James M. Cheverud* & Paul Wilson

Department of Anatomy & Neurobiology, Washington University School of Medicine, St. Louis, Missouri 63110, U.S.A.

Wolfgang P. J. Dittus*

Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington DC 20008, U.S.A. and Institute of Fundamental Studies, Kandy, Sri Lanka

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Primate population studies at Polonnaruwa. III. Somatometric growth in a natural population of toque macaques (*Macaca sinica*)

Growth studies of non-human primates in natural populations are rare due to difficulties in obtaining measurements on animals of known age. We report a cross-sectional analysis of growth in the natural population of toque macaques (*Macaca sinica*) from Polonnaruwa, Sri Lanka, including the timing of growth and physical maturation and the developmental basis of sexual dimorphism.

Twenty-eight measurements were collected from 274 macaques aged 2 weeks to 34 years. Non-parametric spline curves were fit to the distribution of measurement values over age separately by sex. The spline curves suggest four age intervals in which linear regressions of trait on age and analysis of covariance of measurement value with age, sex, and their interaction, can be used to parametrically test specific hypotheses about growth and sexual dimorphism.

Most growth had ceased for both sexes in the adult phase. Prior to this, females had two and males three distinct growth phases. There was little sexual dimorphism in growth rates among infants and young juveniles (birth to 2.5 years). The age limits for subsequent growth periods differed by sex and trait. Thus, skeletal limb growth ceased in juvenile females by about 5.5 years, but continued into an additional subadult phase in males reaching completion by about 7.5 years, whereas muscle mass and weight reached maturity by about 8 and 12 years in females and males, respectively. An adolescent growth spurt was evident only for body weight in males, but cannot be ruled out for other traits. These macaques grow for one and a half to twice as long as macaques from other species in laboratory colonies. Much of the sexual dimorphism among adults arises from bimaturism, although sex differences in growth rates among older juveniles are also responsible for a significant portion of adult dimorphism.

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Introduction

Non-human primate growth has been studied from a comparative evolutionary perspective and as a model for human growth (Watts, 1985a). Nearly all of our information on nonhuman primate growth is derived from laboratory populations due to the need for known-age animals in growth studies. These studies have established that many non-human primates, like humans, display a biphasic growth pattern with distinct early and late growth periods (Laird, 1967; Watts, 1985a; Bogin, 1988) and have suggested the possibility that some non-human primates display an adolescent growth spurt in specific morphological features (Watts & Gavan, 1982; Watts, 1985a; Bogin, 1988). The timing of these growth periods is known primarily from small samples of captive specimens in a few species, including common chimpanzees, macaques and baboons (Watts & Gavan, 1982; Coelho, 1985; Glassman *et al.*, 1984; Coelho *et al.*, 1984). It has become clear from field studies that rates of maturation of primates in their natural habitats are considerably slower than in their well-fed counterparts under captive or semi-captive management (e.g., Dittus, 1975; Dittus & Thorington, 1981; Altmann *et al.*, 1977; Altmann & Alberts, 1987; Phillips-Conroy & Jolly, 1988). Hence, the timing of growth periods under laboratory conditions is of questionable utility for purposes of

*Authors to whom requests for reprints should be addressed.

evolutionary analyses. Unfortunately, information from captive populations is often all that is available (Leigh, 1991).

We report the results of a cross-sectional analysis of growth in a series of somatometric features in the natural population of toque macaques (*Macaca sinica*) from Polonnaruwa, Sri Lanka (Dittus, 1977a, 1988). The population has undergone an intensive but largely non-invasive study of demography, behavior and ecology for nearly 25 years, providing a rich source of basic data which can be combined with somatometric data to study growth. Earlier studies of development in this natural population, based only on body weight, indicated significantly faster growth rates among juvenile males than females aged 0.1 to 5.5 years old, a growth spurt in adolescent males, and continued growth in males and females after 10 and 7 years old, respectively (Dittus, 1977a). The aim of this study was to investigate, in a more comprehensive way, the nature and timing of infant and juvenile growth periods and the timing of somatic maturation in males and females.

In addition to providing basic data on growth in a natural population of non-human primates, we investigate the developmental basis of sexual dimorphism in body measurements. Adult sexual dimorphism can arise from two sources, sexual bimaturism and sex differences in growth rates (Shea, 1986; Gavan & Swindler, 1966). Sexual bimaturism occurs when the sexes reach maturity, or complete growth, at different ages. These two developmental processes may reflect different evolutionary histories and adaptations (Shea, 1986) and differ in their relative importance in a comparative perspective (Leigh, 1991), but are not known in detail for wild populations.

Human sexual dimorphism for weight arises from a combination of these underlying developmental processes, with males growing for a longer period than females and displaying a more exaggerated adolescent growth spurt (Tanner, 1962). Shea (1986) briefly reviewed non-human primate sexual dimorphism, and provided examples in which each developmental process takes precedence in producing sex differences. We examine the extent to which sex differences in toque macaques are due to a bimaturism and rate differences for a variety of somatic characters.

Materials and methods

Population

The toque macaques living at the Nature Sanctuary and Archaeological Reserve at Polonnaruwa, Sri Lanka, have been the subjects of a long-term study by W. Dittus. The population has been observed continuously from September 1968 to May 1972 and from March 1975 through 1991. Periodic observations were made from May 1972 to March 1975. The natural dry evergreen forest inhabited by the macaques and many aspects of their demography, ecology and behavior have been described earlier (Dittus, 1977a, 1977b, 1988).

The population contains approximately 600 individuals in 23 social groups. All animals were individually identified using methods described in Dittus & Thorington (1981). Groups were censused once a month and during the birth season individual females were observed every few days to obtain accurate birth dates. Birth, death and emigration were recorded for each animal. Chronological age at trapping was obtained from known birth dates, although ages of animals born before 1968 were estimated given their level of morphological development as determined in 1968 (Dittus, 1988). At this time, only a few of the oldest animals have estimated ages.

Measurements

Over the last few years, the Polonnaruwa population of macaques have been systematically trapped by social group (and released unharmed) in order to collect genetic, morphological and a variety of biomedical data on the population. Trapping was done following the birth season. To date, twenty-eight measurements, including weight and the length, width and circumference of the head, trunk and extremities, have been collected from 274 animals, 124 males and 150 females, ranging in age from 2 weeks to 34 years (see Appendix 1 for trait definitions). In the trapping process, individuals were held in cages and liberally fed for varying durations prior to being weighed and measured. Variation in weight and other measurements (such as abdominal circumference) due to feeding was therefore likely to be greater than if all animals had been weighed early in the morning prior to feeding. A genetic analysis of these measurements is described in Cheverud & Dittus (1992).

W. Dittus measured approximately half the social groups and research assistants measured the others. All observers practised measurements on several test animals in order to establish both intra- and inter-observer reliability. This involved learning to make minor adjustments in the placement of calipers at specific locations on various anatomical structures used as anchors for measurement. Difficult landmarks, such as the distal margins of rounded condyles, were typically measured several times on a given animal until a consistent measure was obtained. Skeletal lengths and widths had the least error and the effect of error in measuring over articulated segments (such as crown-rump length) was diminished when the lengths were over extended portions of the body. Most error probably involved abdominal circumferences where gut contents could have contributed to the variation. The observations were screened for outliers after data collection by visually inspecting plots of trait score against age separately by sex. Outliers were set to missing values (0.2% of the data) before the analyses reported here.

Age at trapping was obtained from the demographic records. The data analysed here are cross-sectional in nature and thus, may smooth out some of the variability apparent in longitudinal growth studies. It can be particularly difficult to delineate an adolescent growth spurt of small size, as may exist in macaques (Watts & Gavan, 1982; Watts, 1985b), with cross-sectional data due to variation in the timing of the spurt among individual animals (Boas, 1892; Tanner, 1951). Also, the age distribution of the animals tended to be clumped in yearly intervals due to the consistent birth season of the macaques, making judgements about cessation of growth limited to yearly intervals. This constrains the precision with which growth events can be located in time.

Spline curves

Growth was analysed first by fitting a spline curve to the distribution of trait values by age, separately by sex using the algorithm and computer program described by Schluter (1988). The logic of this approach follows, and is drawn largely from Schluter (1988). In order to estimate a growth function, f, from a collection of individual measurements, X_i , and age, A_i we select the function which is most likely given the data at hand:

$$\log(f) = \sum \log(X_i; A_i, f)$$

where $\log(f)$ is the total log likelihood of the function, f, and the term $\log(X_i; A_i, f)$ is the \log_e probability that the measurement equals X at age A given this particular function f. The summation is over all individuals. Regrettably, the function which maximizes this likelihood is any function which passes through each of the individual data points. The function would

be very rough, bouncing up and down to pass through each data point. We do not expect a regular process such as growth to, on average, follow a complex zig-zagging path. Thus, it is usual to include a penalty for roughness in choosing the appropriate function. This is accomplished by maximizing the penalized log likelihood:

$$\log(f) = \sum \log(X_i; A_i, f) - n\alpha \mathbf{J}(f)$$

where *n* is the sample size, α is a non-negative constant refered to as the smoothing parameter and J(f) measures the roughness of the function *f* as its summed squared curvature. Therefore, the more complex the function the greater its penalty and the lower its overall likelihood $\lceil \log(f) \rceil$.

If we assume that measurement values are normally distributed at each age and have constant variance, the function that maximizes the penalized log likelihood at any given α value is a cubic spline. A cubic spline is a function incorporating n+1 cubic polynomials spliced seamlessly at each of the n data points. The value of the smoothing parameter α controls the extent of the penalty for roughness and determines the form of the function f. When α is low, the penalty for roughness is low and the function chosen will be complex while when α is high the function approaches a straight line. So we must have some criterion for choosing a suitable level for the smoothing parameter. A common choice for α is to pick one with maximal predictive power for the data at hand using cross-validation. For any specified α and individual i, let f be the function that maximizes the penalized log likelihood for the data excluding individual i. Then the score of the excluded individual i (X_i) is estimated using f. This is done n times, excluding each individual in turn and using the same level of α to obtain the sum of the squared differences between observed and predicted values for the excluded individuals. The whole procedure is repeated with a series of different α values and the α finally chosen is the one which minimizes the squared difference between the predicted and observed values for excluded individuals.

A spline curve is essentially a running average placed through the middle of the bivariate data distribution. The number of points included in this "running average" varies with the local density of the data. The spline provides a local estimate of the regression surface in contrast to parametric models which provide a global fit to the data and can thus be extremely inaccurate in any given local region. Standard parametric growth curves are special cases of cubic splines and will result from the analysis if they are appropriate for the data.

Spline curves represent a non-parametric approach to growth analysis. No specific model (or growth curve equation) is fit to the data. This has several advantages for growth analysis. First, the shape of the growth curve is free to vary as the data vary, instead of being constrained to follow a particular mathematical model. Laird (1967) found it impossible to fit the entire growth period of macaques to a single mathematical function and instead recommended piecing together separate functions for the infant and juvenile growth periods. As noted by Watts & Gavan (1982), choice of any given equation requires prior knowledge of the growth dynamics. Also, growth curve coefficients obtained from fitting particular models are often quite difficult to interpret in terms of growth rate *vs*. maturational dimorphism. The mathematical models used to fit growth curves require a negative correlation between estimates of growth rate and maturation age. Thus, growth curve models do not allow us to separately evaluate the relative importance of growth rate dimorphism and maturational dimorphism to adult sex differences.

