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Lauren Conrad

University of Arkansas, Fayetteville

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Molar Macrowear as a Proxy for Age in a Captive Sample of *Papio hamadryas*

An *Honors Thesis* submitted in partial fulfillment of the requirements for Honors Studies in
Biological Sciences

By

Lauren Shea Conrad

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J. William Fulbright College of Arts and Sciences

The University of Arkansas

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ABSTRACT

This study is methods-focused, centering around molar crown macrowear and its performance as a proxy for age in a sample of pedigreed, non-human primates. It analyzes the correlation between age-structured variables and molar wear among both males and females in a captive group of baboons. Here, I examined whether wear is significantly correlated with age-related variables (i.e., generations/cohorts) and whether the structure of the “age” dataset differed across wear categories. Because chronological age is unknown, I used documented pedigrees and parent-offspring relationships to group individuals into possible generations. I then used dental development charts to group individuals into cohorts based on tooth eruption patterns observed from dental casts of each individual. A modified version of the Scott System was used to record degree of molar wear. Results indicate significant differences in both age and wear profiles between males and females. However, for both sex-groups, significant relationships exist between M1 and M2 wear and “age” (i.e., cohort/generation membership) that suggest, as expected, wear increases the longer an individual is alive. Results also indicate significant differences in age profiles for males and females across wear categories that might be useful in assigning cohort/generation membership when no pedigree records are available. These findings could be applied by other researchers, especially those wishing to include age as a model covariate in future analyses.

INTRODUCTION

Pedigreed dental cast collections are invaluable resources for dental anthropology. Researchers utilize the combination of “dental data and documented relatedness information” to explore the “biological foundations of tooth variation” (Paul et al., 2022). For example, researchers have analyzed crown size and morphology in twin and family datasets in human (Dempsey & Townsend, 2001; Hughes et al., 2000; Paul et al., 2020, 2021; Stojanowski et al., 2017, 2018, 2019; Townsend & Brown, 1978a, 1978b) and non-human (Baume, 1981; Hardin, 2019a, 2020; Hlusko & Mahaney, 2009; Kelly et al., 2021; Koh et al., 2010) primates to examine patterns of heritability and genetic correlation. Resulting high heritability for most traits indicates genes significantly contribute to their variation and support the use of these data as proxies for genetic information (Paul et al., 2022).

In these genealogical and quantitative genetic analyses, age and age/sex interactions are often included as model covariates. In this way, researchers consider age-dependent variation and trends across birth years, cohorts, or even broad secular change in a population over time. However, age can also be the focus of genealogical investigations of tooth form or dental anthropological research. “Age-structured phenotypic variation” can reveal information about population structure and microevolution (Stojanowski & Schillaci, 2006). For example, a recent study of Solomon Islander individuals used birth year information to examine secular trends in asymmetry. The significant results suggested shifts in sociopolitical dynamics and lifeways over multiple generations impacted health and development as reconstructed from patterns of dental fluctuating asymmetry (Harris, 2021). In an earlier study of this Solomon Islander sample, dental asymmetry was analyzed alongside age data to establish a relationship between maternal age at birth and developmental “stress” reflected in offspring. (Harris, 1977).

Insights of this kind require access to age and/or birth year data. In samples with established genealogies but without documented age information, other lines of evidence must be considered. For example, Schwendeman et al. (1980) used dental characteristics to estimate the age of 49 baboons in a colony with both known and unknown ages. The criteria (eruption, wear, and color of premolars/molars) resulted in precise, ordered age estimates, which aligned with known ages for a subset of the baboons (Schwendeman et al., 1980).

This exploratory study considers whether crown macrowear represents a useful proxy for age in a pedigreed sample of *Hamadryas* baboons. If so, wear might be incorporated into quantitative genetic analyses to detect age-related or secular patterns in dental variation.

Tooth Wear and Age

Tooth macrowear is defined as loss of enamel and dentin observable with the naked eye. These processes are primarily caused by attrition and abrasion (Galbany et al., 2020). Attrition is defined as the loss of tooth structure caused by tooth-on-tooth contact, while abrasion is defined as loss of enamel due to external forces wearing down teeth through mechanical actions (Sperber, 2017). External forces may include food or other foreign body contact (i.e., tooth brushing of humans) (Sperber, 2017). Both can occur as a result of mastication or chewing. As such, macrowear often reflects the relationship between an individual's/species' dietary behavior and environment (Galbany et al., 2020).

Bioarcheologists and dental anthropologists have various ways in which to quantify macrowear, in some cases as a means to approximate age at death in prehistoric human samples. Certain systems focus wear on the anterior dentition (Smith, 1984), while others focus on the molars, specifically (Scott, 1979). Using these established data recording guidelines, researchers

assign ordinal wear categories or “scores” to a tooth based on overall cusp blunting or flattening, enamel loss, dentin exposure, and/or crown destruction (see Methods). While the Smith and Scott Systems are primarily concerned with describing wear patterns, the Brothwell and Miles Systems go one step further in assigning age-estimate ranges to these patterns in the molar row (Brothwell, 1981; Miles, 1958, 1962). These systems are easy to apply, do not require specialized equipment or software, and are fairly useful when applied to a wear-seriated sample.

Tooth Wear in Non-Human Primates

Molar surfaces are used for sheering and grinding in most primates (Kay & Hiiemae, 1974). In their study examining macrowear patterns in non-human primates, it was concluded by Fiorenza et al. (2022) that individuals with more flexible diets (i.e., fruits, insects, leaves, and meat) have the most variable macrowear. On the contrary, non-human primates like gorillas have different macrowear patterns with wear focused in different areas of the crown because of their more specialized diet of mechanically demanding foods (i.e., of leaves, stems, roots, fresh shoots, and bark) (Fiorenza et al., 2022). In a study assessing dental macrowear in wild, non-human primates across different species, it was concluded that wear rates can be explained by a few factors, one being “general diet categories” (Galbany et al., 2020). Species which consumed diets containing mostly fruits (frugivore) had significantly lower tooth wear rates compared to their hard-shelled-organism-consuming (durophagous) and leaf-eating (folivore) counterparts (Galbany et al., 2020). Thus, we can conclude that different diets affect macrowear patterns of non-human primates.

