

Collection locations in Gashaka Gumti National Park, Nigeria

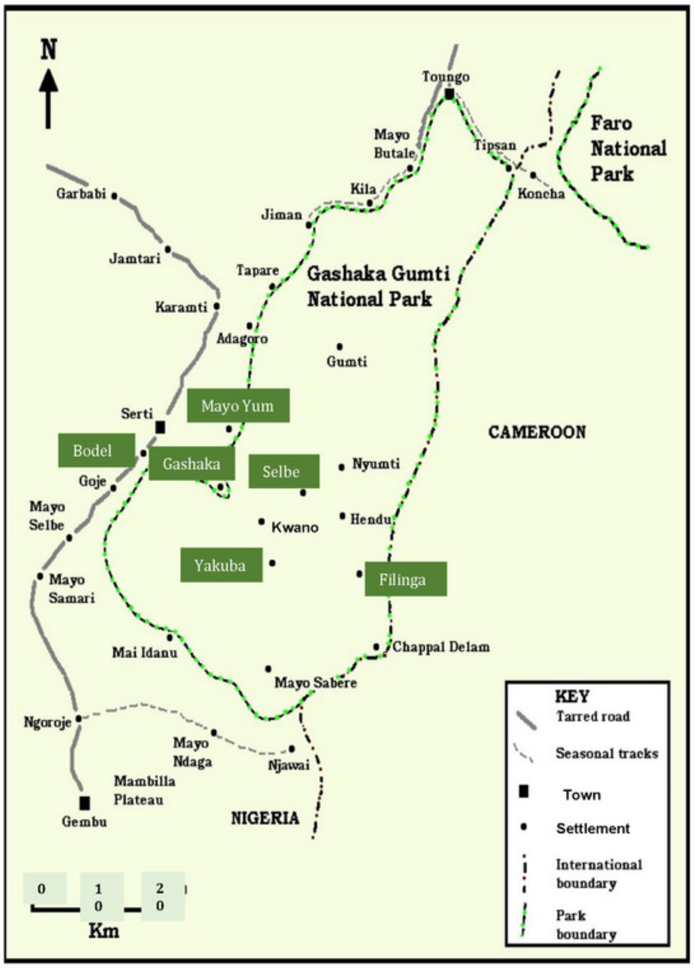

Figure 2

FA10a by Sex

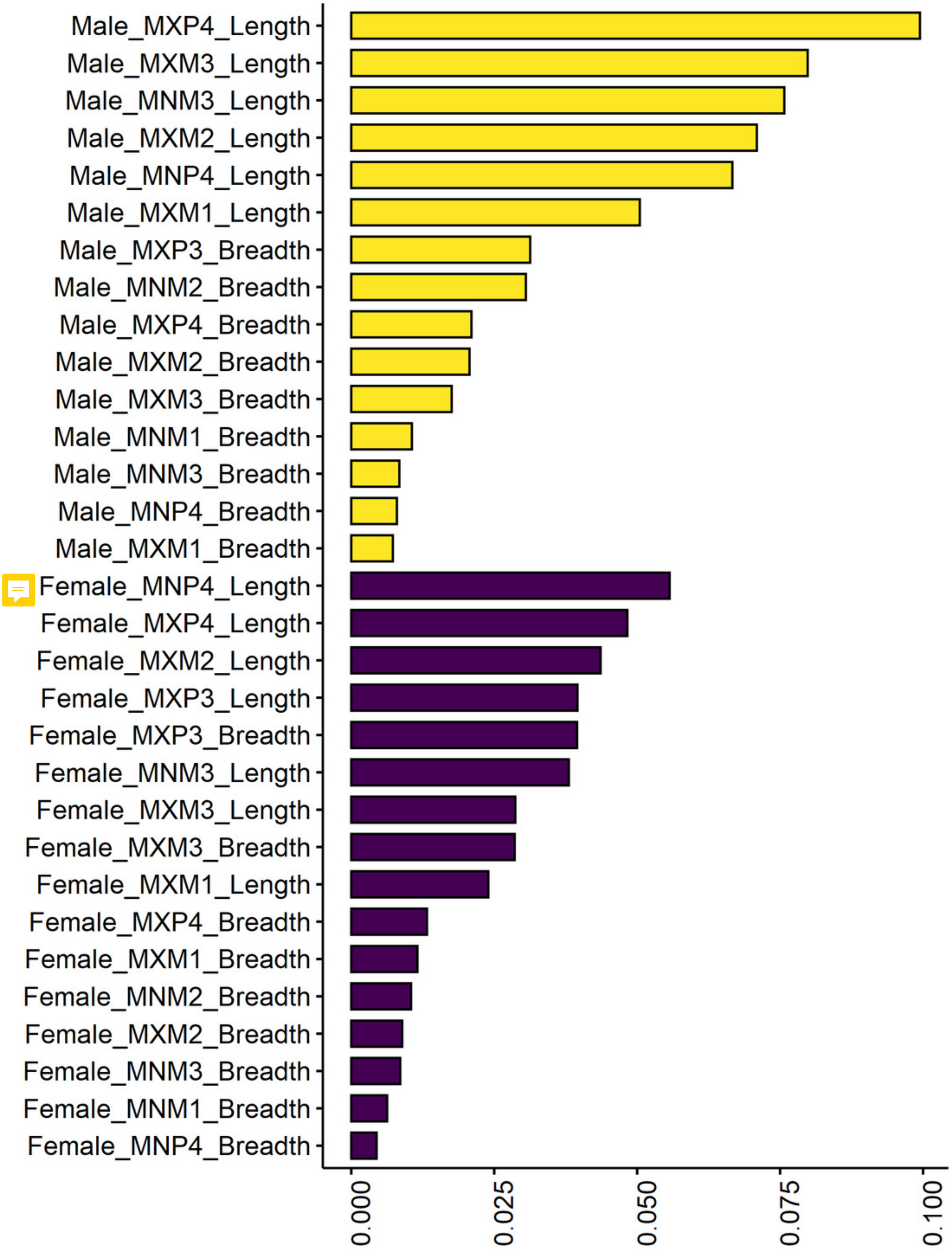
Male_MXP4_Length
Male_MXM3_Length
Male_MNM3_Length
Male_MXM2_Length
Male_MNP4_Length
Male_MXM1_Length
Male_MXP3_Breadth
Male_MNM2_Breadth
Male_MXP4_Breadth
Male_MXM2_Breadth
Male_MXM3_Breadth
Male_MNM1_Breadth
Male_MNM3_Breadth
Male_MNP4_Breadth
Male_MXM1_Breadth
Female_MNP4_Length
Female_MXP4_Length
Female_MXM2_Length
Female_MXP3_Length
Female_MXP3_Breadth
Female_MNM3_Length
Female_MXM3_Length
Female_MXM3_Breadth
Female_MXM1_Length
Female_MXP4_Breadth
Female_MXM1_Breadth
Female_MNM2_Breadth
Female_MXM2_Breadth
Female_MNM3_Breadth
Female_MNM1_Breadth
Female_MNP4_Breadth
0.000
0.025
0.050
0.075
0.100