A disadvantage of the non-parametric spline curve approach to growth analysis is that there are no growth curve coefficients available to compare across the sexes, making quantitative statements about growth difficult to test statistically. For this reason, we first utilize the spline curves and then perform parametric analyses based on the spline curve results. The method also assumes normally distributed residuals of uniform variance across ages. For the data reported here, these conditions are generally true, although heteroscedasticity (increasing variance of residuals with increasing age) is evident for some traits (such as weight). In these cases, the low variance ages should have been weighted more strongly than the high variance ages in constructing the spline, although the overall curve is not likely to be severely affected.

The first step in the analysis is the inspection of the spline curves themselves. This inspection suggests growth dynamics for each of the traits. A judgement was made concerning critical ages at which growth rates appeared to change using both the numerical and graphical results of the spline curve analysis. Both the original spline curves (measurement plotted against age) and pseudo velocity curves derived from the splines (change in measurement divided by change in age plotted against age; Coelho, 1985) were generated and subjectively assessed. The form of the spline curves of the raw data can be used to suggest specific hypotheses about growth rates and maturation age which can be tested with standard statistical models. Spline curves, as with any running average technique, are least reliable at the edges of the bivariate distribution and are also less reliable in regions with relatively little data. Peculiarities of growth curves should not be overinterpreted, especially in regions of sparse data and at the earliest and latest ages at the beginning and end of the curve.

In order to roughly measure the contribution of rate differences and bimaturism to adult sexual dimorphism, the expected measurement difference between the sexes based on the spline curves was recorded for males and females at the age at which female growth was judged to be complete (typically at $5 \cdot 5$ or 8 years, depending on the measurement) and at the age at which male growth was judged to be complete (typically at 7.5 or 12 years, depending on the measurement). The difference in trait values at the female maturation age was then expressed as a percentage of the difference at the male maturation age. This proportional difference is the proportion of adult sexual dimorphism due to dimorphism in growth rates. One minus this percentage was considered as the proportion of adult sexual dimorphism due to continued subadult male growth beyond the age of female maturation, or adult sexual dimorphism due to bimaturism. Determination of a precise age at which growth ceases is somewhat subjective and can be subject to error. Error may be due to age clumping and the cross-sectional nature of the data. Age clumping limits resolution while cross-sectional data tends to smooth over sharp distinctions seen in longitudinal data. Furthermore, growth may slow over several years before finally ceasing, making it difficult to judge a precise age for growth cessation. In these circumstances we tended to choose an age for growth cessation after which growth did not occur, erring on the side of later ages of maturation. Thus, the ages given are likely to be upper bounds for individual growth.

Parametric analyses

Specific hypotheses about the sexual dimorphism of growth were tested using linear regression and analysis of covariance (Sokal & Rohlf, 1981), with the following analysis of covariance model:

$$y_{ijk} = a + sex_i + age_j + (sex \times age)_{ij} + e_{ijk}$$

where y is the trait value, a is a constant, sex represents the effect of male vs. female, age is the linear effect of age in months, $(sex \times age)$ is the effect of the interaction between sex and age on trait values and e is the residual. A significant interaction effect indicates that the growth rate is significantly different between the sexes over the age interval considered. This is the particular significance test of interest for our hypotheses. A significant effect of age indicates that growth takes place during the interval while a significant effect of sex indicates that the sexes are significantly different over the interval considered. The significance tests for sex differences and age (growth) should only be considered when the interaction effect is not significant. The significance tests for growth, irrespective of sex, are not presented because of the predicted heterogeneity of growth across the sexes. Instead, the sex-specific slopes can be tested for statistical significance using their associated standard errors.

Inspection of the spline curves suggests that formal tests of sex differences in growth rates be obtained for four different age periods. First, linear regressions are calculated separately by sex for the infant and early juvenile period, from birth to $2\cdot 5$ years. This is the age by which the first growth period is complete, although it is likely to be a maximum age of completion for individual animals due to the cross-sectional nature of the data. While growth rates may decrease somewhat over this interval, our current data do not allow resolution of the detailed dynamics. A second regression is calculated for the later juvenile period from $2\cdot 5$ years to the age of growth cessation in females (typically $5\cdot 5$ or 8 years, depending on the trait). The third regression covers the subadult period for males and young adult period for females, after female growth has ceased (typically $5\cdot 5$ to $7\cdot 5$ years or 8 to 12 years, depending on the trait). Finally, a regression was fit to the adult data (typically after $5\cdot 5$ or 8 years in females and $7\cdot 5$ or 12 years in males, depending on the trait). Thus, for females, animals included in the third regression are a subset of those used for the regression against adult age. Analyses of covariance were performed for these four age intervals to test for significant sex differences in growth rates.

Results

Age and sex-specific means and standard deviations for the 28 traits are presented in Appendix 2. After 7 years of age, 2-year age intervals were used because of the small samples available for single years. All measurements are significantly different between the sexes in adults as determined by *t*-tests using animals 13 years and older (see Appendix 2). Females have completed growth for all traits by 8 years, while males continue growing to 12 years.

Spline curves

Representative spline curves for both sexes are presented in Figures 1–10. In general, for each trait and both sexes, there is an early period of fast growth (infant and early juvenile period) followed by an extended period of slower growth which continues until growth ceases (late juvenile period in females and late juvenile plus subadult period in males), and finally, a period during which growth has stopped (adult period). The infant and early juvenile growth period extends from birth to about $2\cdot0-2\cdot5$ years. The age of final cessation of growth varied both by sex and measurement.

The postcranial traits fall into two basic categories with regard to the timing of their growth periods as judged from the splines. Linear measurements of the extremities (including arm, forearm, hand, thigh, leg, foot and tail length and foot and hand width) and ventral



Figure 1. Growth curves for body weights in (a) males and (b) females. A spline curve is fit separately for each sex. Growth is complete at 8 years in females and 12 years in males.

trunk length cease growing at about 5.5 years in females and 7.5 years in males. Weight, most measurements of the trunk (including crown-rump length, occipital to tail base, abdominal and thoracic circumferences, and shoulder and hip widths) and circumferences of the extremities (including arm, thigh, and calf circumference) cease growing at about 8 years in females and 12 years in males. Aged animals (20–25 years) tended to have smaller limb circumferences and weights than younger adults, perhaps indicating a loss of muscle tissue at advanced ages. Examples of these growth patterns are shown in Figures 1–6.

Growth in head measurements typically does not follow the patterns observed for the postcranium. Instead, several of the measurements showed unique growth patterns. These traits showed relatively large variability around the spline curves because of the relatively small amount of absolute growth experienced postnatally. Variability around the spline curves hinders interpretation and leads to a general lack of statistical significance in analyses of covariance. Head length and breadth and biorbital and bizygomatic widths follow a growth pattern similar to that found for weight, trunk and limb circumferences, although male growth seems to continue to nearly 15 years of age for head length (see Figure 7) and breadth. Jaw width and upper facial height cease to grow in females at 5 and 7.5 years, respectively, with male growth ceasing at about 10 years (see Figure 8). Lower facial height and nasal width did not show obvious dimorphism in age at maturity in the spline curves, growth slowed in both sexes by 10 and 15 years of age, respectively, in these traits (see Figures 9 and 10). Even so, significant growth in male lower facial height continues throughout adulthood.

Inspection of the pseudo-velocity curves indicated evidence for an adolescent growth spurt in male body weights (see Figure 11). In males, growth rate for weight starts accelerating at about 5 years, peaks at about 6 years, and then decelerates until growth is complete at 12



Figure 2. Growth curves for crown–rump length in (a) males and (b) females. Growth is complete at 8 years in females and 12 years in males.



Figure 3. Growth curves for arm circumference in (a) males and (b) females. Growth is complete at 8 years in females and 12 years in males.



Figure 4. Growth curves for arm length in (a) males and (b) females. Growth is complete at 5.5 years in females and 7.5 years in males.



Figure 5. Growth curves for thigh length in (a) males and (b) females. Growth is complete at 5.5 years in females and 7.5 years in males.



Figure 6. Growth curves for tail length in (a) males and (b) females. Growth is complete at 5.5 years in females and 7.5 years in males.



Figure 7. Growth curves for head length in (a) males and (b) females. Growth is complete at 8 years in females and 15 years in males.



Figure 8. Growth curves for upper facial height in (a) males and (b) females. Growth is complete at 7.5 years in females and 10 years in males.



Figure 9. Growth curves for lower facial height in (a) males and (b) females. Growth is complete at 10 years in females and in males.



Figure 10. Growth curves for nasal width in (a) males and (b) females. Growth is complete at 15 years in females and in males.



Figure 11. Pseudo-velocity curves for weight in (a) males and (b) females. Male curve displays an adolescent growth spurt. While the female curve shows a slight increase in velocity over a restricted age range starting at an age of 4, the increase in velocity is too small and the length of the increased growth period too short for this to be taken as a strong indication of a growth spurt.

Trait	Female age at maturity (year)	Male age at maturity (year)	Growth rate (%)	Age at maturity (%)
Weight	8	12	49	51
Crown-rump length	8	12	50	50
Occipital to tail base	8	12	38	62
Abdominal circumference	8	12	49	51
Thoracic circumference	8	12	55	45
Arm circumference	8	12	51	49
Calf circumference	8	12	34	66
Thigh circumference	8	12	39	61
Trunk length (ventral)	5.5	7.5	12	88
Shoulder width	8	12	30	70
Arm length	5.5	7.5	36	64
Forearm length	5.5	7.5	18	82
Hand length	5.5	7.5	61	39
Hand width	5.5	7.5	32	68
Hip width	8	12	58	42
Thigh length	5.5	7.5	30	70
Leglength	5.5	7.5	25	75
Foot length	5.5	7.5	47	53
Foot width	5.5	7.5	61	39
Tail length	5.5	7.5	32	68
Head length	8	15	45	55
Head breadth	8	15	62	38
Biorbital width	8	12	56	44
Bizygomatic width	8	12	49	51
Jaw width	5	10	4	96
Upper facial height	7.5	10	46	54
Lower facial height	10	10	100	0
Nasal width	15	15	100	0

 Table 1
 Percent of adult dimorphism due to differences in growth rates and age at maturity

years. While there is a slight increase in velocity at 4 years of age in females, this increase is not large or persistent enough to warrant positive identification as a growth spurt. Pseudovelocity curves for the other traits did not provide solid evidence for a growth spurt, although the presence of a spurt cannot be ruled out on the basis of the present cross-sectional data.