Since this study examines a colony of captive non-human primates, it is important to note their diet because of its relevance to wear patterns and degree of wear. The baboons of the

Sukhumi breeding station were fed a diet of flour and fruits, with vegetables, sunflower seeds, nuts, and bread (Baume, 1981). Their diet, in some ways, aligns with frugivorous primates, but it also includes some hard-shelled or tough resources, as well. Importantly, though, there was little variation in how individuals were provisioned within the colony. That is to say, the members of the Sukhumi colony were all fed the same things. Although, it is possible resource access varied based on social factors (rank, social group membership) or health status. This information was not available to me for this study.

RESEARCH ORIENTATION AND HYPOTHESES

The overarching goal of this research is to determine whether degree of gross dental wear is a useful proxy for age. Specifically, my study approaches the following questions: 1) is molar wear related to age-structured variables (i.e., pedigree generation membership, age estimated based on dental stage of dental development, offspring count), and, if so, 2) which aspects of molar wear provide the “best” reflection of age? Because my sample represents a captive colony of *Hamadryas* baboons, it is important to note that a) aspects of population structure were artificially generated, b) the dentitions of all individuals were cast at the same time, and c) presumably, all individuals were fed the same diet. As such, I hypothesize that degree of molar wear will be strongly correlated with other age-structured variables (Bamshad et al., 1994). Aside from outlying cases (e.g., undocumented status-dictated resource access, pathology, trauma), older individuals will have more worn teeth than younger individuals, and macrowear scores will significantly correlate with other age-related markers. If this study can support the hypothesized connection between age-structured categories and macrowear, we can then seriate

wear to generate more specific age estimates for these individuals (e.g., 1.5-2-year cohorts), that will be useful to future researchers analyzing the sample.

MATERIALS AND METHODS

The study sample includes images of dental casts representing a collection of captive, pedigreed baboons (*Papio hamadryas*). These individuals were part of a research colony housed at the Institute of Experimental Pathology and Therapy in Sukhumi, Georgia (formerly the USSR), and their dentitions were cast in 1977 (Baume, 1981). These casts were originally collected to investigate the effects of inbreeding on tooth size and shape and were part of a broader experimental research initiative centered around lymphoma (Baume & Lapin, 1983). A series of pedigree data, primary observation of stone casts of maxillary dentitions, as well as three-dimensional scans and two-dimensional images of these casts were used to gather information about the baboons to categorize them into particular age-relevant groupings (i.e., generations/cohorts) and generate dental wear scores. The available pedigree sample includes 1,371 individuals, although only 461 individuals are represented by casts/images (Figure 1). Some (235) individuals were omitted due to poor cast quality or missing records, resulting in a final sample size of 226 individuals.

A major study complication is that exact chronological age for individuals in this sample is unknown. Birthdates were not included in the pedigree records. The records do, however include parent-offspring relationships which have been used to construct extended, multigenerational genealogies (Figure 1). The individuals in this sample span 72 pedigrees.

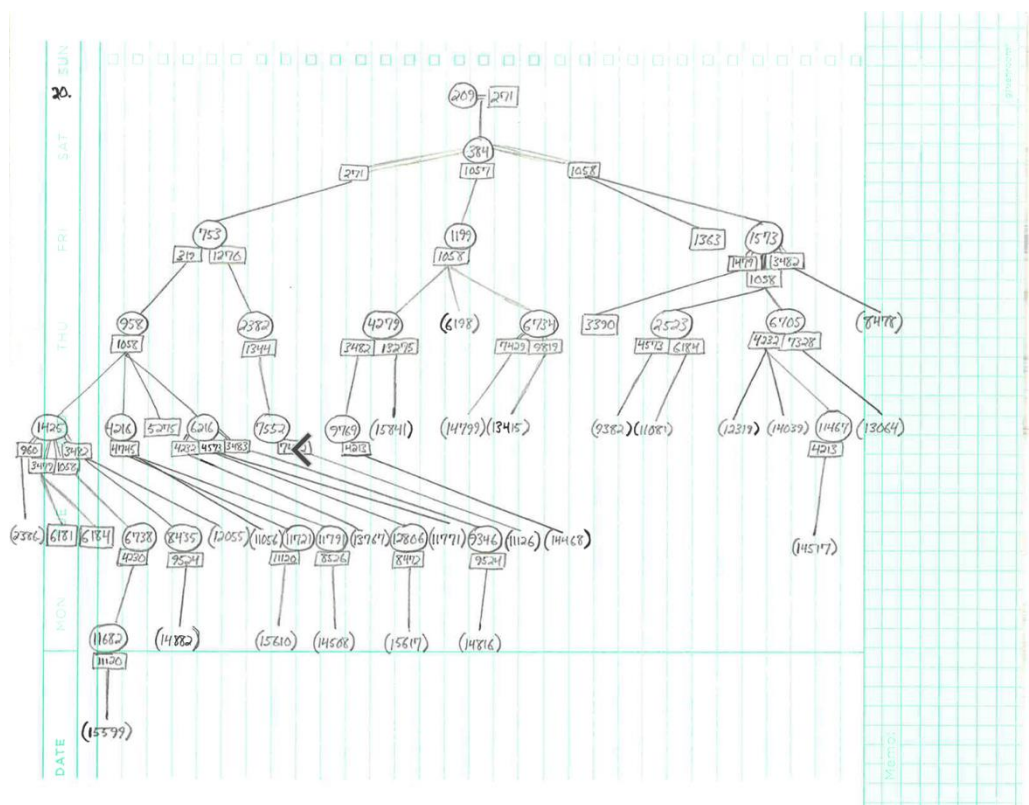


Figure 1. Sample pedigree diagram.

