Morphometric analysis of growth and development in wild-collected vervet monkeys (*Cercopithecus aethiops*), with implications for growth patterns in Old World monkeys, apes and humans

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Abstract

A study was undertaken of a unique sample of 63 wild vervet monkeys *Cercopithecus aethiops* from a single population in Uganda collected over 35 days in 1947. Twenty-five were immature (12 females and 13 males) and 38 were adults (16 females and 22 males). Body mass, external measurements, masticatory and other masses were recorded for each individual at the time of collection, and for a few specimens, the development of the reproductive organs. Each individual was evaluated for cranial capacity, limb length and dental eruption. The comparison of immature and adult animals illustrates the mosaic nature of growth in the different body systems, as well as female–male differences. An ancestral model is proposed for catarrhine growth and development, with particular reference to sex differences. This model provides a framework for assessment of immatures and for the reconstruction of socio-ecological effects on life-history stages in populations of fossil monkeys, apes and early hominids.

Key words: growth, development, primates, sex differences, *Cercopithecus aethiops*

INTRODUCTION

As Old World monkeys, apes and humans (catarrhines) develop, body systems modulate the survival and reproductive strategies of individuals and constrain the overall life-history pattern for the species (Schultz, 1949, 1956, 1969; Hamada, Iwamoto & Watanabe, 1986; Shea, 1986; deRousseau, 1990; Watts, 1990; Zihlman, Morbeck & Goodall, 1990; B. H. Smith, 1991; Pereira, 1993; Pereira & Fairbanks, 1993; Rubenstein, 1993; Bogin & Smith, 1996; Morbeck, 1997*a*; Morbeck, Galloway & Zihlman, 1997). Human body systems develop in a mosaic fashion (Scammon, 1930). Our limited understanding of non-human primate developmental patterns leaves unclear which features constitute a catarrhine pattern of development and which ones are species-specific.

Primate life-history stages are assessed differently by researchers who study living animals and by those who focus on skeletal remains because morphological markers of life stages differ from behavioural ones. Changes in behaviour and external morphology can occur independently of the shuffling and reshuffling of internal organs and tissues. Establishing links among hard tissue markers in the dentition and skeleton, soft tissues and patterns of behavioural development all facilitate the evaluation of species-specific adaptations (Bolter & Zihlman, 2002).

We explore one catarrhine species, the vervet monkey *Cercopithecus aethiops*, collected in the wild by S. L. Washburn in 1947 from one Ugandan population, to document a cross-sectional view of development. Commonly called vervet, green or grivet monkey, *C. aethiops* molecularly sorts as part of the guenon radiation of Old World monkeys (Ruvolo, 1988).

These cross-sectional data sets permit us to examine in detail a single population of vervet monkeys during critical stages of their lives in 'anatomical snap-shots.' The collection provides an extraordinary opportunity to combine individual records of soft tissue, morphometrics and body mass from Washburn's field notes, with additional information on dentition, skeleton, cranial capacity and joint fusion. Such a range of data is likely to remain rare, because animals are no longer collected in large numbers. Consequently, these data may provide unique insights into primate growth and development.

The skeletal collection along with the field notes are held in the Anthropology Laboratories at the University of California, Santa Cruz. There are no official specimen numbers, only the numbers that Washburn assigned as he prepared them.

Our project began with two goals: first, to compare and contrast immature monkeys with adults to establish the patterns of growth in several body systems; second, to refine growth divergences between females and males. The challenge of establishing individual ages led us to add a third goal: the correlation of hard tissue from dental eruption and skeletal fusion to establish age classes in

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Table 1. Various age classes in vervet monkey *Cercopithecus aethiops* studies

Age category	Chronological age (from that study)	Markers	Study
Infant	Birth–6 months		Struhsaker (1967*c*)
Young juvenile	6–18 months		
Juveniles	18–35 months		
Sub-adult	36–47 months		
Adult	48+ months		
Infant 1	Birth to 4–5 months	Locomotion, behaviour, coloration, suckling, external features and vocalizations	Gartlan & Brain (1968)
Infant 2	4–5 to 15–18 months		
Juvenile female	18–35 months		
Juvenile male	18–59 months		
Sub-adult female	36–48 months		
Infant 1	Birth to 4–5 months	Behaviours, play and vocalizations	Bramblett (1980)
Infant 2	4–5 to 18 months		
Juvenile female	18–35 months		
Juvenile male	18–59 months		
Infant			Whitten (1982)
Juvenile 1			
Juvenile 2			
Sub-adult			
Early infancy	0–3 months	Loss of neonatal coat colour	Lee (1984)
Infancy	Birth to 1 year		Cheney *et al.* (1988)
Immature	Females up to 4 years Males up to 5 years	Sexual maturation	Cheney *et al.* (1988)
Juvenile		End of weaning to sexual maturation	Fairbanks (2000)
Juvenile	Females 5–36 months Males 5–48 months	Chronological age	Horrocks & Hunte (1993)
Adult female	About 4–5 years	Body mass	Leigh (1996)
Adult male	About 6–7 years		

vervet monkeys. Soft tissue measurements made at the time of collection expanded the information for the age classes.