Bimaturism vs. growth rate dimorphism

The proportion of adult sexual dimorphism due to growth rate dimorphism (during the infant and juvenile phase) and bimaturism (continued growth of subadult males) as judged from the spline curves is presented in Table 1. For example, the weight predicted from the spline curve at 8 years of age (when female growth ceases) is 3.12 kg in females and 4.40 kg in males, a difference of 1.28 kg. At 12 years (when male growth ceases), the predicted values are 3.07 and 5.69 kg for females and males, respectively, or a difference of 2.62 kg. The ratio of the difference at 8 years to the difference at 12 years measures the proportion of difference due to dimorphism in juvenile growth rates, 49% in this case. Overall, about 40% of adult dimorphism is due to differences in growth rates and 60% is due to differences in maturational age. Bimaturism is particularly important for postcranial body lengths (70% of

Trait	Age ¹	Sex	n	Intercept (S.E.)	Growth rate (S.E.)	Probability of growth rate dimorphism ²
Weight	< 2.5	М	28	0.340 (0.050)	0.760 (0.059)	
	-	F	39	0.326 (0.044)	$0.649\ (0.043)$	0.021
	<8	M	54	0.630 (0.124)	0.450(0.124)	0.000
	< 10	F	4/	0.992 (0.124)	0.291(0.026)	0.000
	<12	M F	14	1.581 (0.579)	0.369 (0.140)	0.009
	> 19	r M	22	5.035 (0·371) 5.025 (0.600)	-0.049(0.038)	0.005
	>12	F	20 58	3.066 (0.110)	0.022 (0.035)	0.664
Crown-rumn	~ 0 ~ 9.5	M	36	20.367 (0.465)	5.740 (0.354)	0.004
length	~2.5	F	49	20.629 (0.450)	4.789 (0.316)	0.025
icingtii	< 8	Ň	51	26.860 (0.155)	1.958 (0.155)	0.025
		F	41	28.537 (0.827)	1.470(0.164)	0.024
	<12	M	14	37.468 (3.392)	0.536(0.346)	
		F	22	40.918 (3.297)	-0.254(0.335)	0.060
	>12	М	17	44·793 (2·862)	-0.001 (0.168)	
	>8	F	55	37.335 (0.548)	0.095 (0.030)	0.315
Occipital to	< 2.5	Μ	36	15.940 (0.568)	5.303 (0.433)	
tail base		F	49	16.264 (0.486)	4.606 (0.341)	0.102
	<8	М	50	20.387 (0.895)	1.953 (0.168)	
		F	41	22.634 (1.413)	1.490 (0.280)	0.073
	<12	M	14	26.777 (4.784)	0.939(0.487)	
		F	21	34.465 (4.829)	-0.185(0.489)	0.063
	>12	м	16	41.979 (4.425)	-0.279(0.260)	
	>8	F M	54	31.612 (0.730)	0.079 (0.040)	0.106
Abdominal	<2.5	M	36	12.122 (0.440)	4.428 (0.336)	0.000
circumerence	- 8	г М	49	11.708 (0.430)	4.387 (0.320)	0.308
	<0	F	52 A1	19.944 (1.030)	1.127 (0.141)	0.252
	< 19	M	14	16.492 (6.089)	1.452 (0.620)	0.333
	<1 <u>2</u>	F	22	22.807 (5.117)	0.387 (0.519)	0.099
	>12	M	18	32.428 (2.642)	-0.065(0.156)	0 000
	>8	F	55	25.439 (0.867)	0.000(0.100) 0.151(0.047)	0.077
Thoracic	<2.5	М	36	15.252 (0.342)	3.676 (0.260)	
circumference		F	49	14.815 (0.308)	3.323 (0.216)	0.148
	< 8	М	51	18.509 (0.669)	1.593 (0.126)	
		F	41	19.201 (0.722)	1.236 (0.143)	0.040
	<12	М	14	24.606 (3.216)	0.908 (0.328)	
		F	22	30.734 (2.021)	-0.219(0.205)	0.002
	>12	М	18	34·717 (2·358)	-0.036 (0.140)	
	>8	F	54	27.941 (0.475)	$0.052 \ (0.026)$	0.936
Arm	<2.5	M	36	5.777 (0.213)	1.474(0.162)	
circumterence	- 0	F	49	5.612 (0.160)	1.274 (0.112)	0.150
	<8	M	32	6.746 (0.462)	0.751 (0.087)	0.011
	<i></i> 19	Г	41 14	7.307 (0.442)	0.438 (0.087)	0.011
	N 12	F	14 99	11.082 (1.518)	-0.128(0.154)	0.007
	>12	M	18	14.097 (1.949)	-0.120(0.134) 0.035(0.115)	0.001
	>8	F	55	10.999 (0.330)		0.542
Calf	< 2.5	M	36	5.924 (0.201)	1.432 (0.153)	0 514
circumference	~~ 0	F	49	5.541 (0.168)	1.303 (0.118)	0.071
	<8	Ň	52	6.949 (0.442)	0.616 (0.084)	
		F	41	7.513 (0.478)	0.381 (0.095)	0.041
	<12	М	14	5-265 (1-868)	0.677 (0.190)	
		r	99	19 195 (0.009)	0.991 /0.101	0.001

Table 2 Linear regressions in male and female toque macaques over limited age ranges representing the infant and early juvenile, later juvenile, subadult male and adult growth periods

Trait	Age	Sex	n	Inter (S.I	cept E.)	Growth rate (S.E.)	Probability of growth rate dimorphism ²
	>12	M	17	13.007	(1.093)	-0.026 (0.064)	
(F))	>8	F	54	10.470	(0·256)	-0.025 (0.014)	0.767
Thigh	< 2.5	M	28	7.456	(0.495)	2.957 (0.360)	
circumference	0	F	27	7.291	(0.510)	2.798 (0.355)	0.377
	<8	M	40	10.457	(0.842)	1.100 (0.151)	0.002
	- 10	r	31	11.590	(0·842)	0.640 (0.170)	0.033
	<12	м	13	10.797	(3.755)	0.951 (0.384)	0.007
	. 10	r M	13	21.189	(3·724)	-0.503(0.387)	0.007
	>12	M	12	23.116	(3.733)	-0.184(0.217)	0.450
712 K. L L	>8	r	30	10.201	(0.793)	-0.042(0.042)	0.459
I runk length	<2.5	M	30	12.001	(0·410) (0.207)	4.778 (0.313)	0.007
(ventral)		r	49	13.346	(0·397) (1.786)	3.955 (0.279)	0.027
	< 5.5	M	32	17.038	(1.730)	1.944 (0.437)	0 192
	-75	r M	28	10.304	(1.343)	2.048 (0.321)	0.433
	< /.5	м	10	18.229	(4·380) (5.492)	1.603 (0.633)	0.104
		r	13	23.330	(3.483)	0.041 (0.837)	0.184
	> / 5	м	35	31.442	(0.752)	0.048 (0.049)	0.191
a 11	> 5.5	F 14	/3	27.495	(0.359)	0.062 (0.022)	0.431
Shoulder	< 2.5	M	30	4.789	(0.198)	1.297 (0.151)	0.000
width		r	49	5.089	(0.177)	0.822 (0.124)	0.008
	<8	M	52	5.778	(0.343)	0.483 (0.065)	0.050
	10	r	41	6.308	(0.00)	0.279(0.111)	0.020
	<12	M	15	2.651	(1.309)	0.802(0.134)	0.001
	10	F	22	8.130	(1.372)	0.147 (0.006)	0.001
	> 12	M	18	13.552	(1.624)	-0.147(0.096)	0.100
A 1 .7	>8	r	22	8.411	(0.204)	0.010 (0.014)	0.129
Arm length	< 2.5	м	30	6.102	(0.109)	1.734 (0.129)	0.007
	- 5 5	r M	49	0.247	(0.201)	0.701 (0.114)	0.091
	< 2.2	M E	31 00	7.731	(0.433)	0.791(0.114) 0.647(0.127)	0.910
	-75	r	28	8.194	(0.574)	0.047 (0.137)	0.218
	< /.2	M	18	10.084	(1.399)	0.418(0.200)	0.940
	. 7 5	r	15	10.788	(1.478)	0.180(0.226)	0.240
	> 7.5	M E	30	13.042	(0.430)	(0.029 (0.033))	0.070
r. 1 .1	> 5.5	r	/3	11.822	(0.143)	0.018 (0.009)	0.879
Forearm length	< 2.5	M	30	6.337	(0.172)	1.504 (0.129)	0.190
	- E E	Г	49	7 200	(0.173)	0.027 (0.114)	0.129
	< 3.2	M	31	7.322	(0.433)	0.937(0.114) 0.720(0.144)	0.140
	-75	r M	28	8.148	(0.002)	0.732(0.144) 0.488(0.202)	0.140
	< 7.5	IVI F	10	9.937	(2.031)	0.200 (0.302)	0.029
	~ 7 5	Г	15	14.025	(1.240) (0.525)	-0.322 (0.109)	0.030
	> 7.5	IVI E	30 72	14.047	(0.333)	-0.011(0.009)	0.750
Hundlength	ر.ر د 9.5	r M	26	5.165	(0.131)	0.016 (0.100)	0.730
riand length	< 2.5	E NI	40	5.073	(0.131)	0.000 (0.004)	0.454
	- 5.5	r M	49	5.407	(0.134) (0.965)	0.591 (0.067)	0.434
	< 5.5	F	- J4 - 98	5.536	(0.203)	0.031 (0.007)	0.009
	- 7.5	r M	20	7.942	(0.397) (1.956)	0.231(0.093) 0.217(0.195)	0.002
	< 7.5	E	10	7.243	(1.200)	0.217 (0.103)	0.996
	7.5	г	15 95	/ 301 0.621	(1.326)	0.094 (0.200)	0.200
	> 7.5	E 141	30 72	7.505	(0.110)	0.024 (0.024)	0.309
Hand width	ن•ن مر 2.5 س	r M	70 36	1.666	(0.038)	0.009 (0.007)	0.002
riana width	< 2.3	IVI E	30 70	1.550	(0.030)	0.239 (0.029)	0.945
	- 5.5	Г	40	1.009	(0.044)	0.200 (0.031)	0.740
	< 5.5	E IVI	97 97	1.005	(0.120)	0.046 (0.041)	0.980
		T.	21	1.203	(0.171)	0.010 (0.011)	0 403

Table 2	Continued.
I apie z	Continuea.

