The Relationship of Tooth Size to Body Size in a Population of Rhesus Monkeys (*Macaca mulatta*)

CAROL LAUER
Department of Anthropology, University of Michigan, Ann Arbor, Michigan

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ABSTRACT Tooth areas correlate significantly with long bone measurements in a skeletal population of rhesus monkeys from Cayo Santiago. Correlations are relatively large for the troop as a whole, as well as for males and females separately. Femur and humerus length measurements show the highest correlations with tooth size.

The literature on the human fossil record is filled with dentition studies that entail deductions about human evolution. It is often implied that tooth size is related to body size, and that species can be separated by dental dimensions. Brace ('65) and Wolpoff ('71a,b) have argued that tooth size differences between gracile and robust australopithecines are due to differences in body size. Weidenreich ('45) and Robinson ('56) have assumed a general relationship between tooth and body size.

Nevertheless, most work on hominids contradicts the assumption that tooth size is significantly related to body size. Filipsson and Goldson's ('63) study of Swedish conscripts demonstrates no significant correlation between incisor and canine breadth, and stature. Garn and Lewis ('58), Garn et al. ('67) and Garn et al. ('68) recount very low correlations between standing height and the length and breadth of canines, incisors and first molars in a sample of Ohioans of Northwest European derivation.

In contrast, Martin ('70) using summed posterior areas on a skeletal collection of 27 gorillas (15 males and 12 females) demonstrates significant correlations between summed posterior areas of maxillary teeth (P^3-M^3) and body size. She uses the sum of humerus and femur length, summed mininum cross sectional area and the summed volumes of the humerus and femur to represent body size. The correlation coefficients for these three measures and tooth size are 0.63, 0.55 and 0.60, respectively. P is less than 0.01 for all three. However, results are only significant for a combined sample of males and females, suggesting that they are linked to the high degree of sexual dimorphism in gorillas.

Kurten ('67) finds significant correlations between tooth and skull size in populations of several mammal species including: *Vulpes vulpes* (European red fox), *Felis silvestris* (European wild cat), *Crocuta crocuta* (spotted hyena) and *Ursus spelaeus* (cave bear).

Martin's study suggests that the inclusion of a wide range of size variation will generate significant tooth and body size correlations even in a random sample of animals. Kurten's positive results in species with little sexual dimorphism may be linked to his use of single populations. Since members of a population live in the same environment, their tooth size is subject to similar selective pressures. The negative results in the human studies can be attributed to non use of whole populations, as well as to inclusion of a small range of size variation. According to Wolpoff ('71a), modern Europeans are under relaxed selective pressure to maintain tooth size, and increased variation is to be expected.

Thus, the studies of modern man are inconclusive regarding tooth and body size relationships. In order to test whether a close relationship (one that is more than a result of sexual dimorphism) exists in primates, one should examine a single population with selection operating on tooth size. However, no matter how positive the results, drawing parallels to fossil man will be problematic because of the non-availability of fossil populations.

The primate population under consideration here is the Group K skeletal collection from Cayo Santiago, housed at the Carribean Primate Center, Punta Santiago, Puerto Rico. These rhesus monkeys (106 in number), while obviously not hominoids, are semi-terrestrial animals adapted to eating a highly diversified diet.

Group K, a free ranging troop resident on Cayo Santiago, was constantly monitored, and a record kept of all births contains the exact age and maternal lineage of each animal. In 1970, a removal program was instituted to reduce the population of Cayo Santiago from around 700 animals to about 300. As part of this plan, Group K was sacrificed, producing a skeletal collection of animals of known sex, age, maternal genealogy and weight. Since animals were provisioned, similar nutritional backgrounds can be assumed.

METHODS

Buccolingual and mesiodistal measurements were taken on the posterior dentition and canines of all Group K members with upper and lower second molars erupted. Areas were calculated, and those of the right and left teeth averaged. Measurements are after Wolpoff ('71a), with length the distance between the contact points of the teeth "in normal tooth position or at the midpoint of the line of contact if interstitial wear occurred" (Wolpoff, '71a). Breadth is the greatest diameter perpendicular to this distance. Vernier calipers were used and diameters recorded to the nearest 0.1 mm.

