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A multivariate comparison of dental variation in wild and captive populations of baboons (*Papio hamadryas*)[☆]

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ABSTRACT

Phenotypic variation is critical to many aspects of biological research. Use of a captive population to address questions concerning the genetics and evolution of dental variation raises the question of how the pattern of phenotypic variation under study compares with that in a wild population of the same species. Differences in the pattern of variation within wild and captive populations may indicate different genetic and non-genetic factors, and also may have implications for how well the captive group can serve as a model for its wild type relatives.

We compared dental size measures from two *Papio hamadryas* populations, one captive and one wild. Lengths and widths of maxillary and mandibular second molars (M2s) were collected from 630 baboons from a captive pedigreed breeding colony housed at the Southwest National Primate Research Center in San Antonio, Texas, and 125 baboons from a wild population culled from a sisal plantation in Kibweze, Kenya.

Although the two populations consistently differed with respect to lengths and widths of the M2s, principal components analyses show that the basic pattern to variation in these molar crown traits is remarkably similar in both populations; and linear functions based on these measures cannot reliably discriminate between the two groups. This similarity in the pattern of variation among these dental crown measures in these two groups suggests that analyses to dissect their genetic architecture in captive populations is likely to be highly relevant to dental variation in wild baboons as well.

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1. Introduction

Captive breeding populations of animals have proven extremely valuable to many areas of scientific research. Their value is primarily attributable to the fact that the researcher can control, limit or, at least, identify and measure reliably the environmental and biological factors that might influence variation in the traits or processes of interest. Given this attribute, animals from captive breeding populations have

served as research models for wild populations of their own species and, in many well-known instances, for humans as well. In either of these two cases, the validity of any captive animal model is a function of the similarity between it and the modeled species.

Captive baboons have been used extensively in anthropological research as model organisms for studies related to dental development, variation, disease, and evolution in humans and other primate species.^{1–3} Although the utility

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of captive baboons in these sorts of studies seems entirely justifiable given their phylogenetic proximity and consequent genetic, anatomic, and physiological similarities to higher primate species, it is incumbent upon the researcher to demonstrate comparability between model and modeled species with respect to each phenomenon of interest (i.e., trait, process, etc.) prior to extrapolation of results. Equally important is ascertaining that captive populations are representative of natural or wild types of their species and not a subpopulation with aberrant traits or phenotypic values (i.e., it is difficult to posit that a captive population is a model for other species if it is not adequately representative of non-captive populations of its own).

We are engaged in studies of the genetics of primate dental variation and evolution using data from captive baboons. Given the highly conserved nature of gene regulatory systems across widely diverse mammalian groups,⁴ the strong genetic similarity between higher primate species—92–95% genetic sequence homology between baboons and humans,³ the genetic similarities between phylogenetically distant taxa such as humans and mice,⁵ and evidence for similar patterns of skeletal morphological integration between closely related primate taxa,^{6–8} we began these studies not expecting significant differences in basic dental biology between wild and captive populations of the same species that have only been isolated for one to five generations. Yet, research of dental eruption times in baboons,^{9–16} for example, shows that this is not always true. Although there is considerable similarity in the timing of dental eruption and emergence across wild populations, these processes occur 1.5 years earlier in captive animals.¹⁵ Such observations motivate our view that, when possible, assessment of the degree of similarity between captive and wild populations with respect to a trait of interest is an important and prudent step in research using model organisms.

Here we report on a comparison of dental variation in a colony of captive, pedigreed, breeding baboons housed at the Southwest National Primate Research Center (SNPRC) to that seen in a wild baboon population from Kenya. Although the amount of variation in each population may not be equal, we hypothesized that this variation results from the same biological process in captive and wild populations of the same species. If true, the structure of the variance revealed through principle components analyses should be the same for both populations.