Trait	Age ¹	Sex	n	Intercept (S.E.)	Growth rate (S.E.)	Probability of growth rate dimorphism ²
	<7.5	М	18	1.656 (0.394)	0.138 (0.058)	
		F	13	1·635 (0·833)	0.097 (0.127)	0.375
	> 7.5	М	35	2.583 (0.108)	0.006 (0.008)	
	> 5.5	F	71	2.252 (0.049)	0.005 (0.003)	0.144
Hip width	< 2.5	М	35	4·318 (0·130)	1.173(0.102)	
		F	49	4.294 (0.113)	1.009 (0.079)	0.102
	<8	M	52	5.112 (0.322)	0.562 (0.036)	
	10	F	40	5-737 (0-288)	0.421 (0.057)	0.066
	<12	M	15	8.468 (1.356)	0.164(0.139)	
	10	F	22	9.629 (0.606)	-0.099(0.062)	0.030
	> 12	M	18	10.860 (0.634)	-0.022(0.038)	
	>8	F	53	8.346 (0.119)	0.028(0.007)	0.671
I high length	<2.5	M	36	6·200 (0·193)	2.237(0.147)	
		F	49	6·460 (0·189)	1.818 (0.133)	0.020
	< 5.2	M	32	8·247 (0·658)	0.973 (0.058)	
		F	27	8.969 (0.524)	0.743 (0.125)	0.164
	< 7.5	M	18	10.127 (1.765)	0.657 (0.260)	
		F	13	15.256 (1.860)	-0.314(0.284)	0.014
	> 7.5	M	35	14.997 (0.539)	0.031 (0.039)	
	> 5.5	F	73	12.895 (0.175)	0.011 (0.011)	0.912
Leg length	<2.5	M	36	6.831 (0.212)	1.870 (0.161)	
		F	49	6·814 (0·246)	1.772(0.173)	0.345
	< 5.5	М	32	8·549 (0·504)	0.881 (0.127)	
		F	28	9.758 (0.884)	0.597 (0.211)	0.129
	< 7.5	M	18	10.560 (2.473)	0.612 (0.365)	
	~ ~	F	13	12.568 (3.097)	0.126(0.473)	0.220
	> 7.5	M	35	15·341 (0·539)	-0.027(0.039)	
	> 5.5	ľ	/3	12.829 (0.187)	0.018(0.011)	0.198
Foot length	<2.5	M	35	7.341 (0.147)	1.422 (0.112)	
		r	49	7.276 (0.131)	1.252 (0.092)	0.121
	< 5.5	M	32	8.543 (0.355)	0.647 (0.089)	
		F	28	8·467 (0·583)	0.538 (0.139)	0.252
	< /.5	M	18	8.768 (1.206)	0.553 (0.178)	
		r	13	10.667 (1.709)	0.055 (0.261)	0.063
	> 7.5	м	35	12.283 (0.266)	0.031(0.019)	0.100
P . 114	> 5.3	r	/3	$11 \cdot 105 (0 \cdot 127)$	-0.003 (0.008)	0.122
root width	< 2.3	M	33	1.556 (0.044)	0.288 (0.033)	0.040
		r	48	1.610 (0.049)	0.202(0.034)	0.040
	< 3.2	M	32	1.723 (0.106)	0.134(0.027)	0.011
	-75	г	20	2.114 (0.190)	0.034(0.043) 0.127(0.054)	0.011
	< 7.5	E	10	1.049 (0.303)	0.137(0.034)	0.000
	> 7.5	Г	13	2.000 (0.039)	-0.003(0.097)	0.022
	> 7.5	E IVI	3 1 79	2.390 (0.103) 9.974 (0.041)	0.007 (0.007)	0.052
Taillonath	× 3· 3	r M	26	2.274 (0.041)	0.007 (0.005)	0.955
i all length	< 2.5	F	30 47	20.033 (1.110)	0.313 (0.700) 7.255 (0.707)	0.176
	~ 5.5	M	20	23.333 (1.110)	1.090 (0.550)	0.170
	< 5.5	E	32 97	33.220 (2.100)	4.009 (0.000)	0.900
	-7.5	r M	4/	37.000 (3.931)	3.100 (U'937) 3.759 (1.474)	0.200
	< / 3	F	10	52.475 (10.00)	51752 (11474) 0.050 (9.120)	0.092
	~ 7.5	r M	13	58,557 (1.000)	0.074 (0.127)	0.000
	> /·J \ 5.5	F	35 71	59,544 (0.077)	0.074 (0.137)	0.960
Head length	∼ J•J ~ 9.5	r M	71 35	52.377 (0.977) 6.160 (0.094)	0.074 (0.001)	0.209
	~ 4 0	741		0 100 10 031	0 301 (0.014)	

Table 2 Continued.

$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	Trait	Age	Sex	n	Intercept (S.E.)	Growth rate (S.E.)	Probability of growth rate dimorphism ²
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		<8	М	52	6.621 (0.126)	0.176 (0.024)	
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $			F	41	6.591 (0.168)	0.124 (0.033)	0.104
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		<15	M	21	7.342 (0.438)	0.083 (0.039)	0.004
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $			F	34	7.830 (0.227)	-0.026(0.020)	0.004
		>15	м	14	8.492 (0.474)	-0.004 (0.023)	0.277
	71 J D J.J	>8	r M	60	7.521 (0.096)	0.002 (0.005)	0.377
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	Head Breadth	< 2.3	M	30 40	5.120 (0.003) 4.889 (0.072)	$0.323 (0.049) \\ 0.329 (0.051)$	0.474
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		<i>~</i> 9	r M	49 50	5.957 (0.191)	0.108 (0.023)	0.111
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		<0	L.	41	5.397 (0.121)	0.107 (0.036)	0.016
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		~ 15	M	21	6.378 (0.333)	0.080 (0.030)	0.010
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		< 15	F	33	6·037 (0·198)	0.005 (0.018)	0.013
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		>15	M	14	7.552 (0.509)	-0.014(0.024)	
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		>8	F	58	6·283 (0·097)	-0.016(0.005)	0.350
	Biorbital	<2.5	M	36	3.714 (0.055)	0.452 (0.042)	
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	width		F	48	3.632 (0.054)	0.429 (0.037)	0.341
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		< 8	М	52	4.002 (0.111)	0.235 (0.021)	
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			F	41	4.341 (0.130)	0.131 (0.026)	0.001
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		<12	М	15	4·548 (0·528)	0.182(0.054)	
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $			F	22	5.482 (0.409)	-0.014(0.042)	0.003
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		>12	М	18	6·514 (0·457)	-0.002(0.027)	0.450
$\begin{array}{c c c c c c c c c c c c c c c c c c c $		>8	F	55	5.227 (0.074)	0.013 (0.004)	0.652
width F 49 3.723 (0.125) 0.666 (0.088) 0.192 < 8 M 52 4.520 (0.211) 0.275 (0.040) F 41 4.564 (0.248) 0.224 (0.049) 0.222 < 12 M 15 2.941 (1.038) 0.448 (0.106) F 22 5.139 (0.692) 0.105 (0.070) 0.004 > 12 M 18 7.481 (0.519) 0.023 (0.031) > 8 F 55 6.117 (0.126) 0.013 (0.007) 0.953 > 8 F 49 2.229 (0.151) 0.337 (0.115; F 49 2.229 (0.151) 0.337 (0.115; F 49 2.229 (0.122) 0.405 (0.078) 0.308 < 5 M 20 2.269 (0.629) 0.309 (0.197) = F 28 2.701 (0.590) 0.145 (0.141) 0.357 < 10 M 34 2.746 (0.595) 0.144 (0.082) = F 31 3.228 (0.493) 0.030 (0.065) 0.140 > 10 M 25 4.225 (0.290) 0.004 (0.016) > 5 F 58 3.367 (0.138) 0.007 (0.009) 0.4496 Upper facial < 2.5 M 36 1.905 (0.050) 0.375 (0.038) height F 49 1.691 (0.042) 0.472 (0.030) 0.0466 < 7.5 M 48 1.866 (0.17) 0.314 (0.023) = F 41 2.039 (0.099) 0.237 (0.020) 0.011 < 10 M 11 2.767 (1.351) 0.314 (0.023) = F 13 4.106 (1.015) -0.046 (0.112) 0.095 > 10 M 11 2.767 (1.351) 0.314 (0.023) = F 13 4.106 (0.189) 0.028 (0.011) < 7.5 F 60 3.512 (0.080) 0.015 (0.005) 0.182 Lower facial < 2.5 M 36 1.366 (0.071) 0.227 (0.043) 0.198 = 10 M 12 2.425 (0.260) 0.001 0.227 (0.043) 0.196 = 10 M 18 2.476 (0.189) 0.028 (0.011) > 10 M 18 2.476 (0.055) 0.148 (0.018) = 10 M 18 2.476 (0.050) 0.188 (0.018) = 10 M 18 2.476 (0.026) 0.011 > 10 M 18 2.476 (0.026) 0.011 > 10 M 18 2.476 (0.026) 0.018 (0.015) > 10 M 18 2.476 (0.026) 0.018 (0.015) > 10 M 18 2.476 (0.266) 0.056 (0.018) = 10 M 18 2.476 (0.266) 0.056 (0.018) = 10 M 18 2.476 (0.266) 0.056 (0.018) > 10 M 18 2.476 (0.266) 0.056 (0.018) > 10 M 18 2.476 (0.266) 0.056 (0.018) > 10 M 18 2.476 (0.266) 0.056 (0.018) = 10 M 60 1.488 (0.013) 0.138 (0.027) > 10 M 18 2.476 (0.266) 0.056 (0.018) = 10 M 18 2.476 (0.266) 0.056 (0.018) = 10 M 18 2.476 (0.266) 0.056 (0.018) = 10 F 43 0.489 (0.035) 0.138 (0.027) > 10 F 43 0.489 (0.035) 0.138 (0.027) > 10 F 43 0.489 (0.035) 0.138 (0.027) > 10 F 438 0.0484 (0.035) 0.138 (0.027) > 10	Bizygomatic	< 2.5	M	36	3.709 (0.136)	0.780 (0.104)	0.100
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	width	0	F	49	3.723 (0.125)	0.001 (0.088)	0.192
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		<8	M	52	4.520 (0.211)	0.275 (0.040)	0.999
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		< 19	r M	41	9.041 (1.029)	0.224 (0.049) 0.448 (0.106)	0.277
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		<12	E IVI	1J 99	5.139 (0.692)	0.105(0.100)	0.004
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		>12	M	18	7·481 (0·519)	0.023(0.031)	0 001
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		>8	F	55	6.117 (0.126)	0.013(0.007)	0.953
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	law width	< 2.5	Ń	36	2.290 (0.151)	0.337 (0.115)	
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Jan main	~~~	F	49	2.229 (0.112)	0.405 (0.078)	0.308
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		<5	М	20	2.269 (0.629)	0.309 (0.197)	
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			F	28	2.701 (0.590)	0.145 (0.141)	0.357
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		<10	М	34	2·746 (0·595)	0.144(0.082)	
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $			F	31	3.228 (0.493)	0.030(0.065)	0.140
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		>10	М	25	4.225 (0.290)	0.004 (0.016)	
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		>5	F	58	3-367 (0-138)	0.007 (0.009)	0.496
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	Upper facial	< 2.5	М	36	1.905 (0.050)	0.375 (0.038)	5 . .
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	height		F	49	1.691 (0.042)	0.472(0.030)	0.046
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		< 7.5	M	48	1.866 (0.117)	0.314(0.023)	0.011
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		- 10	F	41	2·039 (0·099)	0.237 (0.020)	0.011
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		<10	M	11	2.707 (1.331)	0.014 (0.020)	0.005
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		> 10	г	15	4.442 (1.013)	-0.040(0.112) 0.028(0.011)	0.035
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		>10	F	20 60	3.512 (0.080)	0.028 (0.011)	0.182
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Lower facial	- 7.5 - 2.5	M	36	1.366 (0.071)	0.286 (0.054)	0.102
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	height	~2 0	F	49	1.332 (0.061)	0.227 (0.043)	0.196
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		<10	Ň	60	1.468 (0.105)	0.188(0.018)	
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			F	54	1.675 (0.094)	0.080 (0.015)	0.001
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		>10	М	18	2.476 (0.266)	0.056 (0.018)	
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$			F	43	2.439 (0.114)	0.006 (0.006)	0.012
F 48 0.894 (0.032) 0.105 (0.022) 0.176	Nasal width	<2.5	М	36	0.881 (0.035)	0.138 (0.027)	
			F	48	0.894(0.032)	$0.105\ (0.022)$	0.176

Trait	Age ¹	Sex	n	Intercept (S.E.)	Growth rate (S.E.)	Probability of growth rate dimorphism ²
	<15	М	72	1.072 (0.050)	0.060 (0.007)	
		F	75	1.132 (0.039)	0.031 (0.005)	0.001
	>15	М	14	1.608 (0.234)	0.015 (0.011)	
		F	26	1.414 (1.107)	0.005 (0.005)	0.190

Table 2 Continued.