Figure 3

FA10a comparing first molar to other teeth by sex

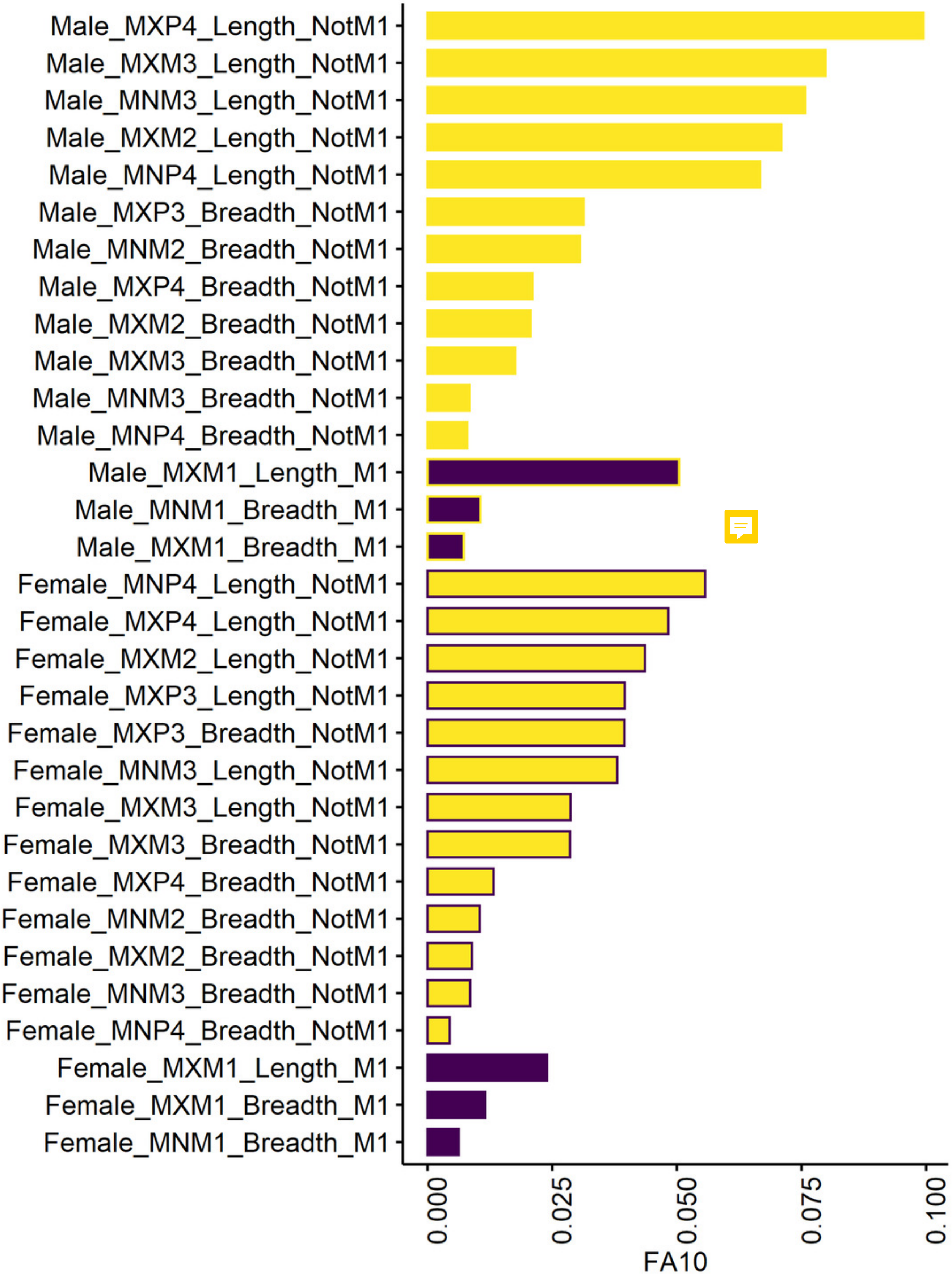
Male_MXP4_Length_NotM1
Male_MXM3_Length_NotM1
Male_MNM3_Length_NotM1
Male_MXM2_Length_NotM1
Male_MNP4_Length_NotM1
Male_MXP3_Breadth_NotM1
Male_MNM2_Breadth_NotM1
Male_MXP4_Breadth_NotM1
Male_MXM2_Breadth_NotM1
Male_MXM3_Breadth_NotM1
Male_MNM3_Breadth_NotM1
Male_MNP4_Breadth_NotM1
Male_MXM1_Length_M1
Male_MNM1_Breadth_M1
Male_MXM1_Breadth_M1
Female_MNP4_Length_NotM1
Female_MXP4_Length_NotM1
Female_MXM2_Length_NotM1
Female_MXP3_Length_NotM1
Female_MXP3_Breadth_NotM1
Female_MNM3_Length_NotM1
Female_MXM3_Length_NotM1
Female_MXM3_Breadth_NotM1
Female_MXP4_Breadth_NotM1
Female_MNM2_Breadth_NotM1
Female_MXM2_Breadth_NotM1
Female_MNM3_Breadth_NotM1
Female_MNP4_Breadth_NotM1
Female_MXM1_Length_M1
Female_MXM1_Breadth_M1
Female_MNM1_Breadth_M1
0.000
0.025
0.050
0.075
0.100
FA10