2. Materials

Right and left second molar metric data were collected from two populations: one held in captivity and one from a more natural habitat. Our taxonomy follows Jolly.¹⁷

The wild baboon data are from a collection of *Papio hamadryas cynocephalus* (yellow baboon) skeletons housed in the Osteology Department of the National Museum of Kenya (NMK). Since 1988 more than 150 baboons have been (and continue to be) culled from 18 sites on the Dwa Sisal Estate (plantation) near Kibwezi in southeastern Kenya (2°26'S, 37°53'E). Given *P. h. cynocephalus* and *P. h. anubis* social grouping patterns, it is reasonable to assume that these animals are

related and form one, or just a few large extended pedigrees similar in nature to that of the SNPRC captive colony used in our quantitative genetic analyses. The NMK data were collected from 125 permanent dentitions, consisting of 68 males, 55 females, and two first molars from juveniles whose sex was indeterminate.

The captive population data were collected from olive baboons (*P. h. anubis*), a few yellow baboons (*P. h. cynocephalus*), and their hybrids¹⁸ housed at the Southwest National Primate Research Center (SNPRC) in San Antonio, Texas. These animals are descendant from founders that were wild caught and matings since have been controlled to inhibit inbreeding. The sample studied has a female to male sex ratio approximating 2:1, and ranges in age from 4.6 to 30 years.

While strict genetic management was (and is) employed to prevent inbreeding, all non-founder animals in this study were the result of matings that were random with respect to phenotype. Since birth or, in the case of some of the oldest of the founders, arrival at the SNPRC colony, all animals have been housed out of doors in social group cages and maintained on monkey chow diets to which they have ad libitum access. Animal care personnel and staff veterinarians provide daily maintenance as well as regular, urgent, and emergent health care to all animals throughout their stay at SNPRC in accordance with the Guide for the Care and Use of Laboratory Animals.¹⁹

Data were collected from dental casts of 630 individuals. Dental molds were collected from anesthetized animals using a protocol described in detail elsewhere²⁰ and approved by the Institutional Animal Care and Use Committee in accordance with the established guidelines. Positive casts were poured with high resolution dental plaster within one week of the mold being made. Dental casts were also produced from skulls of deceased animals that are curated by Dr. J.M. Cheverud at Washington University in St. Louis. All data from the SNPRC population were collected from these plaster casts.

In living monkeys, the gumline obscures the cervix and forms the outer visual boundary for many of the teeth. Therefore, digital images were made of the molar casts following a protocol described in detail elsewhere²⁰ and the outline of each tooth was established as 1 mm below the lowest point of the mesial and distal fovea rather than at the gumline. This was measured by sinking the tooth into a pool of titanium beads of approximately 0.15 mm diameter that acted like a liquid, filling in around the molar at the designated level. Following this protocol, the outer line of the tooth was standardized and could be used for all measurements collected. Replicability of the digitizing protocol was tested for 14 molars. Measurements of the same tooth in repeated images were found to be 1.5–1.7% different.

3. Data collection methods

This study focuses on the maxillary and mandibular second molars (M^2 and M_2 , respectively), as these are the largest of the datasets.

The NMK molars were measured using fixed-jawed dental calipers (Mitutoyo[®] Model NTD12-6" C). Mesiodistal lengths (md) and buccolingual widths (mesial width = mw; distal width = dw) were measured following standard definitions.¹³

Data from the SNPRC baboon molars were collected from digital images of the casts (described above). Mesiodistal length was measured as the maximal length of the molar. Buccolingual distance was measured as the maximal width of the tooth oriented through the two mesial cusps, defined on the buccal and lingual sides by the contact with the titanium beads. Measurements were not taken from teeth that were worn below the landmark defined by the mesial/distal foveal depth.

Measurement errors for the caliper-metric protocols ranged between 1 and 5% of the average measurement. Measurement error for the data collected from the digital images ranged between 1 and 2%.²¹

The measurements collected for these two populations are not identical, making comparisons of actual size estimates between them inappropriate. However, measurement error for all of the protocols used here are low and comparable, and the protocols were consistent within each population. Therefore, comparing the univariate distributions and multivariate structure between the two populations is not affected by the somewhat differing data collection procedures.