Incisors and P_3 were not measured since great wear means that no accurate assessment can be made of unworn areas. An error analysis, made by repeating measurements on 13 individuals, indicates average error in tooth area due to reproducibility is less than 2%.

Six measurements were recorded for estimating body size: maximum anatomical femur length, head diameter, mid shaft diameter of the femur, anatomical humerus length, diameter at the deltoid tuberosity and body weight. Animals were measured if the proximal end of the femur was fused, and the distal end at least partially fused. Weights, which were taken at capture, were available for some animals. Lengths and diameters were obtained using an osteometric board, spreading calipers and vernier calipers, and all measurements were recorded to the nearest 1.0 mm. Repetitions of all measurements on six animals show average error due to reproducibility to be around 1%. Finally, distal long bones have been excluded since they are often traumatized, and their adult form is more a function of juvenile experience than of inherited size.

Regressions and correlations were calculated to estimate the relationship between tooth area and body size.

RESULTS

Descriptive statistics, calculated for males and females and the population as a whole, reveal some sexual dimorphism, but generally low variability. Table 1 lists the coefficients of variation for the macaque population, and those for a sample of gorillas measured by Dr. Paul Mahler at the Cleveland Museum of Natural History. Note the higher variability in the gorillas for all teeth except the canines. The coefficients of variation for the separate gorilla sexes show that the gorillas' relatively high variability is not just due to sexual dimorphism. The lower coefficients of variation for canines in the separated macaque sexes suggests that macaques are more sexually dimorphic in canine size than are gorillas. Since the macaques are part of a single breeding unit, their low variability is expected. The gorillas are random sample from a variety of regions in Africa.

Measurement of body size

A recent study done on Cayo Santiago indicates a 0.93 correlation with 248 degrees of freedom ($p < 0.001$) between sitting height and weight in adult male rhesus monkeys (D. Sade and C. DeRousseau, personal communication). No study was done on females, and my own observations on Cayo Santiago suggest greater variability in female weight. The descriptive statistics for Group K support this conclusion. The coefficient of variation for female weights is approximately 20, and for males is 15. Because of these male, female differences, and because weights were not available for all animals, another size measure was sought. In males, correlations calculated between weight and bone measurements are signifi-

TABLE 1

Coefficients of variation for tooth areas in a sample of gorillas[1] *and in the Group K population of rhesus monkeys*

Tooth	Gorillas			Macaques					
	Males	Females	Males + females	Males		Females		Males + females	
	N = 30	N = 20	N = 40 [2]	N	C.V.	N	C.V.	N	C.V.
C-	21.2	15.4	39.2	16	15.9	28	11.4	32 [2]	40.9
P^3	14.2	14.2	16.5	26	8.9	27	7.9	53	9.4
P^4	12.5	14.0	14.6	26	9.1	29	6.2	55	8.4
M^1	12.4	13.1	13.6	26	7.6	29	5.9	55	7.6
M^2	12.8	14.7	15.3	26	8.3	29	6.8	55	8.9
M^3	12.7	16.3	17.8	15	8.2	17	7.4	32	10.7
P^3-M^3	12.8	13.4	14.6	15	7.6	16	5.5	31	9.0
C_	17.2	13.4	40.0	19	14.6	28	10.1	38 [2]	46.7
P_4	14.4	13.0	18.2	26	8.5	28	8.2	54	8.5
M_1	12.1	10.5	16.0	26	10.3	29	6.2	55	9.1
M_2	13.9	11.0	19.0	26	9.3	29	7.3	55	9.4
M_3	15.0	13.1	21.2	15	9.4	20	9.3	35	12.0
P_4-M_3	12.7	10.5	17.6	15	9.3	19	6.2	34	9.3

[1] Gorilla data provided by Dr. Paul Mahler.
[2] Animals have been randomly eliminated so that number of males is approximately equal to number of females.

cant. These correlations are also significant for females (table 2), though slightly lower than in males, due to the greater variability in female weights. Correlations for the whole group are given.