Data Collection Methods

Generating Age-Related Categories. Individuals from these pedigrees were compared with casts present in the lab and then grouped according to generation based upon whether they had offspring and/or parents. Baboons were categorized into generations following the sequence of Generation 0 (founding generation, grandparent), Generation 1 (next generation, parent), Generation 2 (grandchild), and so on. Baboons were found in pedigrees up to Generation 7. Developmental information was also used to group individuals into an alternative set of rough age categories. Tooth eruption charts were referenced to determine stage of dental development for all individuals. The first chart outlines average age at tooth eruption for I¹, I², C, P³, P⁴, M¹,

and M^2 for humans and baboons (Hlusko & Mahaney, 2009) (Figure 2). The second chart presents a chronology of dental development in *Papio hamadryas* (among other species) for I^1 , I^2 , C, P^3 , P^4 , M^1 , M^2 , and M^3 (Figure 3). Since tooth eruption can be assessed with reference to the casts, the combination of the two charts was used to generate more fine-grained age categories. Upon first examination of development, those whose dentitions were still developing when casted were assigned to the youngest generation (e.g., Generation 2), which was mapped across genealogies. Parents of these individuals were grouped into the next youngest generation (e.g., Generation 1), and grandparents into the next (e.g., Generation 0). After further investigation into pedigree data, individuals were grouped into generations with respect to their presence and positions across pedigrees, ranging from Generation 0-7. Because these generations do not map cleanly across all pedigrees, it is possible some individuals fall “in between” these generations.

One of the main determinants for estimating age based on dental development was the presence of the third molar, which indicates an individual is over the age of seven (Figures 2-3). For dentally immature individuals, eruption stages were used to (roughly) estimate age in years. To account for uncertainty surrounding these estimates, individuals were assigned to broader cohort groupings: Cohort 1 (<2 years), Cohort 2 (2-3.5 years), Cohort 3 (3.5-5 years), Cohort 4 (5-7 years), and Cohort 5 (7+ years). Three cohort variables were included in the ultimate analysis: one in which cohorts were assigned based on the minimum age in the range generated based on development, another in which cohorts were assigned based on the median age in the range generated based on development, and another in which cohorts were assigned based on the maximum age in the range generated based on development (for definitions of study variables, see Supplemental Table 1).

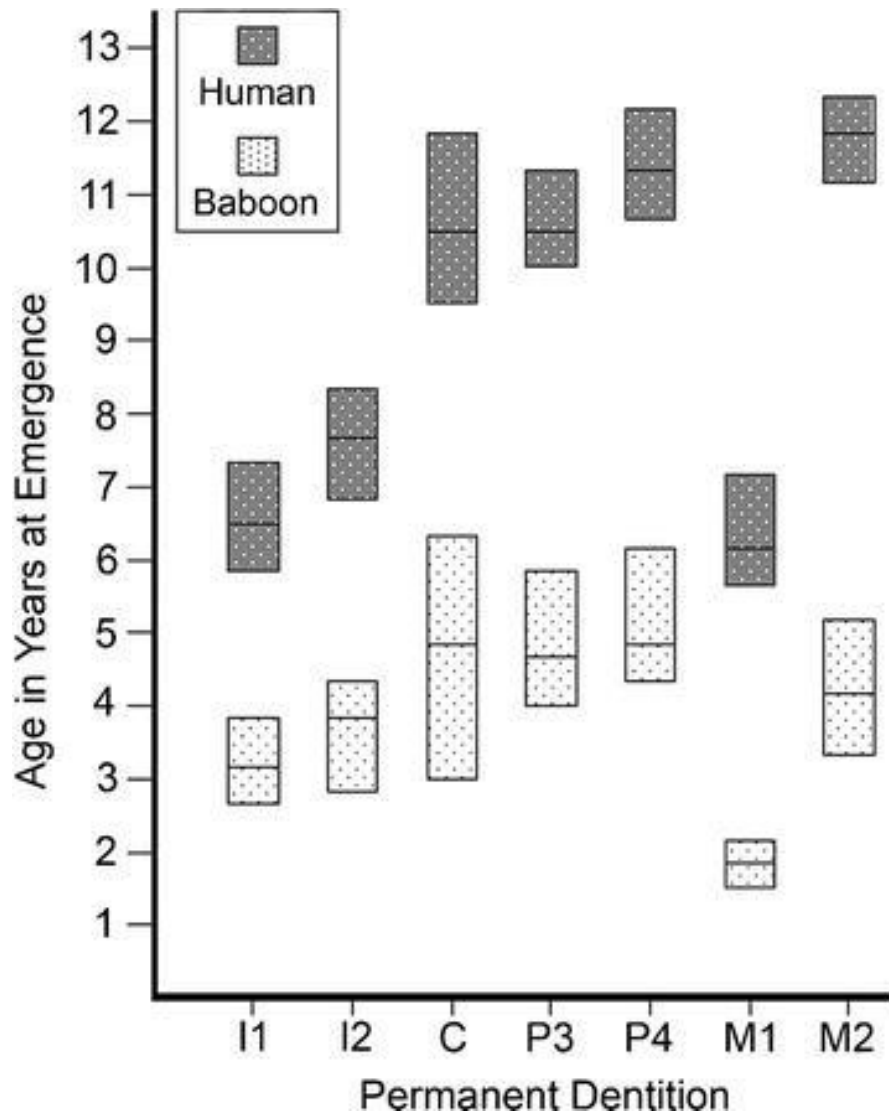


Figure 2. Human and baboon eruption ages for permanent dentition; line represents average age at eruption (from Hlusko & Mahaney, 2009).

Quantifying Tooth Wear. Both crown wear and stage of dental development were assessed from three-dimensional cast scans. These images were curated as .STL files generated using a Medit T-500 blue light table-top orthodontic scanner and viewed in MeshLab's 3D mesh processing software for data collection (Figure 4).