'The maximum age in the regression, the minimum age being the maximum for the previous regression model. The last of the regressions are for adults and include all animals above the specified age. Age in years.

²Probabilities are for growth rate differences during the specified age interval (growth rate dimorphism).

adult dimorphism due to bimaturism, not including hands and feet) while it is less important for weight and postcranial circumferences and widths (54% of adult dimorphism due to bimaturism). Growth of the head displayed a variety of results from no bimaturism (lower facial height and nasal width) to nearly complete bimaturism (jaw width).

Parametric analyses

The regression equations, appropriate standard errors and probabilities of growth rate differences by sex are presented for each trait in Table 2 for separate regressions during the infant and early juvenile, late juvenile, subadult male or young adult female and adult periods.

Comparing growth rates among the ages. In general, growth rates declined with age, being highest during the infant and early juvenile period. Growth during the late juvenile period was usually about half the rate observed during the earlier period for males and about one-third the rate observed during the earlier period for females. Males grew less rapidly during the subadult than during the late juvenile period. In keeping with our selection of age categories based on the splines, female age-mates to subadult males (young adult females) had stopped growing altogether. Males showed several exceptions to the trend for lower growth rates with increasing age. Abdominal, arm and calf circumferences, shoulder width, hand width and bizygomatic width had slightly higher growth rates in the subadult phase than in the preceding late juvenile growth period.

Comparing growth rates across the sexes. Growth rates during the infant-early juvenile period were only rarely significantly different between the sexes (7 of 28 traits). Even so, all of the 20 postcranial measurements bar one (abdominal circumference) grew faster in males than in females, and six of these were statistically significant. One-half of the eight cranial measurements indicated faster growth in males, the other half in females, but only upper facial height grew significantly faster in females. These results indicate that growth rate differences by sex may develop early in life, especially for postcranial traits, but that these early rate differences are relatively small and contribute only a small proportion to adult dimorphism.

During the late juvenile period males nearly always grew at a faster rate than females (only ventral trunk length grew slightly faster in females than in males) and this was statistically significant for 13 of 28 measurements at the 5% level. The differences in growth rate also

tended to be larger than in the earlier period. These results indicate significant sex differences in growth rate during the juvenile period for many measurements.

As expected given our delineation of age groups based on inspection of the splines, the largest differences in growth rates occurred in the subadult male and early adult female period, when female growth had stopped and male growth continued. During the young adult period, females did not grow for any measurement. For measurements with positive (but not statistically significant) female growth rates, males grew more than twice as fast as females (hand width is the only exception to this trend). Fourteen of 28 measurements showed significant sex differences in growth rates at the 5% level and 20 were significant at the 10% level, even though this growth rate comparison had the smallest sample sizes of the four tested. The measurements not showing a significant difference at the 10% level displayed significant male growth but not significant female growth (except for hand length, in which neither sex showed significant growth). Differences in growth rate during the subadult male—young adult female period are due to differences in the age of physical maturation in males and females. Adult sexual dimorphism arises, in part, from these differences in maturational age.

Discussion

Growth patterns and timing

Not surprisingly, we found distinct infant and juvenile growth periods for wild toque macaques. This corresponds to earlier results for rhesus macaques from Laird (1967) and Watts & Gavan (1982), for baboons (Glassman *et al.*, 1984; Coelho, 1985), chimpanzees (Laird, 1967; Watts & Gavan, 1982) and humans (Tanner, 1962; Bogin, 1988). The first period lasted from birth to, at most, 2.5 years. This is similar to the age of 23 months given by Laird (1967) for the end of early growth patterns in rhesus macaques using longitudinal data. The early period did not appear to differ in length among the various measurements studied. There is some potential for heterogeneity in growth rates within this age range which cannot be adequately resolved with this data, but this awaits further study.

The period of later juvenile growth differed among the measurements, with measures related to muscle mass (weight, dorsal trunk lengths, trunk breadths, extremity circumferences) growing several years longer than linear skeletal measures of limb size. Skeletal measurements complete growth by about 5.5 years in females and 7.5 years in males, while muscle mass measures continue growing to about 8 years in females and 12 years in males. The age of growth cessation found here for skeletal measures agrees reasonably well with the ages of epiphyseal fusion reported for the rhesus macaques from Cayo Santiago (Cheverud, 1981).

Somatometric measurements of the Cayo Santiago rhesus macaques (Turnquist & Kessler, 1989) provide very similar results to those found here for toque macaques. While not a laboratory colony, the rhesus macaques of Cayo Santiago are liberally provisioned and thus cannot be considered as a feral population in terms of somatic growth. The animals in this population are likely to be larger than animals from a feral population of rhesus macaques. Even so, Turnquist & Kessler (1989) found the same pattern of growth difference between skeletal and muscle mass traits, skeletal traits (arm, forearm, hand, thigh, leg and foot lengths) ceasing growth between 4–6 years in females and 6–10 years in males, while traits reflecting muscle mass (weight, crown-rump length, arm and thigh circumference) appear to

continue to grow until 10–14 years in both sexes. While the timing of growth is similar in the Cayo rhesus macaques and the Sri Lankan toque macaques, the Cayo rhesus macaques grow to about twice the body weight in the same period of time. The size differences between members of these two populations are largely due to differences in growth rates, not to ages of maturation or size at birth. Whether the same results would be obtained for a comparison of feral rhesus and toque macaques depends on whether the free-ranging but provisioned macaques on Cayo Santiago mature at the same age as a feral rhesus macaque population.

Baboons also seem to grow on a schedule similar to that found for macaques (Sigg *et al.*, 1982), suggesting that much of the size variation among papionins may be due to differences in growth rates. These interspecific comparisons are in contrast to comparisons between sexes within species where bimaturism is the most important cause of size differences.

The results of growth studies for laboratory populations of non-human primates differ importantly from those reported here. Growth is greatly accelerated in laboratory populations. Data from laboratory-reared rhesus macaques suggest that growth in weight is complete by about 6 years in females and 8 years in males (Kirk, 1972). This is 2–4 years earlier than in the provisioned free-ranging rhesus macaques of Cayo Santiago or the feral toque macaques of Polonnaruwa. Laboratory-reared baboons complete growth of weight and crown-rump length by about 6–7 years (Coelho, 1985). Again, this is much earlier than reported for feral baboons, in which females complete weight growth at about 6–7 years, while males continue growing to about 12 years (Sigg *et al.*, 1982). Altmann & Alberts (1987) found that the growth rate for weight reported for captive baboons was double the rate they observed in wild animals. Dental eruption is also greatly accelerated in captive baboons (Phillips-Conroy & Jolly, 1988; Kahumbu & Eley, 1991).

There is no good evidence for an adolescent growth spurt in the data reported here, except for male body weight. This is not surprising given the cross-sectional nature of the data, age clumping in the sample due to natural birth peaks and small size of the spurt expected for macaques (Watts & Gavan, 1982). Thus, we cannot rule out the possibility of growth spurts for other traits or for female weight based on our present data. The magnitude of the juvenile growth spurt for skeletal dimensions suggested by earlier studies of non-human primates is so small that its existence has been appropriately questioned (Bogin, 1988). However, the evidence seems more secure for weight and muscle mass measurements (Bogin, 1988), especially in male baboons (Coelho, 1985). We have a similar result in this study for male body weight. However, longitudinal growth studies of this population will be needed to confirm this finding.

The limb circumferences and weight also display a tendency to decrease at advanced ages, perhaps indicating the effects of muscle wastage and decline in condition at this period of life (see Figure 3). The same trend appears in the data from the free-ranging colony of rhesus macaques on Cayo Santiago (Turnquist & Kessler, 1989). However, longitudinal data would be necessary to confirm this decline among aged animals since secular trends could also produce this result.

Developmental bases of sexual dimorphism

The developmental bases of adult sexual dimorphism in these body characters include both rate and maturation age dimorphism. Bimaturism dominates, especially for body lengths. The average proportion of adult dimorphism due to bimaturism for postcranial body lengths is 70% (if the hands and feet are not included). This proportion is likely to be underestimated due to the difficulty in identifying a precise age at which growth stops. The evolution of

sexual dimorphism for body lengths appears to be due, primarily, to the prolongation of male growth during the subadult period, or conversely, the contraction of the female juvenile growth period, with relatively little modification of growth rates. The difference in growth periods for males and females corresponds to differences in epiphyseal fusion and is accomplished by delayed epiphyseal fusion in males relative to females, especially at the elbow and knee joints (Cheverud, 1981).

In contrast, sexual dimorphism in postcranial circumferences and widths are due to rate and maturation dimorphism in nearly equal proportions (54%) of adult dimorphism due to maturational differences). Most of the significant differences among older juveniles concern rates of growth for widths, circumferences and weight. This tallies with an earlier estimate indicating that juvenile males gain weight faster than their female peers (Dittus, 1977*a*). Even so, the proportion due to growth rate dimorphism is likely overestimated due to the difficulties in precisely assessing when growth stops. This bias may be particularly strong for females and postcranial circumferences and widths due to the relatively long period of declining growth rates in female muscle mass measurements. Thus, taking female morphology as primitive and male as derived, sexual dimorphism in body widths and circumferences, largely reflecting muscular development, have evolved through a combination of increased juvenile male growth rates and prolonged subadult male growth.

Measurements of the head display a variety of developmental bases for adult dimorphism. For some measurements adult dimorphism is produced solely by rate differences (lower facial height, nasal width) while for others adult dimorphism is almost entirely caused by differences in age at maturity (jaw width). In general, head measurements tend to differ more in growth rates between the sexes than postcranial measurements. In a cross-sectional growth study of rhesus macaque crania, Cheverud & Richtsmeier (1986) found that the face grows nearly twice as fast in males as it does in females during the juvenile growth period (about 3–7 years), while differences in age of maturation appear minor. Sirianni (1985) found that facial measurements grow approximately two to three times faster in juvenile male pigtailed macaques (*Macaca nemestrina*) than in juvenile females. These results correspond to our findings for lower facial height, nasal width and other facial measurements.