I expected femur and humerus length to be good estimators of stature, but I wanted some general functional measure also dependent upon weight. Therefore, femur and humerus volume were calculated as π (0.5 diameter)^2 $\times$ maximum anatomical length. There is a 0.78 correlation (N = 21) between weight and humerus volume in males ($p < 0.001$), and a 0.80 correlation between weight and femur volume (N = 18, $p < 0.001$).

The problem of tooth wear

Since ages are known, dividing the animals into age groups and comparing average tooth areas in these groups should reveal the effects of wear on tooth size. Because of wear, size was expected to decrease with age. This expectation was not borne out, as data for P_4 (which is representative) show: in females there is no noticeable trend, and older males tend to have larger teeth. The correlation is 0.42 ($p < 0.1$) between summed superior area (P^3-M^3) and age in the male subgroup.

The apparent increase in male tooth size is perhaps the result of males changing troops frequently. Most Group K males were not natal to that troop. Since the sample size is small, the apparent increase in tooth size with age could result from the chance joining of several old males who had large teeth. Alternately, if larger teeth correlate with larger body size, males with greater body size may be more likely to be-

TABLE 2

Correlations between bone measurements and weight in Group K rhesus monkeys

Bone measurement	Males		Females		Males + females	
	N	r	N	r	N	r
Femur length	18	0.45 [1]	23	0.50 [2]	41	0.70 [3]
Femur diameter	21	0.90 [3]	23	0.77 [3]	44	0.86 [3]
Head diameter	21	0.51 [2]	23	0.03	44	0.51 [3]
Humerus length	21	0.69 [3]	23	0.65 [3]	44	0.71 [3]
Diameter at deltoid tuberosity	21	0.75 [3]	23	0.63 [2]	44	0.75 [3]

[1] Indicates significance at the 0.05 level.
[2] Indicates significance at the 0.01 level.
[3] Indicates significance at the 0.001 level.

come adult members of a troop. In this model, large bodies are selected for, and tooth size correlations with age are a chance by-product. My observations on Cayo Santiago suggest the latter is unlikely. Obviously, one can draw no firm conclusions from these limited data.

Tooth and body size correlations

There is a generally low level correlation between weight and tooth measurements in males. In females the correlations are negative, as expected, due to many overweight females: this condition, related to child bearing, is aggravated by provisioning. Combining males and females provides enough range of weight variation to make correlations with teeth significant. In the mandibular canines $r = 0.62$ ($p < 0.001$) and in the maxillary canines $r = 0.49$ ($p < 0.005$). The great sexual dimorphism in tooth area produces significant correlations with the considerable sexual dimorphism in weight.

Weight is only partially useful as an indicator of body size. By turning to long bone measurements, the sample size is increased, and females can be used without extensive qualifications. Table 3 gives tooth area and long bone length correlations for males, females and the whole troop. Generally, the trend is for higher correlations between humerus and femur length, and third molars and summed superior areas. The high correlation, in the pooled sample, between canines and long bone lengths is due to great sexual dimorphism in tooth area and bone length. The low correlation between femur length and M_3 area in males is the result of one outlyer. The third molar's late development, and thus its exposure in formation to the same environmental stresses as the long bones, may explain its high correlation with femur and humerus length. The negative correlations between bone lengths and canine areas in females are due to higher variability in tooth area than in humerus and femur length.

Summed superior area (P^3-M^3) correlates more highly with most long bone measurements than does summed inferior area (P_4-M_3), because the maxillary sum gives a better estimate of maximum grinding space. Because P_3 works with the upper canine as a shearing mechanism, it is not a true grinding tooth, and thus is not included in summed inferior areas. Wolpoff ('71a) has argued that these sums are good functional measures of the mastication apparatus. Assuming similar diets, a larger animal must be able to grind up more food than a smaller animal to maintain body size.