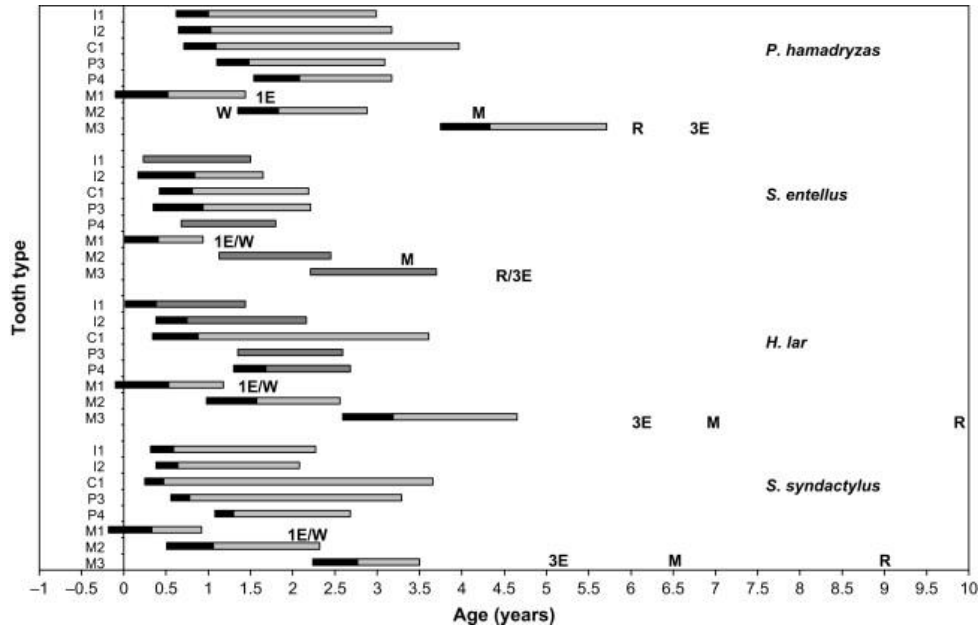


Figure 3. W = weaning; M = menarche; R = first reproduction; 1E = first molar emergence; and 3E = third molar emergence plotted against dental development in female *P. hamadryas*, *S. entellus*, *S. syndactylus*, and *H. lar*. Black bars = cuspal enamel formation; light gray bars = non-cuspal enamel formation; dark gray bars = all enamel formation (from Dirks & Bowman, 2007).

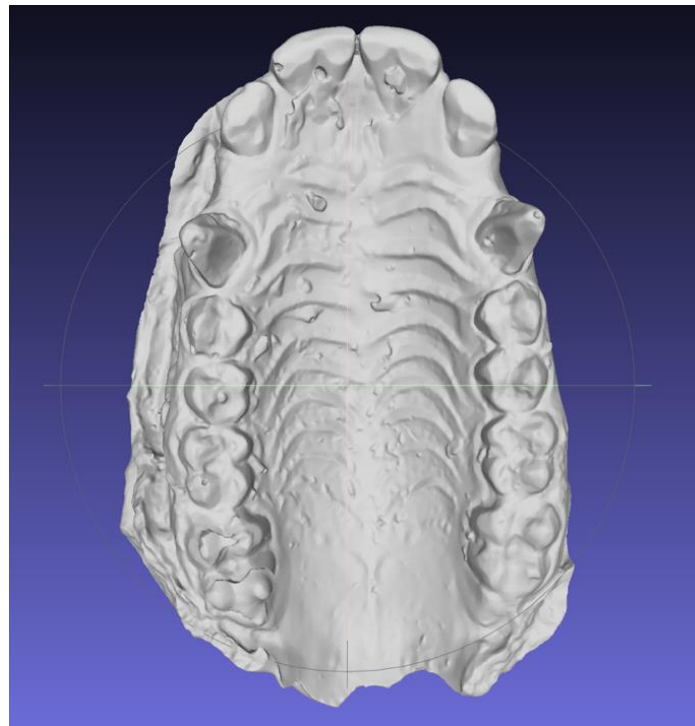


Figure 4. Three-dimensional scan of dental cast viewed in Meshlab.

Macrowear was quantified or “scored” without reference to generation membership. It was necessary to use macrowear as opposed to microwear because the casts are not of the highest quality; there are numerous casting errors, bubbles in the casting material, and breaks/chips that could be mistaken for wear if analyzed using topographic surface mapping. Instead, primary macrowear data collection was prioritized from the permanent maxillary first, second, and third molars (M^1 , M^2 , and M^3). Molars are used heavily for mastication and should wear at a fairly steady rate (Kubo & Eisuke, 2014). The first molar is also present in most individuals, as it is the earliest to erupt in the permanent dentition; even individuals with mixed dentitions (including both deciduous or “baby teeth” and permanent or “adult” teeth) are likely to have first molars erupted (see Figure 2). Both the left and right M^1 , M^2 , and M^3 s were analyzed in case individuals exhibited sided chewing behavior, and the maximum, minimum, and mean wear scores were included in the analysis (Tables 1-2 and S1). Deciduous left and right m^1 and m^2 data were collected for younger, developing baboons with either deciduous or mixed dentitions. However, due to small sample sizes, these data were not included in the analysis.

While I collected wear data for much of the sample, I was granted access to an existing dataset compiled by a previous Dental Phenomics Laboratory member (Park, 2022). In order to combine these datasets and increase sample size, an error study was conducted on a subset of individuals. This helped reveal intra- and interobserver discrepancies before beginning data collection. The molars of fifteen arbitrarily chosen individuals were scored twice with a three-day separation to a) assess intraobserver error between sessions of data collection, and b) assess interobserver error between researchers.