4. Analytical methods

Initial data processing and management were done using routines implemented in the computer pedigree database program PEDSYS.²² All statistical analyses were conducted using routines implemented in the NCSS 2004 software program.²³ Prior to analysis and within each sample, a linear regression procedure was used to regress out the effects of sex on each measure. All analyses described below were conducted on sex-adjusted residuals. We compared the wild Kenyan to captive pedigreed baboons on the basis of the 12 M2 crown metrics in three ways: (1) univariate inferential statistical comparisons on a measure-by-measure basis, (2) multivariate descriptive statistical comparisons based on latent structure of the data, and (3) multivariate inferential statistical comparisons.

4.1. Unrelated founder sample for inferential statistics

The data from the captive baboons come from related individuals, violating the assumption of independence on which the interpretation of the results of many statistical tests rely. By contrast, we have no accurate knowledge of the patterns of kinship that may exist within the wild Kenyan sample. To address these issues, we identified a subset of 65 unrelated animals with dental data in the captive baboon population. These animals essentially are founders for the 11 pedigrees from which the captive animals in this study were obtained. We used pedigree analysis and kinship estimation routines implemented in the computer programs PEDSYS²² and SOLAR²⁴ to identify these individuals. Each comparison between the wild and captive baboon populations were repeated by comparison with the captive founder sub-sample. All reports of significance, however, are based on comparisons with the captive founder sub-sample. No result from the latter comparison was accepted or reported if inconsistent with that from the former comparison with the larger pedigreed sample.

4.2. t-Tests

We used Student's two-sample t-test (with Aspin-Welch adjustment for unequal variances) to compare the means of the sex-adjusted residuals of each measure from the wild Kenyan and captive pedigreed populations. We considered test statistics with $P < 0.05$ to be evidence of a significant difference.

4.3. Principal components analysis

We used the multivariate data reduction method, principal components analysis (PCA), to further aid in the comparison of the M2 metrics in the wild and captive populations. We used PCA to decompose the covariance among the sex-adjusted residuals for the 12 dental crown measures in each population, reducing the dimensionality of their M2 datasets while retaining the characteristics of each dataset that contribute most to its variance. The goal was to obtain for each population a set of low-order components: i.e., synthetic variables that are linear transformations of the original data containing the "more important" aspects of the data and account for a majority of the variance in them. We selected as the more salient components, (1) those which incremental contribution to the variance distinguished them from the others in a scree curve and (2) those with eigenvalues approximating or greater than 1.²⁵

Prior to the principal components analyses, we eliminated an animal's data from consideration if all three measures were not available for at least one of the four permanent M2s. Further, we eliminated from the study data from animals with too many missing measurements to support the following missing multivariate normal data estimation procedure. A regression analysis was conducted using the variable containing the missing value as the dependent variable and all variables with non-missing data from an animal as independent variables. The values of the non-missing variables from the animal containing the missing value were used in the regression equation to compute a predicted value for the missing value. This process was iterated 1000 times for each value using the imputed missing values from one run during the estimation phase of the next.

Lastly, we conducted linear discriminant analyses of the sex-adjusted residuals for these permanent M2 metric data to determine if we could obtain a set of prediction equations that would classify the individuals into their appropriate groups: i.e., wild or captive. Group membership was used as the criterion variable and the M2 crown metrics were used as the predictor variables. We used graphical and statistical analyses of the resultant discriminant function and canonical variate scores to assess whether the two groups could be separated on these metrics or whether, as expected, they overlap.

5. Results

Summary descriptive statistics for each sample—wild caught baboons from Kenya, captive baboons from SNPRC, and a sub-sample made up of founders for the pedigrees into which the captive baboons are organized—are presented in [Table 1](#). Mean

Table 1 – Permanent second molar crown dimensions (in mm) in wild and captive baboons: sample descriptive statistics