Several other goals also emerged: to focus on growth and development from the whole body perspective; to provide an in-depth look at developmental patterns and life stages of this Old World monkey population, and to extend a growth and development framework to the other catarrhines, extant or extinct.

ASSESSING LIFE STAGES

It is crucial for the field researcher to understand the fundamentals of growth and development for several reasons: to assess basic demographic variables like group composition and age at reproductive maturity; to establish age-cohorts; to follow changes in individuals as they mature; to examine the influence of ecological constraints in a primate population (J. Altmann, Altmann, Hausfater & McCuskey, 1977; J. Altmann, Altmann & Hausfater, 1981; S. Altmann, 1998). However, as the systems develop independently, status assessment may vary within a species or even within one population depending on whether physical or behavioural criteria are used (Bramblett, 1980), or which attribute or series of traits is used (see Table 1).

MATERIALS AND METHODS

The 63 skeletons of Ugandan *Cercopithecus aethiops* consist of both sexes and all ages. Vervets have a birth season (Butynski, 1988), and because collection was made over a short period, not every age class is represented in the sample. For example, 1 and 2 year olds are present but not 1.5 year olds.

Methods in the field

Each monkey was weighed at once, linear anthropometric measurements were taken, and external features noted. Washburn's handwritten field notes record the sex (visual assessment), measurements on trunk length, chest circumference and breadth, lengths of tail, hand and foot (anthropometrics after Schultz, 1929).

Body mass and testes weights, observations of ovarian maturity and weights on masticatory muscles were collected in the field. For muscle weights, Washburn individually dissected the temporalis and masseter muscles from origin to insertion and weighed each (see Zihlman & McFarland, 2000 for methods on soft tissue collection).

Table 2. Revised age classes for sub-adults and adults[a]. *, Age classes represented in this sample

| Revised age class | This sample | | Life-history stage | Tooth eruption | Age (months) based on Fairbanks |
	Female	Male			
0	0	0	Infant	None	0–5 days[b]
1*[c]	1	4		Deciduous	6–115 days
2*	5	1	Juvenile	M1 (upper/lower)	12–14
3*	1	2		I1, I2	22–27
4	0	0		M2	26–31
5	0	0		P3[d], P4	32–40
6*	1	3		C	38–41
7*	4	3		M3 (proximal humerus unfused)	38–67
8*	15	21	Adult	All teeth fully erupted (proximal humerus fused)	>38

[a] Fewer age classes than in the study of Turner et al. (1997), based on Ockerse (1959) dental eruption chronologies.
[b] Based on Ockerse (1959) first dentition at 6 days.
[c] Note that age class 1 includes two of five males with only partial deciduous dentition compared to the three others that had full deciduous dentition. These two individuals were considerably smaller than others in this age class and are probably closer to newborn age. The other three males and the one female in age class 1 are estimated to be older.
[d] Note that catarrhines (Old World monkeys, apes and humans) only have two premolars per quadrant (two upper quadrants in the maxilla, two lower quadrants in the mandible). However, they are abbreviated as "P3" and "P4". This recognizes that the mammalian ancestors of these primates had 4 premolars per quadrant (P1, P2, P3, P4). In the course of catarrhine evolution, they have lost the P1 and P2 teeth. See also Fig. 1.

Methods in the laboratory

In biological anthropology, maximum lengths of adult long bones are most commonly taken for comparison and are therefore preferred, as presented here. Studies of sub-adult individuals, in contrast, involve immature bones; epiphyses are often missing because they have not yet fused onto the long bones. In these cases, only diaphyseal (bone shaft without epiphyses) lengths can be measured. For growth and development studies, we propose that the methodology for obtaining diaphyseal lengths of Bromage et al., (in prep) be used as the standard. The method can be used on immatures without epiphyses and on mature (adult) bone with epiphyses.

The volume of the cranial capacity was measured as an indirect indicator of brain size. A non-invasive technique was used that may be performed at museums or in non-specialized laboratories. The crania were filled with mustard seed, the skull tilted to distribute them throughout, the skull tapped twice to settle its contents, and then filled to the plane of the foramen magnum rim. The seed was then poured into a flask and recorded to the nearest ml. The measurement was performed 3 times, and the mean taken.