The correlation of humerus and femur length with tooth area could result from their close relationship with body size, i.e., stature. The other long measurements do

TABLE 3

Correlation coefficients for femur length (FL) and humerus length (HL), and tooth areas in Group K monkeys

Tooth	Males				Females				Males + females			
	FL		HL		FL		HL		FL		HL	
	N	r	N	r	N	r	N	r	N	r	N	r
C^{-}	16	0.35	16	0.50 [1]	28	−0.12	28	−0.12	44	0.88 [3]	44	0.85 [3]
P^3	26	0.46 [2]	26	0.58 [3]	27	0.20	27	0.09	53	0.55 [3]	53	0.58 [3]
P^4	26	0.35 [1]	26	0.43 [1]	29	0.21	29	0.15	55	0.48 [3]	55	0.50 [3]
M^1	26	0.27	26	0.39 [1]	29	0.23	29	0.23	55	0.47 [3]	55	0.53 [3]
M^2	26	0.34 [1]	26	0.44 [1]	29	0.31 [1]	29	0.25	55	0.58 [3]	55	0.61 [3]
M^3	15	0.53 [1]	15	0.56 [1]	17	0.71 [3]	17	0.67 [3]	32	0.81 [3]	32	0.81 [3]
P^3-M^3	15	0.52 [1]	15	0.64 [3]	16	0.51 [1]	16	0.55 [1]	31	0.75 [3]	31	0.80 [3]
C_{-}	19	0.12	19	0.40 [1]	28	−0.17	28	−0.02	47	0.85 [3]	47	0.83 [3]
P_4	26	0.15	26	0.31	28	0.21	28	0.20	54	0.21	54	0.24 [1]
M_1	26	0.22	26	0.31	29	0.27	29	0.14	55	0.39 [3]	55	0.43 [3]
M_2	26	0.37 [1]	26	0.47 [2]	29	0.48 [3]	29	0.35 [1]	55	0.57 [3]	55	0.60 [3]
M_3	15	0.21	15	0.42	20	0.69 [3]	20	0.65 [3]	32	0.68 [3]	35	0.69 [3]
P_4-M_3	15	0.18	15	0.41	19	0.28	19	0.17	31	0.57 [3]	34	0.63 [3]

[1] Indicates significance at the 0.05 level.
[2] Indicates significance at the 0.01 level.
[3] Indicates significance at the 0.005 level.

TABLE 4

Correlation coefficients for femur diameter (FD), femur head diameter (FHD) and humerus diameter at the deltoid tuberosity (DDT), and molar areas in Group K monkeys

Tooth	Males				Females				Males + females			
		FD	FHD	DDT		FD	FHD	DDT		FD	FHD	DDT
	N	r	r	r	N	r	r	r	N	r	r	r
M^1	26	0.22	0.24	0.16	29	0.27	0.19	0.08	55	0.42[3]	0.48[3]	0.32[2]
M^2	26	0.28	0.19	0.14	29	0.39[1]	0.30	0.24	55	0.52[3]	0.56[3]	0.40[3]
M^3	15	0.53[1]	0.03	−0.29	17	0.38[1]	0.35	0.19	32	0.62[3]	0.66[3]	0.49[3]
M_1	26	0.15	0.28	0.21	29	0.28	0.22	0.14	55	0.34[2]	0.44[3]	0.33[2]
M_2	26	0.34[1]	0.40[2]	0.28	29	0.21	0.16	0.22	55	0.55[3]	0.55[3]	0.43[3]
M_3	15	0.03	0.05	−0.19	17	0.08	0.06	0.26	35	0.67[3]	0.49[3]	0.46[3]

[1] Indicates significance at the 0.05 level.
[2] Indicates significance at the 0.01 level.
[3] Indicates significance at the 0.005 level.

not work as well, partly because they include too small a range of variation. Further, the maximum diameters are the result of muscle markings that can vary during an animal's lifetime from weight and activity level changes. When comparing younger and older adults, a time lag between muscle growth and bone remodeling is also a factor. Bone length is less subject to the vicissitudes of the environment and, given similar diet, has a smaller norm of reaction. Table 4 gives molar area and bone diameter correlations for males and females. In the male and female samples combined, correlations are generally significant at the 0.05 or higher level. Sexual dimorphism produces good correlations in the combined sample, but even when considering males and females separately, humerus and femur lengths correlate significantly with tooth size.