Molar wear was scored with reference to the Scott System, as well as a modified version of this system. The Scott System was designed for quantifying macrowear in humans and was

originally developed for application to archaeological contexts (Scott, 1979). Under this system, molar wear is quantified using quadrant scores. Molars are separated into four sections/cusps, and each is scored on a scale from 1-10 (Figure 5). The sum of the four quadrant scores provides a total score for the tooth crown, ranging from 0-40. Wear scores are determined by the amount of enamel present in each quadrant. This system is easy to use, so it is broadly applied to bioarcheological skeletal samples (Scott, 1979). Park (2022) collected data from this sample using a simplified version of the Scott System, characterized by wider “bins” of wear scores. This modified Scott System yields ordinal data (range: 0 to 3), in which 0 indicates no available wear data, 1 designates no wear or slight blunting of cusps/pinprick of dentin exposure (*light wear*), 2 corresponds with moderate blunting of cusps/significant dentin exposure (*moderate wear*), and 3 indicates flattening of cusps/extreme dentin exposure (*heavy wear*) (Park, 2022).



Figure 5. Scott System data collection form with examples on human molars.

Analytical Methods

Through analyzing the wear scores of several individuals from different multigenerational families, the goal was to determine whether a) there is a strong correlation between generation/cohort membership (age) and wear, and b) whether age (as approximated by these variables) significantly differs across wear scores.

Error Analysis. Observer error was evaluated with reference to maximum and mean difference, as well as absolute difference between scoring sessions and observers. Because wear data are ordinal, correspondence was assessed using non-parametric Kendall's tau-b correlations. A Wilcoxon signed-rank test was used to test for significant differences in the paired datasets.

Wear Analysis. To determine whether there was sex-specific wear patterning that would prevent me from analyzing males and females together, I conducted a series of Mann-Whitney U tests for age-structured categories and wear scores. Next, I generated Kendall's tau-B correlation matrices representing the relationship between age-structured variables and wear variables. Using those with the strongest relationships (see Results), I conducted a series of Kruskal-Wallis tests with molar wear scores as the independent variables and age-structured variables as the dependent variables. Multiple pairwise comparisons were made using Dunn's procedure with application of a Bonferroni correction to account for family-wise error. A multivariate approach could not be applied, due to differing patterns of missing data across variables.

RESULTS

Error Analysis

All wear scores under the modified Scott System were significantly correlated across observer datasets ($\tau = 0.61-0.76$, $p = 0.01-0.03$). There was one exception: the second round of

left molar scoring. In this instance, values between observers were not significantly correlated ($\tau = 0.46, p = 0.10$). However, results of the interobserver error analysis (both left and right molars) indicate observer scores under this system did not significantly differ ($W = 5.00; W_{standardized} = 0.00; p = 1.00$). This justified the pooling of datasets for the modified Scott System.

In terms of intraobserver error, the correlation coefficients were significant for both the left and right wear scores for both data collection sessions using the augmented scoring system ($\tau = 0.60-0.73, p = 0.01-0.03$). Wilcoxon tests indicated no significant differences between scoring sessions ($W = 1.50-2.00; W_{standardized} = -0.58-0.00; p = 0.56-1.00$). When using the original Scott System, data from the two scoring sessions were significantly correlated ($\tau = 0.46-0.65, p < 0.01-0.03$). However, the Wilcoxon tests indicated significant difference in Scott scores for the paired right molar samples ($W = 13.00; W_{standardized} = -2.29; p = 0.02$); results for the paired left molar samples also approached significance ($W = 8.00; W_{standardized} = -1.74, p = 0.083$). Due to low repeatability for the original Scott System, I conservatively used only the modified Scott System for data collection. While this limited overall variation in wear across the sample (range of 0-3 versus range of 0-40), it did allow me to pool my data and the existing dataset (Park, 2022), due to our strong correspondence using the augmented system.

Sex-Specific Patterns

Results indicate males and females differ in patterns of wear. For both the right and left M1, females exceed males in wear score (RM1 mean: female = 1.94, male = 1.43; LM1 mean: female = 1.94, male = 1.52). The same is true for the M2 (RM2 mean: female = 1.87, male = 1.52; LM2 mean: female = 1.90, male = 1.39), but not consistently true for the M3 (RM3 mean: female = 1.86, male = 1.92; LM3 mean: female = 2.01, male = 1.69), which had a limited sample size.

These differences are significant based on Mann-Whitney U tests (p-value range: <0.001-0.02). However, it is important to note that the overall sample size for males is smaller than that for females (M = 56, F = 158).

Further, males and females differ in their cohort distribution (p-value range: 0.00-0.01), but not their generational distribution (p-value range: 0.06-0.66). Males were skewed to represent younger cohorts (maximum age cohort mean: female = 4.34, male = 3.95; minimum age cohort mean: female = 3.88, male = 3.25; median age cohort mean: female = 4.26, male = 3.79). Based on this result, males and females were analyzed separately. This ensured that age-related (based on cohort membership) wear trends did not capture sex-dependent dietary or behavioral trends.

Age and Wear Correlations

According to the female matrix, there was significant correlation between all age-structured and wear variables for M1 and M2, but none for M3. M3 data were not significantly correlated with any of the generational groupings nor cohort groupings, possibly due to the smaller M3 sample size and the nature of cohort assignment based on dental development (see Discussion). Generation correlations are negative because older generations are represented by lower numbers (founding/oldest generation = 0) and often correspond with values of higher wear, making the correlation negative. The opposite is true for cohort correlations; these correlation values are positive because the older individuals are assigned to higher numbered cohorts. This, in and of itself, suggests the general (and anticipated) trend of increasing wear with age.

The bolded values in Tables 1 and 2 represent correlation coefficients that significantly differ from 0 ($\alpha = 0.05$). The generation and cohort variable most strongly correlated with wear are highlighted for each tooth (M1 = yellow; M2 = green; M3 = blue). The strongest of the

correlations across collapsed left side/right side wear variables (minimum wear, maximum wear, mean wear) are darkly shaded if significant (Table 2).