The developmental bases of sexual dimorphism vary considerably with the kind of measurement considered. Postcranial skeletal dimensions show a considerable degree of bimaturism while sexual dimorphism in muscle mass and cranial features are due to both rate differences and bimaturism.

Summary and conclusions

Somatic growth in the wild toque macaques from Polonnaruwa, Sri Lanka, is similar in pattern to that reported for laboratory populations of macaques and baboons, but growth is prolonged by several years. The period of infant and early juvenile growth ends at about 2.5 years, followed by a later juvenile growth period which varies in length by sex and type of measurement. Weight and measurements influenced by muscle mass complete growth by 8 years in females and 12 years in males, while skeletal lengths of the extremities complete growth by 5.5 years in females and 7.5 years in males. An adolescent growth spurt was detected for male body weight.

Sexual dimorphism is due primarily to bimaturism, males growing for a prolonged period relative to females, although growth rate dimorphism during the later juvenile period when both sexes are still growing also contributes significantly to adult dimorphism. Bimaturism was particularly important for skeletal length measurements. During the infant and early juvenile period, growth rate estimates for postcranial traits were slightly, but consistently, faster in males than in females.

Preliminary information comparing toque macaque growth to other macaques and baboons indicates that much of the variation among adult papionins may be due to differences in infant and juvenile growth rates with relatively little contribution from variation in age at maturity. However, due to acceleration of growth likely in laboratory and provisioned colonies, more data from feral macaque and baboon populations is required to make secure interspecific comparisons.

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Appendix 1

- Body measurements collected from the toque macaques at Polonnaruwa. Measurements were recorded in cm except for weight which was recorded in kg.
- Weight: weight in kg at trapping (scale).
- Crown-Rump length (CRNRMP): distance between the vertex (top of the head) and the caudal tip of the ischial tuberosities (caliper).
- Occiput to tail base (OCCTBS): dorsal trunk length from the base of the skull to the base of the tail (caliper).
- Trunk length (ventral) (TRL): distance between suprasternale (the upper border of the sternal notch) and symphysion (the midsagittal point along the cranial border of the pubic symphysis) (caliper).
- Abdominal circumference (ABDCIRC): circumference of the abdomen measured above the pelvis (tape measure). Thoracic circumference (THORCIRC): circumference of the thoracic cavity measured at the level of the breast (tape measure).
- Biacromial width (shoulder width) (BAW): distance between right and left acromion (most lateral point of the upper extremity) (caliper).
- Bitrochanteric width (hip width) (BTW): distance between the right and left trochanterion laterales (most lateral point on the greater trochanters of the femur) measured with legs held together in flexed position (caliper).
- Arm circumference (BICPCIRC): maximum circumference on the arm (tape measure).
- Arm length (ARL): distance from acromion to radiale [the most lateral and proximal point of the radial head (at elbow)] (caliper).
- Forearm length (FAL): distance from radiale to stylion (the most distal point on the radial styloid process) (caliper).
- Hand length (HNL): distance from stylion to chirodactylion (the most distal tip of the third digit) (caliper).
- Hand width (HNW): distance from metacarpale mediale (head of the second metacarpal) to metacarpale laterale (head of the fifth metacarpal) (caliper).
- Calf circumference (CLFCIRC): maximum circumference of the calf (tape measure).
- Thigh circumference (THGHCIRC): maximum circumference of the thigh (tape measure).
- Thigh length (THL): distance from trochanterion laterale to femorale (most distal point of the femur's lateral condyle at knee) (caliper).
- Leg length (LEL): distance between tibiale (most proximal point on the medial condyle of the tibia at the knec) and sphyrion (the most distal point on the medial malleolus of the tibia at the ankle) (caliper).
- Foot length (FTL): distance from pternion (heel) to pododactylion (most distal point on the third digit) (caliper).
- Foot width (FTW): distance from metatarsale mediale (medial point of the head of the second metatarsal) to metatarsale laterale (the lateral side of the fifth metatarsal head) (caliper).
- Tail length (TL): distance from the base of the tail to the tip of the most caudal vertebra (tape measure).
- Head length (HDL): distance from glabella (most anterior point on the frontal bone) to inion (most posterior point on the occipital) (caliper).

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Head breadth (HDB); maximum transverse distance between right and left parietal bones (caliper).

Biorbital width (BOW): distance between the lateral margins of the orbits (caliper).

Bizygomatic width (BZW): maximum distance between the lateral surfaces of the zygomatic arches (caliper).

Bigonial width (BGW): maximum distance between the right and left angles (gonia) of the mandible (caliper).

Upper facial height (UFH): distance between nasion (depression below brow ridges) and intradentale superior (gingiva between upper medial incisors) (caliper).

Lower facial height (LFH): distance between the most inferior point of the mandibular symphysis and intradentale inferior (gingiva between lower medial incisors) (caliper).

Nasal width (NSW): maximum distance between the lateral margins of the nostrils (caliper).