Parameter	XLM2			XRM2			DLM2			DRM2		
	mdl	mw	dw	mdl	mw	dw	mdl	mw	dw	mdl	mw	dw
Wild population												
N	91	89	88	94	90	88	87	86	85	87	89	86
Mean	12.25	11.47	10.40	12.22	11.38	10.38	12.12	10.09	9.93	12.22	10.09	9.86
S.D.	0.84	0.75	0.69	0.87	0.79	0.71	0.82	0.74	0.74	0.83	0.70	0.65
Minimum	10.1	9.6	8.8	10.2	9.5	8.8	10.1	8.6	8.4	9.9	8.6	8.3
Maximum	14.2	13.3	11.9	14.1	13.2	11.8	14.0	12.1	11.9	14.1	12.0	11.1
Captive population												
N	649	647	637	643	638	623	590	581	572	593	585	575
Mean	12.51	10.12	9.13	12.43	10.09	9.07	12.29	9.35	8.79	12.34	9.35	8.79
S.D.	0.84	0.87	0.82	0.84	0.87	0.83	0.82	0.77	0.83	0.79	0.74	0.77
Minimum	10.10	8.33	7.23	9.10	7.55	7.19	8.20	7.50	5.80	9.88	7.20	7.00
Maximum	15.7	13.3	11.9	15.5	13.2	11.9	15.3	12.1	11.9	15.4	11.9	11.3
Captive population, founders only												
N	60	57	57	59	59	58	52	51	51	54	54	53
Mean	12.13	9.60	8.70	12.09	9.75	8.76	11.96	8.94	8.38	11.99	9.04	8.45
S.D.	0.57	0.59	0.58	0.57	0.52	0.52	0.54	0.49	0.54	0.54	0.51	0.42
Minimum	10.9	8.3	7.2	11.1	8.6	7.8	11.0	7.8	7.2	10.8	7.7	7.6
Maximum	13.4	11.9	11.2	13.7	10.9	8.9	13.2	10.2	10.0	13.8	10.1	9.6

X = maxillary; D = mandibular; R, L = side of the arcade; mdl = mesiodistal length; mw = mesial buccolingual width; dw = distal buccolingual width.

permanent M2 crown widths (bucco-lingual diameters) of the wild Kenyan baboons were consistently larger than those of the captive bred animals from SNPRC, while the contrary is true for the mesio-distal lengths. However, t-tests of the residuals (after regressing out the effects of sex) of these metrics reveal no significant differences between the wild Kenyan animals and the unrelated founders of the pedigrees to which the captive baboons belong (i.e., all $P > 0.21$).

Principal components analysis in which we decomposed the covariance among the 12 permanent M2 measures revealed very similar results for the two. The first five components account for approximately 99.7 and 99.8% of the variance in the Kenyan and captive animals, respectively. The first through third principal components, identified as the most salient by having eigenvalues greater than or equal to 1 and by inspection of the scree plot, account for approximately 71, 15, and 7–8% of the variance in these measures in each population. Examination of the component loadings from

these analyses (Tables 2 and 3) amplifies the similarities between the two groups. The first principal component reflects magnitude or size; the second is a component contrasting crown length and crown width; and the third contrasts maxillary and mandibular measures. Principal components analyses of the data from the sub-sample of founders for the captive population's pedigrees revealed the same pattern of results (not shown).

Both forward and backward stepping linear discriminant analyses failed to identify a subset of measures that could distinguish the two groups, so all M2 crown measures were used. The best linear function based on these 12 M2 crown measures from the two groups were incapable of reliably discriminating between the wild Kenyan and captive pedigreed baboons (Fig. 1). Application of this function results in 44.8% of the wild baboons being classified as "captive" and 46.1% of the "captives" being classified as "wild." The results of the associated canonical correlation analysis—i.e., a single

Table 2 – Principal components analysis of permanent second molar crown dimensions in wild baboons from Kenya: component loadings

Variables	Component 1	Component 2	Component 3	Component 4	Component 5
xlm2md	−0.77943	−0.53332	−0.01256	−0.08156	−0.22932
xlm2mbw	−0.86867	0.255708	−0.12851	0.173102	−0.06018
xlm2dbw	−0.77075	0.192203	−0.49384	−0.11103	0.082942
xrm2md	−0.80989	−0.51882	−0.03191	−0.04514	−0.22866
xrm2mbw	−0.85141	0.282559	−0.14545	0.231601	−0.07939
xrm2dbw	−0.72171	0.175055	−0.51202	−0.02565	0.060899
d1m2md	−0.79084	−0.527	0.062638	0.081663	0.229861
d1m2mbw	−0.79023	0.273822	0.339985	0.223214	−0.02582
d1m2dbw	−0.75328	0.309623	0.258975	−0.19408	0.043193
drm2md	−0.78802	−0.49016	0.110185	0.014954	0.232852
drm2mbw	−0.82543	0.27725	0.354729	0.058524	0.00335
drm2dbw	−0.75215	0.296817	0.170628	−0.39647	−0.00567