Among females, the strongest correlations for M1 data were between M1 maximum wear and youngest generation and M1 maximum wear and minimum age cohort (Table 1). The strongest correlations for M2 data were between M2 minimum wear and youngest generation and M2 minimum wear and minimum age cohort (Table 1). For males, the correlation matrix indicated significant correlation between some age-structured wear variables and some M1 and M2 wear variables. Again, there were no significant correlations between age related variables and M3 wear variables. Among males, the strongest correlation for M1 was between M1 maximum wear and minimum age cohort (Table 2). The strongest correlations for M2 were between M2 maximum wear and oldest generation and M2 minimum wear and median age cohort (Table 2).

Variables	M1 Min Wear	M1 Max Wear	M1 Mean Wear	M2 Min Wear	M2 Max Wear	M2 Mean Wear	M3 Min Wear	M3 Max Wear	M3 Mean Wear
Oldest Generation	-0.421	-0.521	-0.477	-0.46	-0.467	-0.468	-0.208	-0.215	-0.217
Youngest Generation	-0.431	-0.541	-0.493	-0.483	-0.472	-0.478	-0.116	-0.137	-0.126
Best Guess Age Cohort Based on Max Age (Cohort 1 (<2), Cohort 2 (2-3.5), Cohort 3 (3.5-5), Cohort 4 (5-7), Cohort 5 (7+))	0.484	0.508	0.502	0.59	0.608	0.609	0.178	0.201	0.195
Best Guess Age Cohort Based on Min Age	0.522	0.528	0.531	0.611	0.596	0.608	0.182	0.197	0.196
Best Guess Age Cohort Based on Median Age	0.493	0.509	0.507	0.587	0.606	0.608	0.178	0.201	0.195

Table 1. Correlation matrix (Kendall's Tau B) / Group F (Female).

Variables	M1 Min Wear	M1 Max Wear	M1 Mean Wear	M2 Min Wear	M2 Max Wear	M2 Mean Wear	M3 Min Wear	M3 Max Wear	M3 Mean Wear
Oldest Generation	-0.245	-0.419	-0.351	-0.368	-0.462	-0.384	-0.354	-0.161	-0.286
Youngest Generation	-0.19	-0.119	-0.126	-0.064	-0.151	-0.073	-0.183	0.037	-0.133
Best Guess Age Cohort Based on Max Age (Cohort 1 (<2), Cohort 2 (2-3.5), Cohort 3 (3.5-5), Cohort 4 (5-7), Cohort 5 (7+))	0.126	0.266	0.227	0.481	0.303	0.399	0.299	0.395	0.358
Best Guess Age Cohort Based on Min Age	0.213	0.291	0.271	0.435	0.289	0.363	0.299	0.395	0.358
Best Guess Age Cohort Based on Median Age	0.15	0.285	0.247	0.519	0.354	0.457	0.299	0.395	0.358

Table 2. Correlation matrix (Kendall) / Group M (Male).

These variables with the highest correlations were selected for Kruskal-Wallis tests. The female KW results were significant for M1 maximum wear and youngest generation ($K = 32.21$,

$p < 0.01$). Post hoc analyses indicate significant differences between those categorized as M1 maximum wear score 1 and M1 maximum wear scores 2 and 3, even after accounting for family-wise error (Table 3). The mean generation for those with a wear score of 1 was 3.80 versus those with wear scores of 2 and 3 whose mean generation values were 1.72 and 0.70, respectively (Table 4). Since a wear score of 0 indicates there is no wear data, and there was only one individual who scored a 0, these results are meaningless to the broader analysis.

	0	1	2	3
0	0	16.950	36.860	51.176
1	-16.950	0	19.910	34.226
2	-36.860	-19.910	0	14.316
3	-51.176	-34.226	-14.316	0

	0	1	2	3	
0		1	0.468	0.113	0.027
1		0.468	1	0.004	<0.0001
2		0.113	0.004	1	0.015
3		0.027	<0.0001	0.015	1

Bonferroni corrected significance level: 0.0083

Table 3. Post-Hoc Results: Female M1 Max / Youngest Generation. (Differences shown above and p-values shown below.)

The female results were also significant for M1 maximum wear and minimum age cohort ($K = 36.89, p < 0.01$). Post hoc analyses indicate the difference driving this result is between those categorized as M1 maximum wear score 3 and M1 maximum wear scores 1 and 2 (Table 5). The

mean cohorts for these different categories are 3.05 for maximum wear score 1, 3.84 for maximum wear score 2, and 4.84 for maximum wear score 3 (Table 4).

Variable	Observations	Obs. with missing data	Obs. without missing data	Minimum	Maximum	Mean	Std. deviation
Youngest Generation M1 Max Wear-0	1	0	1	6	6	6	0
Youngest Generation M1 Max Wear-1	20	0	20	0	7	3.8	2.067
Youngest Generation M1 Max Wear-2	25	0	25	0	6	1.72	2.072
Youngest Generation M1 Max Wear-3	37	0	37	0	5	0.703	1.412
Best Guess Age Cohort Based on Min Age M1 Max Wear-0	1	0	1	5	5	5	0
Best Guess Age Cohort Based on Min Age M1 Max Wear-1	20	0	20	1	5	3.05	0.887
Best Guess Age Cohort Based on Min Age M1 Max Wear-2	25	0	25	1	5	3.84	1.281
Best Guess Age Cohort Based on Min Age M1 Max Wear-3	37	0	37	3	5	4.838	0.553

Table 4. Summary Statistics (Data / Subsamples). Female M1 Wear

	0	1	2	3
0	0	37.575	21.580	3.243
1	-37.575	0	-15.995	-34.332
2	-21.580	15.995	0	-18.337
3	-3.243	34.332	18.337	0

	0	1	2	3	
0		1	0.081	0.314	0.879
1	0.081		1	0.011	<0.0001
2	0.314	0.011		1	0.001
3	0.879	<0.0001	0.001		1

Bonferroni corrected significance level: 0.0083

Table 5. Post-Hoc Results: Female M1 Max / Minimum Age Cohort. (Differences shown above and p-values shown below.)