	Crown len	-rump gth	Occip tail l	ital to base	Abdo circum	minal ference	Tho circum	racic ference	Ar circum	m lerence
Age	W	F	W	ш	M	F	W	Ĩ	Μ	F
0-1 1-2 3-4 4-5 5-6 6-7 7-9 9-11 11-13 13-15 15+	22.36 (1.69) 31.98 (1.75) 31.98 (1.75) 33.98 (2.43) 36.71 (1.75) 37.80 (0.94) 37.80 (0.94) 39.11 (1.45) 41.45 (1.69) 42.24 (1.70) 44.90 (1.73) 44.40 (1.62) 44.83 (2.03)	$\begin{array}{c} 22\cdot24 \ (2\cdot18)\\ 28\cdot54 \ (1\cdot14)\\ 31\cdot12 \ (1\cdot86)\\ 33\cdot40 \ (1\cdot16)\\ 35\cdot46 \ (1\cdot15)\\ 37\cdot30 \ (1\cdot15)\\ 37\cdot30 \ (1\cdot15)\\ 37\cdot37 \ (0\cdot91)\\ 38\cdot52 \ (1\cdot93)\\ 38\cdot52 \ (1\cdot93)\\ 38\cdot32 \ (1\cdot28)\\ 38\cdot32 \ (1\cdot23)\\ 38\cdot46 \ (1\cdot23)\\ 39\cdot47 \ (1\cdot75)\\ 39\cdot47 \ (1\cdot75)\\ \end{array}$	$\begin{array}{c} 17\cdot74 \ (1\cdot94)\\ 26\cdot03 \ (2\cdot05)\\ 26\cdot03 \ (2\cdot05)\\ 27\cdot66 \ (1\cdot80)\\ 27\cdot66 \ (1\cdot80)\\ 31\cdot89 \ (1\cdot96)\\ 32\cdot94 \ (2\cdot48)\\ 32\cdot05 \ (1-98)\\ 32\cdot94 \ (2\cdot33)\\ 33\cdot84 \ (2\cdot78)\\ 33\cdot84 \ (2\cdot78)\\ 33\cdot84 \ (2\cdot78)\\ 36\cdot87 \ (3\cdot01)\\ \end{array}$	$\begin{array}{c} 17.67\ (2.02)\\ 26.05\ (1.97)\\ 27.33\ (1.97)\\ 27.33\ (1.98)\\ 31.49\ (2.20)\\ 31.49\ (2.20)\\ 32.95\ (1.91)\\ 32.35\ (1.91)\\ 32.48\ (1.98)\\ 32.56\ (2.02)\\ 33.56\ (2.02)\\ \end{array}$	$\begin{array}{c} 13\cdot63 \ (1\cdot63) \\ 13\cdot63 \ (1\cdot92) \\ 21\cdot39 \ (1\cdot92) \\ 22\cdot39 \ (1\cdot64) \\ 22\cdot39 \ (1\cdot64) \\ 22+69 \ (1\cdot71) \\ 22+69 \ (1\cdot71) \\ 22\cdot57 \ (2\cdot66) \\ 22\cdot64 \ (1\cdot85) \\ 32\cdot28 \ (3\cdot13) \\ 32\cdot59 \ (3\cdot19) \\ 32\cdot59 \ (3\cdot19) \end{array}$	$\begin{array}{c} 13\cdot43 \ (2\cdot23) \\ 21\cdot77 \ (1\cdot55) \\ 21\cdot77 \ (1\cdot55) \\ 221\cdot37 \ (1\cdot55) \\ 221\cdot37 \ (1\cdot55) \\ 221\cdot37 \ (1\cdot55) \\ 221\cdot37 \ (1\cdot57) \\ 221\cdot37 \ (1\cdot68) \\ 221\cdot37 \ (1\cdot68) \\ 221\cdot37 \ (1\cdot67) \\ 221\cdot37 \ (1\cdot67) \\ 221\cdot37 \ (1\cdot67) \\ 221\cdot37 \ (2\cdot41) \ (2\cdot41) \\ 221\cdot37 \ (2\cdot41) \ (2\cdot41) \\ 221\cdot37 \ (2\cdot41) \ (2\cdot41) \ (2\cdot41) \\ 221\cdot37 \ (2\cdot41) \$	$\begin{array}{c} 16\cdot48 \ (1\cdot14) \\ 22\cdot12 \ (100) \\ 23\cdot12 \ (100) \\ 23\cdot51 \ (0.84) \\ 25\cdot57 \ (1\cdot27) \\ 25\cdot57 \ (1\cdot27) \\ 27\cdot24 \ (0.98) \\ 33\cdot36 \ (1\cdot74) \\ 33\cdot36 \ (1\cdot74) \\ 34\cdot15 \ (1\cdot74) \\ 34\cdot15 \ (1\cdot36) \\ 34\cdot54 \ (2\cdot04) \end{array}$	$\begin{array}{c} 16\cdot 10 & (1\cdot 67) \\ 16\cdot 10 & (1\cdot 67) \\ 22\cdot 33 & (1\cdot 06) \\ 22\cdot 32 & (0\cdot 91) \\ 25\cdot 09 & (0\cdot 94) \\ 25\cdot 09 & (0\cdot 94) \\ 25\cdot 75 & (1\cdot 11) \\ 27\cdot 75 & (1\cdot 11) \\ 27\cdot 75 & (1\cdot 95) \\ 28\cdot 85 & (0\cdot 95) \\ 28\cdot 85$	$\begin{array}{l} 6\cdot28 & (0\cdot65)\\ 8\cdot95 & (0\cdot65)\\ 8\cdot95 & (0\cdot74)\\ 9\cdot17 & (0\cdot22)\\ 10\cdot43 & (1\cdot35)\\ 10\cdot26 & (0\cdot97)\\ 11\cdot35 & (0\cdot65)\\ 11\cdot35 & (0\cdot65)\\ 11\cdot35 & (0\cdot65)\\ 12\cdot84 & (1\cdot25)\\ 11\cdot35 & (0\cdot65)\\ 12\cdot84 & (1\cdot25)\\ 11\cdot5\cdot0 & (1\cdot66)\\ 14\cdot50 & (1\cdot42)\\ 14\cdot50 & (1$	$\begin{array}{c} 6.07 & (0.67) \\ 7.61 & (0.57) \\ 8.48 & (0.62) \\ 8.78 & (0.45) \\ 9.73 & (0.76) \\ 9.73 & (0.76) \\ 10.26 & (0.97) \\ 10.46 & (0.83) \\ 10.24 & (0.68) \\ 10.24 & (0.63) \\ 10.24 & (0.95) \\ 10.25 & (1.09) \\ 10.55 & (1.09) \end{array}$
Age	Calf circu M	ımference F	Thigh circ M	umference F	Ventral tr M	unk length F	Should	er width F	Arm l M	ength F
0-1 1-2 3-4 5-5 6-7 6-7 1-9 11-13 13-15 15+	$\begin{array}{c} 6.40 & (0.67) \\ 8.27 & (0.87) \\ 8.71 & (0.63) \\ 8.81 & (0.67) \\ 8.81 & (0.67) \\ 10.26 & (1.13) \\ 10.13 & (1.42) \\ 11.61 & (1.03) \\ 11.61 & (1.03) \\ 11.81 & (1.03) \\ 11.82 & (0.76) \\ 12.58 & (0.42) \\ 12.58 & (0.88) \end{array}$	$\begin{array}{c} 6\cdot05 \ (0\cdot74) \\ 7\cdot49 \ (0\cdot52) \\ 8\cdot61 \ (0\cdot71) \\ 8\cdot55 \ (0\cdot65) \\ 9\cdot35 \ (0\cdot93) \\ 10\cdot06 \ (0\cdot49) \\ 10\cdot06 \ (0\cdot72) \\ 10\cdot32 \ (1\cdot08) \\ 10\cdot32 \ (1\cdot08) \\ 9\cdot92 \ (0\cdot84) \\ 9\cdot92 \ (0\cdot84) \end{array}$	$\begin{array}{c} 8.21 & (0.97) \\ 12.39 & (1.47) \\ 13.26 & (1.40) \\ 14.07 & (1.61) \\ 16.22 & (1.53) \\ 16.73 & (1.81) \\ 16.73 & (1.81) \\ 17.33 & (1.61) \\ 17.33 & (1.65) \\ 19.29 & (1.26) \\ 19.29 & (1.26) \\ 22.33 & (2.26) \\ 22.35 & (1.00) \\ 19.68 & (2.44) \\ 19.68 & (2.44) \\ \end{array}$	$\begin{array}{c} 8.18 & (1\cdot40) \\ 11\cdot73 & (1\cdot69) \\ 13\cdot66 & (0\cdot99) \\ 13\cdot66 & (0\cdot99) \\ 14\cdot53 & (0\cdot80) \\ 15\cdot50 & (1\cdot00) \\ 15\cdot50 & (1\cdot00) \\ 15\cdot57 & (2\cdot09) \\ 15\cdot73 & (1\cdot37) \\ 15\cdot38 & (1\cdot11) \\ 15\cdot56 & (2\cdot55) \\ 15\cdot73 & (1\cdot60) \end{array}$	$\begin{array}{c} 14\cdot35 \ (1\cdot68) \\ 19\cdot93 \ (1\cdot47) \\ 22\cdot67 \ (1\cdot42) \\ 22\cdot57 \ (1\cdot42) \\ 23\cdot21 \ (3\cdot94) \\ 25\cdot50 \ (2\cdot07) \\ 27\cdot31 \ (0\cdot97) \\ 27\cdot31 \ (0\cdot97) \\ 27\cdot31 \ (0\cdot97) \\ 31\cdot70 \ (1\cdot13) \\ 31\cdot70 \ (1\cdot13) \\ 32\cdot42 \ (1\cdot39) \\ 32\cdot42 \ (1\cdot39) \end{array}$	$\begin{array}{c} 14\cdot 90 \ (1\cdot 68) \\ 20\cdot 17 \ (1\cdot 12) \\ 21\cdot 93 \ (1\cdot 14) \\ 23\cdot 55 \ (1\cdot 03) \\ 25\cdot 54 \ (1\cdot 27) \\ 27\cdot 54 \ (1\cdot 27) \\ 27\cdot 54 \ (1\cdot 17) \\ 27\cdot 54 \ (1\cdot 18) \\ 28\cdot 04 \ (1\cdot 82) \\ 28\cdot 06 \ (1\cdot 62) \\ 28\cdot 23 \ (1\cdot 08) \\ 28\cdot 92 \ (1\cdot 11) \\ 28\cdot 92 \ (1\cdot 46) \end{array}$	$\begin{array}{c} 5\cdot23 \ (0\cdot60)\\ 6\cdot80 \ (0\cdot71)\\ 7\cdot21 \ (0\cdot80)\\ 7\cdot63 \ (0\cdot79)\\ 7\cdot91 \ (1\cdot01)\\ 8\cdot37 \ (0\cdot80)\\ 9\cdot32 \ (0\cdot62)\\ 9\cdot32 \ (0\cdot62)\\ 9\cdot32 \ (0\cdot62)\\ 9\cdot32 \ (0\cdot61)\\ 11\cdot2\cdot15 \ (0\cdot44)\\ 11\cdot23 \ (1\cdot32)\\ 11\cdot23 \ (1\cdot32)\\ 10\cdot91 \ (1\cdot18)\end{array}$	$\begin{array}{c} 5\cdot44 & (0\cdot73) \\ 6\cdot31 & (0\cdot74) \\ 6\cdot82 & (0\cdot70) \\ 7\cdot38 & (0\cdot81) \\ 7\cdot44 & (1\cdot102) \\ 8\cdot44 & (1\cdot14) \\ 7\cdot88 & (0\cdot91) \\ 8\cdot15 & (0\cdot41) \\ 8\cdot56 & (0\cdot81) \\ 8\cdot56 & (0\cdot81) \\ 8\cdot75 & (0\cdot71) \\ \end{array}$	$\begin{array}{l} 6\cdot72\ (0\cdot80)\\ 8\cdot79\ (0\cdot24)\\ 9\cdot77\ (0\cdot24)\\ 10\cdot59\ (0\cdot22)\\ 11\cdot45\ (0\cdot90)\\ 11\cdot98\ (0\cdot50)\\ 11\cdot98\ (0\cdot50)\\ 12\cdot80\ (0-62)\\ 13\cdot38\ (0-69)\\ 13\cdot38\ (0-69)\\ 14\cdot13\ (1\cdot18)\\ 14\cdot24\ (0\cdot75)\\ 14\cdot24\ (0\cdot75)\ (0\cdot75)\\ 14\cdot24\ (0\cdot75)\ (0$	$\begin{array}{c} 667 \ (0.80) \\ 8.667 \ (0.75) \\ 9.38 \ (0.75) \\ 9.33 \ (0.62) \\ 10.37 \ (0.64) \\ 11.28 \ (0.35) \\ 11.53 \ (0.71) \\ 11.53 \ (0.73) \\ 12.01 \ (0.70) \\ 11.70 \ (0.73) \\ 11.96 \ (0.54) \\ 11.96 \ (0.54) \\ 11.96 \ (0.54) \\ 12.30 \ (0.59) \end{array}$

SOMATOMETRIC GROWTH IN TOQUE MACAQUES

	Forearn	n length	Hand	length	Hand	vidth	Hip	vidth	Thigh	length
Age	M	Н	W	<u>Б</u>	M	H	W	ы	W	F
<u>9-1</u>	6.96(0.71)	6.75 (0.76)	5.51(0.60)	5.37(0.47)	1·75 (0·14)	1.64(0.16)	4·71 (0·44)	4.64(0.53)	7.02(0.77)	7.03(0.87)
12	8-99 (0-54)	8-87 (0-61)	6.52(0.32)	6.57(0.58)	2.04(0.07)	1.86(0.15)	6.17(0.41)	5.93(0.37)	9.54(0.82)	9.56(0.49)
2–3	9.82(0.50)	9.47(0.50)	7.01(0.40)	(0.50)	2·20 (0·18)	2.07(0.18)	6.76(0.57)	6.53(0.33)	10-83 (0-74)	10-35 (0-70)
3-4	10-69 (0-69)	10-72 (0-68)	7-36 (0-43)	7.43(0.39)	2.16(0.12)	2.14(0.18)	7.07 (0.85)	7.07 (0.31)	11.72(0.96)	11.52(0.42)
4-5	11-81 (0-47)	11.56(0.55)	8-20 (0-32)	7.63(0.33)	2·44 (0·14)	2.21 (0.17)	7·63 (1·00)	7-79 (0-60)	13-00 (0-76)	12.64 (0.47)
5-6	12-11 (0-86)	11-91 (0-26)	8-39 (0-36)	7-66 (0-44)	2.31(0.16)	2.22(0.16)	7-85 (0-71)	8·28 (0·33)	13.30(1.29)	12·94 (0·67)
6-7	13-32 (0-87)	12.09(0.34)	8-75 (0-52)	7-61 (0-37)	2.60(0.05)	2.28(0.24)	8.75 (0.77)	8.55(0.42)	14-38 (0-85)	13-11 (0-51)
62	13.61 (0.66)	11-74 (0-59)	8-77 (0-54)	7.49 (0.48)	2.67 (0.18)	2.35(0.18)	9-55 (0-64)	8-58 (0-56)	15.02(0.50)	13.04(0.35)
9-11	13-88 (1-08)	12.12 (0.66)	8-76 (0-57)	7-88 (0-45)	2.62 (0.17)	$2 \cdot 24 (0 \cdot 19)$	10-01 (0-74)	8-64 (0-33)	15.29(0.75)	12-96 (0-77)
11 - 13	14-03 (0-76)	11-95 (0-53)	8.63 (0.15)	7.78 (0.36)	2.50(0.16)	2.34(0.21)	10.20 (0.26)	8-60 (0-27)	15-50 (1-02)	12-93 (0-73)
13-15	14-22 (0-97)	11.54(0.46)	8-87 (0-55)	7.44 (0.45)	2.78 (0.19)	2.30(0.20)	10.50(0.45)	8-66 (0-18)	15-20 (1-08)	12-75 (0-72)
15 +	13-81 (1-13)	12-15 (0-57)	9-13 (0-79)	7.82(0.43)	2.74(0.21)	2-38 (0-17)	10.66(0.53)	9.04(0.41)	15-73 (1-28)	13-17 (0-76)
	Leg l	ength	Foot l	ength	Foot v	vidth	Taill	ength	Head	ength
Age	M	F	W	Гт.	М	F	W	ír,	M	ſщ
0-1	7.47 (0.94)	7-42 (1-26)	7-82 (0-52)	7.70 (0.61)	1.63 (0.11)	1.67 (0.17)	33·44 (2·81)	32·37 (4·32)	6.30(0.40)	6·21 (0·59)
1–2	9-86 (0-66)	9-76 (0-72)	9-69 (0-47)	9.38(0.53)	2.08 (0.10)	1.96(0.16)	43·27 (3·24)	$41.92(2\cdot24)$	6.08 (0.27)	6.62(0.46)
2^{-3}	10.80(0.50)	10.59 (0.76)	10-28 (0-37)	9-91 (0-37)	2·15 (0·13)	2.06(0.17)	46·71 (4·01)	45-31 (6-08)	7·05 (0·19)	6.90(0.25)
3-4	11.46(0.66)	11-97 (1-04)	10-70 (0-61)	10-20 (0-58)	$2 \cdot 21 \ (0 \cdot 19)$	2.26(0.28)	45·76 (4·27)	47.77(2.31)	7.26 (0.27)	6.93(0.33)
4-5	12.82 (0.69)	12·53 (0·76)	11-75 (0-54)	11.19 (0.58)	2.45(0.13)	2.28 (0.09)	52·81 (3·06)	53-50 (4-76)	7-46 (0-21)	7·18 (0·28)
5-6	13.31 (0.89)	12-96 (0-61)	11-79 (0-49)	11-01 (0-21)	2.50(0.21)	2.30(0.15)	54.31(2.51)	51-25 (1-51)	7.51 (0.28)	7-37 (0-24)
6.7	14.63 (1-34)	13-35 (0-73)	12-39 (0-56)	11-08 (0-43)	2.54(0.15)	2.33(0.16)	57.33 (5.58)	51.69 (4.18)	7.75(0.36)	7.39(0.22)
62	14.99(0.62)	13.02 (0.95)	12-71 (0-48)	11.18 (0.50)	2.68(0.15)	2.33(0.18)	60.59(2.90)	53.44(3.28)	8.00(0.38)	7.50(0.33)
9-11	15.23(1.03)	12.83(0.69)	12.57(0.41)	11.22(0.57)	2.64(0.20)	2.32(0.22)	57.28(3.54)	$54 \cdot 19 (3 \cdot 42)$	8-04 (0-44)	7-58 (0-24) 7 55 (0.00)
11-13	14-90 (0-57)	12-83 (0-74) 10-47 (0-21)	12-72 (0-21)	11-04 (0-57)	2-60 (0-27)	2-30 (0-19)	(97-5) (7-70 (97-5) (7-70 (97-5) (7-7)	53-U0 (5-12)	(11.0) 04.9	(77.0) 60-7
13-15 15+	14-87 (0-86) 14-98 (1-21)	12·4/ (0·61) 13·40 (0·64)	12-/3 (0-53) 12-84 (0-61)	10-79 (0-52) 11-06 (0-53)	2.568 (0.20) 2.71 (0.18)	2·39 (0·10) 2·44 (0·13)	00-35 (3-47)	54-32 (1-04) 54-32 (4-27)	8-48 (0-42) 8-42 (0-35)	7-58 (0-38)
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Appendix 2 Continued.