A scatter plot of femur length against summed superior area (fig. 1), or humerus length (fig. 2) show linear trends. F statistics calculated from this data also indicate linearity. For the former set of variables, $F = 37.79$, with $p < 0.001$, and for the latter, $F = 52.87$ and $p < 0.001$. Regressions represent these relationships well. The regression of summed superior area on femur length is $49.34 + 1.2 \times$ femur length = summed superior area. $R^2 = 0.57$, and the standard error of the estimate = 15.89. Regressing this summed

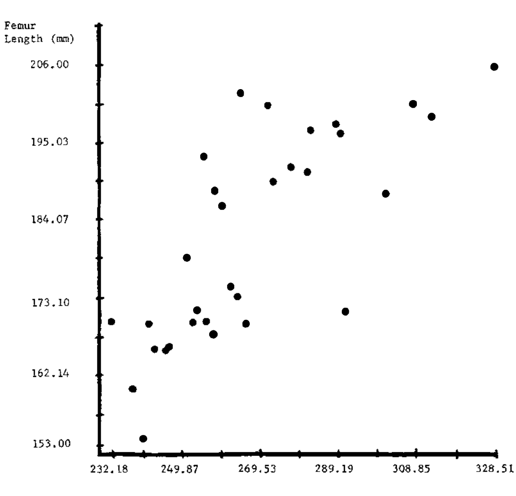

Fig. 1 Femur length as a function of summed superior area (P^3-M^3) in Group K monkeys.

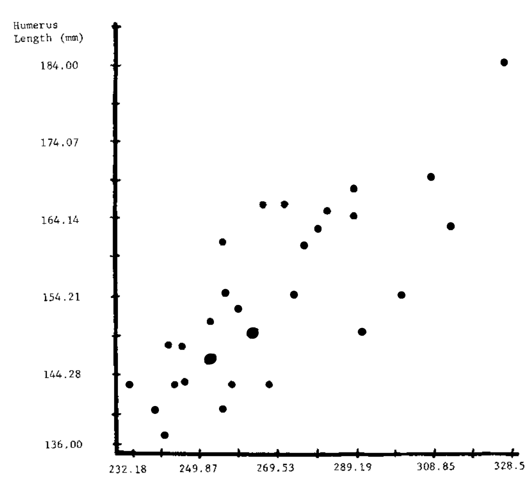

Fig. 2 Humerus length as a function of summed superior area (P^3-M^3) in Group K monkeys.

area on humerus length, 1.82 + 1.73 × humerus length = summed area. R^2 = 0.65, and the standard error = 14.35. Regressions computed separately for males and females do not work as well since the range of variation is small.

There is a positive relationship between femur and humerus volume and tooth areas. Table 5 shows that these correlations are only significant for the troop as a whole. When these volumes were recalculated using a water displacement technique, the results were not significantly different from those presented in table 5. Generally, humerus and femur length provide better correlations, e.g.. the regression of femur volume on summed superior area, −193.48 + 0.003 × femur volume = summed area. R^2 = 0.45, and the standard error of the estimate = 19.93. This may reflect the greater stability of bone length than bone volume. Bone volumes are constantly remodelled in response to stress, and are highly dependent upon weight and the size of muscle attachments.

Weight dependency at first appears to be a positive attribute in a discussion of body size, but weights, particularly under provisioning, can vary during a lifetime. Selection for a tooth size and body weight relationship would work on the totality of food an individual consumes during his life, i.e., how long it took to wear down his teeth. An animal's weight at any instant might not be indicative of lifetime average food consumption.

CONCLUSIONS

Tooth area correlates significantly with stature in the whole troop and in the separate sexes. These results do not imply that body size differences account for all tooth size differences. Furthermore, one should not make cross environmental comparisons, since different diets select for different tooth and body sizes.