Results were significant for M2 minimum wear and youngest generation, with the difference driving these results between those categorized as M2 minimum wear score 3 and M2 minimum wear score 1, but not score 2 ($K = 25.86, p < 0.01$) (Table 6). The mean value for M2 minimum wear score 1 was 3.03, while the value for score 3 was 0.55 (Table 7). Since the generations began with 0 as the oldest and 7 as the youngest, these results make sense. The female minimum age cohort distribution differed between M2 minimum wear categories, as well ($K = 38.67, p < 0.01$). Post hoc results indicate significant difference between those categorized as M2 minimum wear score 1 and M2 minimum wear scores 2 and 3 (Table 8). The mean cohorts for these wear scores were 3.36, 4.61, and 4.86, respectively (Table 7).

	0	1	2	3
0	0	14.591	31.333	42.155
1	-14.591	0	16.742	27.564
2	-31.333	-16.742	0	10.822
3	-42.155	-27.564	-10.822	0

	0	1	2	3
0	1	0.517	0.169	0.062
1	0.517	1	0.010	<0.0001
2	0.169	0.010	1	0.104
3	0.062	<0.0001	0.104	1

Bonferroni corrected significance level: 0.0083

Table 6. Post-Hoc Results: Female M2 Min / Youngest Generation. (Differences shown above and p-values shown below.)

Variable	Observations	Obs. with missing data	Obs. without missing data	Minimum	Maximum	Mean	Std. deviation
Youngest Generation M2 Min Wear-0	1	0	1	5	5	5	0
Youngest Generation M2 Min Wear-1	33	0	33	0	7	3.03	2.338
Youngest Generation M2 Min Wear-2	18	0	18	0	6	1.556	2.121
Youngest Generation M2 Min Wear-3	29	0	29	0	4	0.552	1.183
Best Guess Age Cohort Based on Min Age M2 Min Wear-0	1	0	1	3	3	3	0
Best Guess Age Cohort Based on Min Age M2 Min Wear-1	33	0	33	1	5	3.364	0.962
Best Guess Age Cohort Based on Min Age M2 Min Wear-2	18	0	18	3	5	4.611	0.778
Best Guess Age Cohort Based on Min Age M2 Min Wear-3	29	0	29	1	5	4.862	0.743

Table 7. Summary statistics (Data / Subsamples). Female M2 Wear.

	0	1	2	3
0	0	-8.030	-31.917	-38.086
1	8.030	0	-23.886	-30.056
2	31.917	23.886	0	-6.170
3	38.086	30.056	6.170	0

	0	1	2	3
0	1	0.696	0.125	0.065
1	0.696	1	<0.0001	<0.0001
2	0.125	<0.0001	1	0.310
3	0.065	<0.0001	0.310	1

Bonferroni corrected significance level: 0.0083

Table 8. Post-Hoc Results: Female M2 Min / Minimum Age Cohort. (Differences shown above and p-values shown below.)

As for the males, Kruskal-Wallis results were significant for M1 maximum wear and minimum age cohort ($K = 7.16$, $p = 0.03$), with differences between those categorized as M1

maximum wear scores 1 and 3, but not 2, driving the output (Table 9). The mean cohorts for these wear scores are 2.96 for maximum wear score 1 and 4.33 for maximum wear score 3 (Table 10).

	1	2	3
1	0	-4.610	-17.241
2	4.610	0	-12.630
3	17.241	12.630	0

	1	2	3
1	1	0.260	0.008
2	0.260	1	0.056
3	0.008	0.056	1

Bonferroni corrected significance level: 0.0167

Table 9. Post-Hoc Results: Male M1 Max / Minimum Age Cohort. (Differences shown above and p-values shown below.)

Variable	Observations	Obs. with missing data	Obs. without missing data	Minimum	Maximum	Mean	Std. deviation
Best Guess Age Cohort Based on Min Age M1 Max Wear-1	27	0	27	1	5	2.963	1.126
Best Guess Age Cohort Based on Min Age M1 Max Wear-2	23	0	23	1	5	3.304	1.02
Best Guess Age Cohort Based on Min Age M1 Max Wear-3	6	0	6	3	5	4.333	1.033

Table 10: Summary statistics (Data / Subsamples). Male M1 Wear.

Significant results were also obtained for M2 minimum wear and median age cohort ($K = 17.23, p < 0.01$), although this was not the case for the model including M2 maximum wear and

oldest generation ($K = 5.22$, $p = 0.07$). Post hoc analyses revealed significant difference between those categorized as M2 minimum wear scores 1 and 2 (Table 11). The mean cohort for these wear scores were 3.68 and 4.50, respectively (Table 12). The results indicating that a wear score of 0 is significantly different are likely meaningless, because a wear score of 0 indicates no data present or no wear and only accounts for three males in the population.

	0	1	2	3
0	0	14.591	31.333	42.155
1	-14.591	0	16.742	27.564
2	-31.333	-16.742	0	10.822
3	-42.155	-27.564	-10.822	0

	0	1	2	3
0	1	0.069	0.002	0.002
1	0.069	1	0.006	0.014
2	0.002	0.006	1	0.597
3	0.002	0.014	0.597	1

Bonferroni corrected significance level: 0.0083

Table 11. Post-Hoc Results: Male M2 Min / Median Age Cohort. (Differences shown above and p-values shown below.)

Variable	Observations	Obs. with missing data	Obs. without missing data	Minimum	Maximum	Mean	Std. deviation
Best Guess Age Cohort Based on Median Age M2 Min Wear-0	3	0	3	2	3	2.667	0.577
Best Guess Age Cohort Based on Median Age M2 Min Wear-1	37	0	37	2	5	3.676	0.818
Best Guess Age Cohort Based on Median Age M2 Min Wear-2	10	0	10	4	5	4.5	0.527
Best Guess Age Cohort Based on Median Age M2 Min Wear-3	4	0	4	4	5	4.75	0.5

Table 12: Summary statistics (Data / Subsamples). Male M2 Wear.