Figure 4

FA10a comparing third molar to other teeth by sex

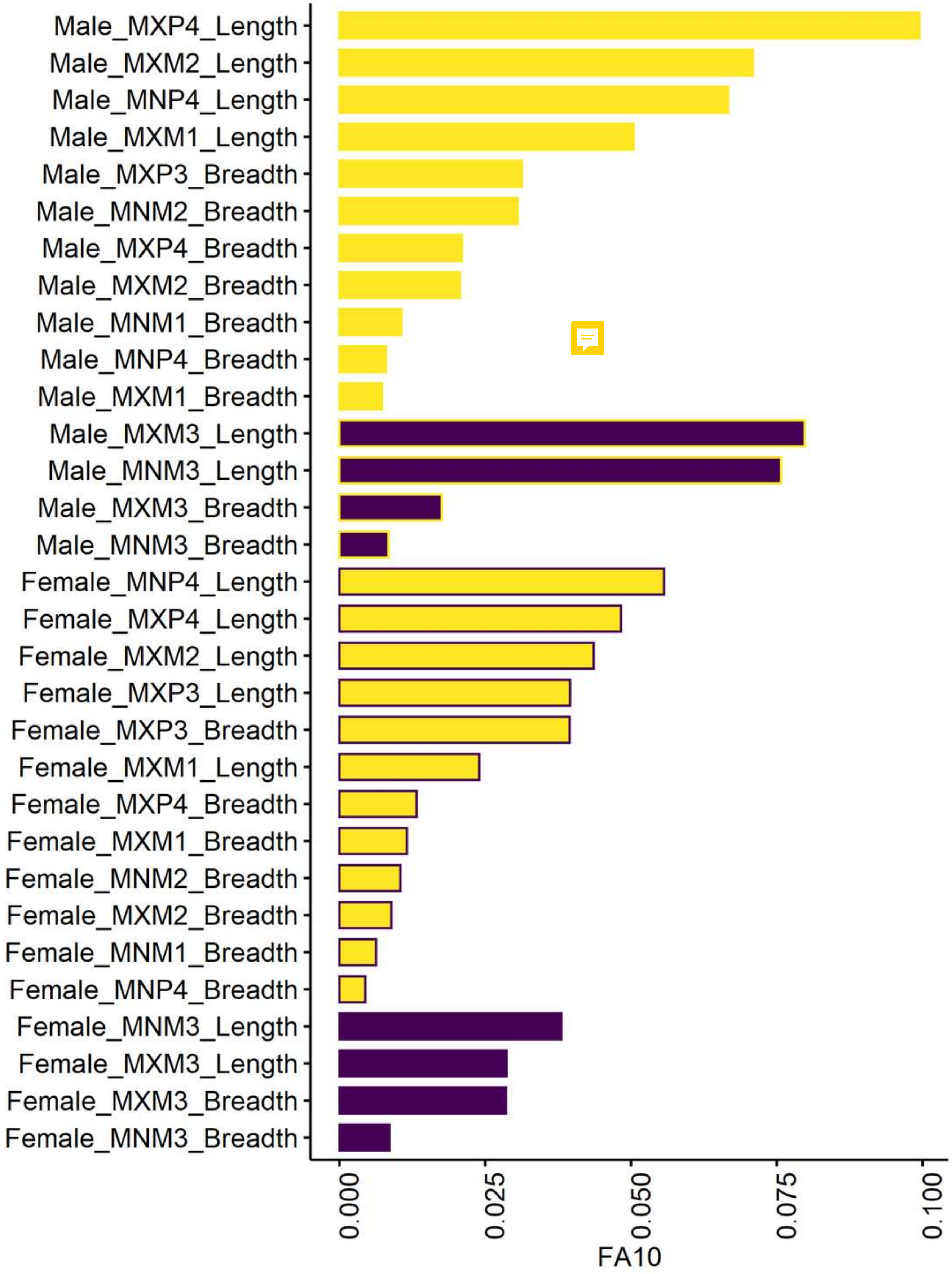
Male_MXP4_Length
Male_MXM2_Length
Male_MNP4_Length
Male_MXM1_Length
Male_MXP3_Breadth
Male_MNM2_Breadth
Male_MXP4_Breadth
Male_MXM2_Breadth
Male_MNM1_Breadth
Male_MNP4_Breadth
Male_MXM1_Breadth
Male_MXM3_Length
Male_MNM3_Length
Male_MXM3_Breadth
Male_MNM3_Breadth
Female_MNP4_Length
Female_MXP4_Length
Female_MXM2_Length
Female_MXP3_Length
Female_MXP3_Breadth
Female_MXM1_Length
Female_MXP4_Breadth
Female_MXM1_Breadth
Female_MNM2_Breadth
Female_MXM2_Breadth
Female_MNM1_Breadth
Female_MNP4_Breadth
Female_MNM3_Length
Female_MXM3_Length
Female_MXM3_Breadth
Female_MNM3_Breadth
0.000
0.025
0.050
0.075
0.100
FA10