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 $\begin{array}{c} 2.44 & (0.15) \\ 2.73 & (0.17) \\ 2.84 & (0.20) \\ 3.10 & (0.12) \\ 3.37 & (0.13) \\ 3.60 & (0.13) \end{array}$ $\begin{array}{c} 3.69 \\ 3.70 \\ 3.70 \\ 0.31 \\ 3.66 \\ 0.18 \\ \end{array}$ 3.60(0.22)3.89(0.28)(0.21)Upper facial height ſ. ·87 $\begin{array}{c} 2.04 \ (0.15) \\ 2.46 \ (0.20) \\ 2.73 \ (0.20) \\ 2.90 \ (0.42) \\ 3.26 \ (0.17) \\ 3.63 \ (0.17) \\ 3.84 \ (0.34) \\ 4.31 \ (0.28) \end{array}$ $\begin{array}{c} 4.80 \\ 4.83 \\ 6.28 \\ 5.04 \\ (0.31) \end{array}$ (0.44) Σ 4-65 ($\begin{array}{c} 2.32 \ (0.35) \\ 2.98 \ (0.36) \\ 3.12 \ (0.52) \\ 3.66 \ (0.71) \\ 3.56 \ (0.71) \\ 3.53 \ (0.50) \\ 3.53 \ (0.50) \\ 3.53 \ (0.50) \\ 3.53 \ (0.50) \\ 3.53 \ (0.50) \\ 3.53 \ (0.50) \\ 3.53 \ (0.51) \\ 3.56 \$ (L Ġ. Sample size Jaw width $\begin{array}{c} 3\cdot53 & (0\cdot55) \\ 3\cdot98 & (0\cdot74) \\ 4\cdot10 & (0\cdot69) \end{array}$ $\begin{array}{c} 2\cdot37 \,\,(0\cdot59)\\ 2\cdot93 \,\,(0\cdot52)\\ 3\cdot03 \,\,(0\cdot49)\end{array}$ $\begin{array}{c} 3\cdot33 \\ 3\cdot07 \\ 3\cdot07 \\ 3\cdot50 \\ 0\cdot38 \end{array}$ (0.20)(0.20)(0.48)Σ Σ 4.40(3-94 (4-37 ($\begin{array}{c} 3.89 & (0.52) \\ 4.94 & (0.31) \\ 5.02 & (0.47) \\ 5.26 & (0.42) \\ 5.73 & (0.37) \\ 5.73 & (0.37) \\ 5.89 & (0.42) \\ 6.04 & (0.28) \\ 5.88 & (0.50) \\ 6.24 & (0.33) \end{array}$ $\begin{array}{c} (0\cdot19)\\ (0\cdot16)\\ (0\cdot20)\\ (0\cdot20)\\$ (0.42)(0.30)(0.40)Bizygomatic width . بىت ۲r. 3.02 ($\begin{array}{c} 6.04 \\ 6.04 \\ 6.24 \\ 6.25 \\ 6.28 \\ 6.28 \\ 6.42 \\ \end{array}$ 0-59 (1.26 1.69 1.89 2.45 2.71 2.89 3.08 3.16 3.09 30 Weight $\begin{array}{c} 1.79 \\ 2.11 \\ 0.28 \\ 2.60 \\ 0.38 \\ 3.54 \\ 0.33 \\ 3.54 \\ 0.33 \\ 3.51 \\ 0.53 \\ 5.02 \\ 0.71 \\ 0.52 \\ 5.71 \\ 0.52 \\ 0.$ $\begin{array}{c} 3\cdot 99 \; (0\cdot 54) \\ 4\cdot 90 \; (0\cdot 53) \\ 5\cdot 33 \; (0\cdot 28) \\ 5\cdot 57 \; (0\cdot 34) \end{array}$ 5.62(0.53)6.03(0.60) $\begin{array}{c} 6\cdot10 & (0\cdot33) \\ 6\cdot75 & (0\cdot66) \\ 7\cdot15 & (0\cdot62) \end{array}$ 0.76**J·63** (0·13) 1-40 (0-15) 3-05 (0-24) 7-82 (0-42) 91 (0-39) Σ Σ 9.66 $\begin{array}{c} 0.92 & (0+12) \\ 1.07 & (0+10) \\ 1.15 & (0+14) \\ 1.122 & (0+14) \\ 1.224 & (0+10) \\ 1.338 & (0+14) \\ 1.338 & (0+14) \\ 1.338 & (0+14) \\ 1.346 & (0+12) \\ 1.360 & (0+22) \\ 1.53 & (0+12) \\ 1.54 & (0+12) \\ 1.55 & (0+12) \\$ $\begin{array}{c} (0\cdot 23) \\ (0\cdot 20) \\ (0\cdot 16) \\ (0\cdot 28) \\ (0\cdot 28) \end{array}$ (0·19) (0.15)(0.29)(0.19)(0.21)(0.26)(0.23) í. (L $\begin{array}{c} 3\cdot 78 \ (\\ 4\cdot 57 \ (\\ 4\cdot 811 \ (\\ 4\cdot 811 \ (\\ 5\cdot 95 \ (\\ 5\cdot 351 \ (\\ 5\cdot 351 \ (\\ 5\cdot 551 \ (\ 5\cdot$ **Biorbital** width Nasal width $\begin{array}{c} 3.86 \ (0.22) \\ 4.46 \ (0.12) \\ 4.64 \ (0.17) \\ 4.83 \ (0.18) \\ 5.03 \ (0.26) \\ 5.19 \ (0.19) \\ 5.64 \ (0.34) \\ 5.81 \ (0.32) \end{array}$ $\begin{array}{c} 1.08 & (0.14) \\ 1.19 & (0.14) \\ 1.18 & (0.14) \\ 1.42 & (0.25) \\ 1.42 & (0.25) \\ 1.42 & (0.13) \\ 1.53 & (0.11) \\ 1.54 & (0.21) \\ 1.54 & (0.24) \\ 1.77 & (0.02) \\ 1.77 & (0.02) \\ 1.77 & (0.01) \\ 1.91 & (0.18) \\ 1.91 &$ (0.24)(0.59) (0.24)(0.27) **J-93** (0-12) Σ Σ 6-28 (i 6-43 (i 5.65 (55 $\begin{array}{c} 5.44 & (0.17) \\ 5.57 & (0.22) \\ 5.76 & (0.25) \\ 5.73 & (0.42) \\ 5.73 & (0.42) \\ 5.99 & (0.17) \\ 6.07 & (0.13) \\ 6.01 & (0.41) \end{array}$ $\begin{array}{c} 6\cdot 10 & (0\cdot 23) \\ 6\cdot 11 & (0\cdot 16) \\ 6\cdot 08 & (0\cdot 18) \\ 5\cdot 94 & (0\cdot 42) \end{array}$ $\begin{array}{c} 1.41 & (0.23) \\ 1.71 & (0.20) \\ 1.83 & (0.30) \\ 1.81 & (0.14) \end{array}$ $\begin{array}{c} 2\cdot31 & (0\cdot21) \\ 2\cdot34 & (0\cdot14) \\ 2\cdot40 & (0\cdot20) \\ 2\cdot59 & (0\cdot30) \end{array}$ 1-92 (0-31) 2-07 (0-31) (0.37)0-27 2-46 (0-20 Lower facial height ſr. ĹŦ. Head breadth <u>9</u>.00 2.61 $\begin{array}{l} 5\cdot23\ (0\cdot20)\\ 5\cdot62\ (0\cdot26)\\ 5\cdot86\ (0\cdot20)\\ 5\cdot90\ (0\cdot25)\\ 6\cdot12\ (0\cdot28)\\ 6\cdot12\ (0\cdot28)\\ 6\cdot50\ (0\cdot23)\\ 6\cdot57\ (0\cdot44)\end{array}$ $\begin{array}{l} 1.49 & (0-23) \\ 1.68 & (0-35) \\ 2.02 & (0-18) \\ 1.98 & (0-45) \\ 1.98 & (0-45) \\ 2.37 & (0-11) \\ 2.58 & (0-20) \\ 2.74 & (0-29) \\ 2.93 & (0-41) \\ 3.11 & (0-19) \end{array}$ (0.10)(0.20)(0.38)(0.31)(0.15)(0.28)(0.33)Σ Σ 7-27 7-22 7-27 7-27 3.14 (3.10 (3.54 ($\begin{array}{c} 4-5\\ 5-6\\ 6-7\\ 7-9\\ 9-11\\ 9-11\\ 11-13\\ 13-15\end{array}$ 9-11 11-13 13-15 $1-2 \\ 2-3 \\ 3-4$ 5 1-23-45-67-97-95+ -1 2 + 5 Age Age

SOMATOMETRIC GROWTH IN TOQUE MACAQUES

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