DISCUSSION

Many casts in this sample are not represented in the drawn pedigrees, which means that approximating age based on generational data is not possible. Approximating age based on stage of development is useful, but this approach is limited in application to dentally immature or subadult individuals. By that I mean, individuals with erupted M3s are all lumped into a single cohort representing the upper end of the age distribution (approximately 7+ years). This study explored whether crown macrowear might represent a useful proxy for age for application to the entire sample, even older aged individuals.

Importantly, our results show differences in both age-related variables and wear across sexes. The sample was predominantly female, which may have contributed to these results. Some differences among males and females may be due to characteristics of the colony. The Sukhumi baboon colony represents an artificially maintained population. We do not have documents outlining whether or not the colony underwent culling events that targeted males or females or particular age groups, although this is a possibility. Further, researchers may not have cased older males in the population; they may have focused on younger males for safety reasons. I made the conservative choice to analyze male and female data separately in case differences in wear represented sex-specific diets, behaviors, resource access, or masticatory factors.

The strength of correlation between age-related and wear variables varied considerably. This is important, because it indicates that the choice of how to quantify wear impacts its usefulness as a proxy for age. M3 data were not significantly correlated with any generational or cohort groupings. This is not surprising due to the limited M3 sample size. Additionally, it is difficult to detect trends based on M3 data due to the method of cohort assignment based on dental development. An individual with M3 data was automatically placed into Cohort 5 (individuals 7 years of age and older), the oldest cohort. Thus, one of the age-related categories has an upper limit based on M3 eruption; wear of the M3 is, therefore, uninformative with respect to cohort membership as assigned in this study. In a future study, M3s could be analyzed separately to determine whether there are possible generational/cohort groupings within M3 wear categories. However, this might require use of the original Scott System for data collection, which yields a broader range of wear scores (0-40) than the modified Scott System, which includes only scores of 0-3.

The correlations for M1 and M2 are important, as each proved to have different wear variables of importance. This might provide guidance on how best to quantify wear for future studies. For example, in females, M1, *maximum* wear was most strongly correlated with age-related variables, while M2 *minimum* wear was most strongly correlated with age-related variables. Perhaps it would be most useful for a combination of M1 maximum wear and M2 minimum wear data to serve as proxies for age in females. For example, younger individuals may only have M1s erupted. After seriating the sample based on maximum left-right wear, these individuals could be grouped into cohorts or age-relevant categories based on macrowear for this tooth only. Alternatively, if we were to only have access to an individual's M2s (perhaps this

individual is missing their M1s), we could reference sample-seriation based on minimum left-right wear, because it yielded the most meaningful results in the current study.

In most analyses, I noted a significant difference in the “age” profiles between individuals characterized by a wear score of 1 and individuals characterized by a wear score of 3 and, in some cases, 2. These differences led me to conclude that individuals with lower wear scores are significantly younger (with differing age and cohort “cut offs” depending on the M1 or M2 wear variable of interest). This is important because the cast sample includes individuals without solid pedigree data. This allows us to group them into age cohorts based on their wear (and development) data, a desired outcome of our study. However, the groupings are fairly crude and inclusive, limiting the precision of age estimation using this line of evidence.

There are significant differences between age-related variables across only certain wear scores. For example, in females, there is a difference of about 1.5 cohorts (based on minimum developmental age) between individuals with a minimum M2 wear score of 1 (mean cohort = 3.36) and 2 (mean cohort = 4.61) or 3 (mean cohort = 4.86) (Table 12). However, there is no significant difference between individuals with wear scores of 2 and 3 in terms of minimum age cohort groupings. These results suggest we can use wear to determine whether individuals are younger than a particular cohort/generation or older than a particular cohort/generation. Individuals can now be seriated based on relevant wear variables to assign cohort membership as a proxy for age—an essential covariate in future studies.

The hypothesis that degree of molar wear is strongly correlated with other age-structured variables is supported in certain instances—in particular when considering M1 and M2 wear. As expected, higher wear scores generally corresponded with older individuals (based on pedigree and dental development information). An important future direction for this research is to

develop a precise way to collect wear data using the Scott System, which will increase variability across the dataset to generate more nuanced age-categories. Because macrowear has been shown to track age-related variables, we could then seriate individuals assigned to the oldest developmental cohort by wear scores to yield more fine-grained age categories.

CONCLUSION

The goal of this study was to determine whether dental wear could be used as a proxy for age utilizing a combination of pedigree data, casts, and scans. From the casts and scans, I used a modified data collection system to score crown macrowear for all three maxillary molars on both the left and right sides of the dentition and grouped individuals into cohorts based upon dental development. Using the pedigree information, I assigned generation membership to all individuals in the sample. I found significant correlations between age-structured variables and wear in the M1 and M2 that are consistent with the expected trend of increasing wear with age. While males and females differed significantly in their age and wear profiles, both sex groups saw significant shifts in cohort and generation profiles across wear scores (often between wear scores 1 and 3 or wear scores 1 and 2/3). These findings can be utilized in future dentition-based studies when age is unknown. For example, M1 and/or M2 wear could be included as covariates in quantitative genetic studies of the sample as a way to capture the effects of age.

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SUPPLEMENTAL TABLES

	Definition
Minimum Wear	The minimum augmented Scott System score assigned to either left or right side.
Maximum Wear	The maximum augmented Scott System score assigned to either left or right side.
Minimum Age Cohort	Cohort assignment based on the minimum possible age in the range generated by assessing stage of dental development.
Median Age Cohort	Cohort assignment based on the median age in the range generated by assessing stage of dental development.
Maximum Age Cohort	Cohort assignment based on the maximum possible age in the range generated by assessing stage of dental development.
Youngest Generation	Generation assignment based on the youngest possible generation for an individual from all generational memberships in pedigrees.
Oldest Generation	Generation assignment based on the oldest possible generation for an individual from all generational memberships in pedigrees.

Table S1. Definitions for wear and age-related variables.