Given similar environments, a range of tooth sizes will probably accommodate a particular body size, and selection will operate to keep areas within that range. Thus, in a series of specimens of similar stature or body size, one would expect insignificant tooth and body size correlations. The greater the range of body sizes, the higher should be the correlations with tooth size. In the Cayo Santiago population, combining the sexes increases the range of size variation and produces higher correlations than consideration of the less variable sexes separately. In the gorilla data, a great deal of sexual dimorphism, and thus a wide range of size variation, produces significant results even though a random collection of animals is analyzed. This connection breaks

TABLE 5

Correlation coefficients for humerus volume (HV), femur volume (FV), and tooth areas in Group K monkeys

Tooth	Males				Females				Males + females			
	FV		HV		FV		HV		FV		HV	
	N	r	N	r	N	r	N	r	N	r	N	r
C⁻	16	0.59 [2]	16	0.46 [1]	28	−0.07	28	−0.10	44	0.86 [3]	44	0.81 [3]
P^3	21	0.27	26	0.40 [1]	27	0.07	27	−0.01	48	0.49 [3]	53	0.45 [3]
P^4	21	0.21	26	0.18	27	0.24	27	0.20	49	0.47 [3]	55	0.36 [3]
M^1	21	0.20	26	0.22	28	0.12	29	0.11	49	0.46 [3]	55	0.39 [3]
M^2	21	0.27	26	0.21	28	0.37 [1]	29	0.26	49	0.60 [3]	55	0.47 [3]
M^3	15	0.25	15	−0.11	17	0.49 [1]	17	0.29	32	0.72 [3]	32	0.59 [3]
P^3-M^3	15	0.27	15	−0.06	16	0.29	16	0.18	31	0.67 [3]	31	0.56 [3]
C_	19	0.20	19	0.23	28	0.03	28	0.14	47	0.81 [3]	47	0.77 [3]
P_4	21	−0.02	26	0.10	28	0.15	28	0.08	49	0.21	54	0.18
M_1	21	0.01	26	0.24	28	0.11	29	0.13	49	0.34 [2]	55	0.37 [3]
M_2	21	0.23	26	0.33 [1]	28	0.19	29	0.24	49	0.53 [3]	55	0.49 [3]
M_3	15	0.10	15	−0.06	19	0.42 [1]	20	0.35	34	0.58 [3]	35	0.52 [3]
P_4-M_3	15	−0.03	15	−0.07	19	0.26	19	0.04	34	0.52 [3]	34	0.46 [3]

[1] Indicates significance at the 0.05 level.
[2] Indicates significance at the 0.01 level.
[3] Indicates significance at the 0.005 level.

down if one limits the size range by segregating the sexes. Within males and females in the Cayo Santiago sample, tooth area correlations with limb bone lengths are generally significant in spite of less variability than in the gorillas. The significance of this relationship in macaques seems linked to use of a single population as the unit study. This suggests the importance of the population as focal unit when dealing with relatively homogeneous or non sexually dimorphic species.

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LITERATURE CITED

Brace, C. L., and M. F. A. Montagu 1965 Man's Evolution. Macmillan, New York.

Filipsson, R., and L. Goldson 1963 Correlation between tooth width, width of the head length of the head and stature. Acta Odontologica Scandanavia, *21*: 359–365.

Garn, S. M., and A. B. Lewis 1958 Tooth size, body size and "giant" fossil man. Amer. Anthro., *60*: 874–880.

Garn, S. M., A. B. Lewis and R. Kerewsky 1968 The magnitude and implications of the relationship between tooth size and body size. Arch. of Oral Biol., *13*: 129–131.

Garn, S. M., S. Swindler, A. B. Lewis and R. Kerewsky 1967 Genetic control of sexual dimorphism in tooth size. J. of Dent. Res., *46*: 963–972.

Kurten, B. 1967 Quantitative approaches to dental microevolution. J. of Dent. Res., *46*: 817–828.

Martin, J. 1970 The relationship of posterior tooth size and body size in gorillas. Unpublished manuscript.

Robinson, J. T. 1956 The Dentition of the Australopithecinae. Transvaal Mus. Mem. No. 9.

Weidenreich, F. 1945 Giant early man from Java and southern China. Anthro. Papers from Amer. Mus. of Nat. Hist., *40*: 5–138.

Wolpoff, M. F. 1971a A functional measure of tooth size. SW. Jour. of Anthro., 27: 279–286.

——— 1971b Metric Trends in Hominid Dental Evolution. Case Western Reserve Stud. in Anthro., No. 2.