Table 1(on next page)

ME summary by replicate set

Table 1: ME summary by replicate set

Replicates	ME3	Mean	Median	Minimum	Maximum	Range
9-10	12%	25%	22%	10%	51%	41%
5-6	12%	24%	22%	9%	47%	38%
6-9	7%	16%	16%	5%	33%	29%
2-5	7%	18%	16%	7%	37%	30%
4-7	8%	18%	15%	5%	51%	46%
3-8	6%	13%	12%	5%	36%	31%
2-9	4%	10%	9%	4%	31%	27%
1-10	4%	8%	8%	3%	21%	18%

Table 2(on next page)

FA10a Index Values for Hypothesis Testing

Table 2: FA10a Index Values for Hypothesis Testing

Sex	**Metric**	**Tooth**	**FA10a**	**n**[1]
Female	Breadth	MNM1	0.01	20
Female	Breadth	MNM2	0.01	16
Female	Breadth	MNM3	0.01	20
Female	Breadth	MNP4	0.00	14
Female	Breadth	MXM1	0.01	31
Female	Breadth	MXM2	0.01	30
Female	Breadth	MXM3	0.03	34
Female	Breadth	MXP3	0.04	26
Female	Breadth	MXP4	0.01	31
Female	Length	MNM3	0.04	20
Female	Length	MNP4	0.06	15
Female	Length	MXM1	0.02	31
Female	Length	MXM2	0.04	32
Female	Length	MXM3	0.03	32
Female	Length	MXP3	0.04	27
Female	Length	MXP4	0.05	31
Male	Breadth	MNM1	0.01	17
Male	Breadth	MNM2	0.03	16
Male	Breadth	MNM3	0.01	14
Male	Breadth	MNP4	0.01	15
Male	Breadth	MXM1	0.01	31
Male	Breadth	MXM2	0.02	34
Male	Breadth	MXM3	0.02	34
Male	Breadth	MXP3	0.03	25
Male	Breadth	MXP4	0.02	29
Male	Length	MNM3	0.08	14
Male	Length	MNP4	0.07	15
Male	Length	MXM1	0.05	33
Male	Length	MXM2	0.07	35
Male	Length	MXM3	0.08	33
Male	Length	MXP4	0.10	29

[1] The sample size from which the FA10 index was created.

Table 3(on next page)

FA10A Trends

Table 3: FA10a Trends

Model	F-value	df	p-value	Sig
FA10~Tooth	1.78	8.00	0.14	
FA10~Class	0.19	1.00	0.67	
FA10~Arcade	0.26	1.00	0.61	
FA10~Metric	8.48	1.00	0.01	*

Table 4(on next page)

Results of Hypothesis Testing

Table 4: Results of Hypothesis Testing

Hypothesis	Result	Model	F	df	p
Sex Differences	Significant sex differences	FA10~Sex	10.602	1	**0.003**
Weaning	No difference	FA10:M1~Tooth Type	1.670	1	0.207
	Significant sex differences	FA10:M1~Tooth Type*Sex	6.696	3	**0.002**
Reproduction	No difference	FA10:M3~Tooth Type	0.064	1	0.802
	Significant sex difference	FA10:M3~Tooth Type*Sex	4.313	3	**0.013**