Table 3 – Principal components analysis of permanent second molar crown dimensions in captive baboon population: component loadings

Variables	Component 1	Component 2	Component 3	Component 4	Component 5
xlm2md	-0.76367	-0.49165	-0.13236	0.002662	0.046523
xlm2mbw	-0.78332	0.301105	-0.23389	0.188956	0.036853
xlm2dbw	-0.78	0.317631	-0.29681	-0.14044	0.25375
xrm2md	-0.78692	-0.46715	-0.12605	-0.03185	-0.01307
xrm2mbw	-0.79128	0.37138	-0.20619	0.159822	-0.18897
xrm2dbl	-0.74871	0.357057	-0.25075	-0.1883	-0.02908
d1m2md	-0.73535	-0.54224	-0.02214	0.02476	-0.00512
d1m2mbw	-0.79554	0.158103	0.292876	0.297911	0.03914
d1m2dbw	-0.73571	0.081858	0.417771	0.024419	0.279188
drm2md	-0.7528	-0.51411	-0.01046	-0.01489	-0.07476
drm2mbw	-0.8081	0.208107	0.24715	-0.0361	-0.24498
drm2dbw	-0.7511	0.172871	0.332795	-0.31116	-0.0789

canonical variate, canonical $R = 0.0667$, $R^2 = 0.0045$, Wilks' Lambda = 0.9955—emphasize further the inability to discriminate between these two groups based on the 12 M2 crown measures.

6. Discussion

The primary goal for this study was to determine whether the pattern of variation in M2 crown dimensions in captive populations of baboons was similar enough to that in wild populations of the same species to justify use of the former to study the genetics and evolution of the latter. Our results demonstrate a considerable degree of similarity between the captive and wild baboon populations in the variation of these 12 dental metrics. This is perhaps most evinced by the inability to construct linear discriminant functions that reliably differentiate between the two populations.

This result is perhaps not surprising given that quantitative genetic analyses have shown similarities in the genetic variance of numerous wing shape and life history phenotypes in captive and wild populations of milkweed bugs,²⁶ and that genetic correlations yield similar patterns of craniofacial

modularity across primate species²⁷ and genera.^{6,7} Although our analyses do not yield information about the underlying genetics, a common genetic architecture could return the similarities in phenotypic variation that we find in these two baboon populations.

We interpret the results presented here as evidence that dental variation in captive baboons does reflect dental variation in wild baboons. As such, quantitative genetic analyses of molar size variation in these captive baboons are appropriate as a model for non-captive baboon biology. Further analyses are needed to determine whether or not these phenotypic similarities exist for other regions of the dentition (such as the canine complex²⁸) and more complicated phenotypes such as those that describe cusp orientation.²⁹

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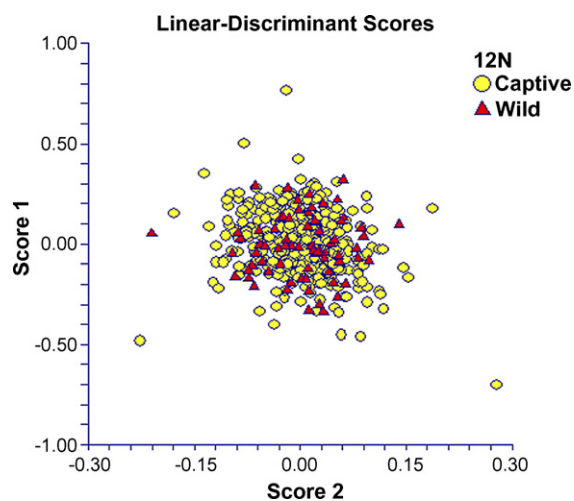


Fig. 1 – Plot of linear discriminant function scores from analysis of 12 M2 crown metrics in wild (triangle) and captive pedigreed baboons (circle).

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