In the laboratory, dental eruption and epiphyseal fusion (especially the proximal humerus and pelvis) were assessed. Dental eruptions were visually assessed and assigned the following scores based on Wintheiser, Clauser & Tappen (1977): 1, unerupted; 2, partial eruption; 3, full eruption. Skeletal fusion stages of the long bones and pelvis were assigned according to Wintheiser et al. (1977) methods: 1, no union; 2, partial union; 3, full union.
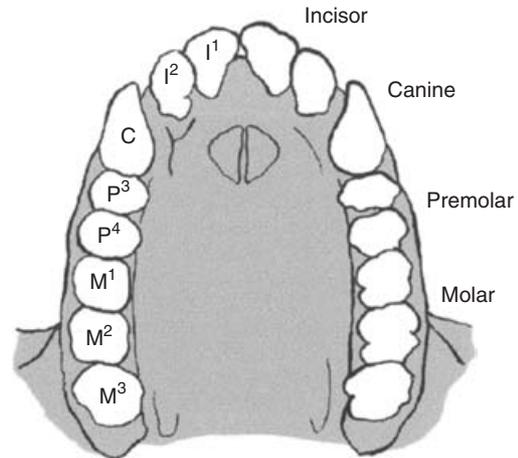

Fig. 1. Dental abbreviations in catarrhines.

Age class assignment

Each individual was assigned a dental age class based on the number and kinds of teeth erupted after the classification of Turner, Anapol & Jolly (1997) (see Fig. 1), which was modified in 3 ways. First, dental eruption chronologies were refined from an additional live captive vervet colony housed at the UCLA-VA Vervet Research Center (L. Fairbanks, pers. comm.), which differs from the chronologies used by Turner et al. (1997; based on Ockerse, 1959). Smith, Crummett & Brandt (1994) predicted that the Ockerse data contained errors (particularly the premolar eruption chronologies). A revised age class chronology based on the Fairbanks dental eruptions (see Table 2) is posited, and these age classes are used in our analysis.

Second, a stage of humeral fusion was added to further refine the animals with fully erupted third molars. Because the proximal humerus is typically the last long bone to fuse in monkeys (Washburn, 1943; Shigehara, 1980), we used this union as a way to separate the immature and mature. Those lacking a fully fused (stage 3) proximal humerus were classified as immature. For comparison, animals with stage 3 fully erupted third molars and stage 3 fully fused proximal humerus were considered adult. There were no specimens with a fully fused proximal humerus with a partially erupted third molar.

Third, we classified animals without permanent dentition as 'infant,' specimens with fully erupted molars and fused proximal humeri as 'adult' and the rest of the specimens as 'juvenile.' This grouping allowed statistical analyses between females and males, juveniles and adults. Means, standard deviations and analysis of variance (ANOVA) were calculated.

RESULTS

Means and standard deviations for mass and linear measurements are presented by sex for juveniles and adults (see Table 4).

Skeleton and body proportions

Complete union of the female pelvis was achieved in all elements, including the ischio-pubic ramus and the three borders of the acetabulum, before males of comparable dental stage. For long bones, the females had a different fusion sequence than males, most notably at the knee joint (i.e. distal femur, proximal tibia and fibula). These knee elements in females fused before full dentition, and before the completed fusion of the upper limb (wrist and shoulder joints).

Humerus lengths differ significantly between female and male adults (ANOVA: $F_{1,27} = 86.42$, $P < 0.001$), but as juveniles the difference is not quite statistically significant (ANOVA: $F_{1,14} = 4.454$, $P = .052$). Females of age class 7 are all within 1 SD of the adult female humerus mean ($n = 3$; 115, 107, and 109 mm), and two of three males in age class 7 were within 1 SD ($n = 3$; 121, 123, 127 mm), but none of the humeral lengths of males in age class 6 are within the range of the adult mean ($n = 3$; 110, 99, 119 mm).

Femur lengths are significantly different between female and male juveniles (ANOVA: $F_{1,17} = 7.068$, $P = .016$), and the significance increases with adulthood (ANOVA: $F_{1,29} = 140.75$, $P < 0.001$). As with the humerus, it appears that the femur length growth is completed in females by age class 7 ($n = 4$, 136, 129, 129, 136 mm), but has not finished growing in all age class 7 males ($n = 3$, 146, 156, 159 mm).

Measurements for sex differences in juvenile vervet hand (ANOVA: $F_{1,16} = 9.798$, $P = 0.006$) and feet (ANOVA: $F_{1,15} = 14.064$, $P = 0.002$) followed a similar pattern in that significance increased with adulthood
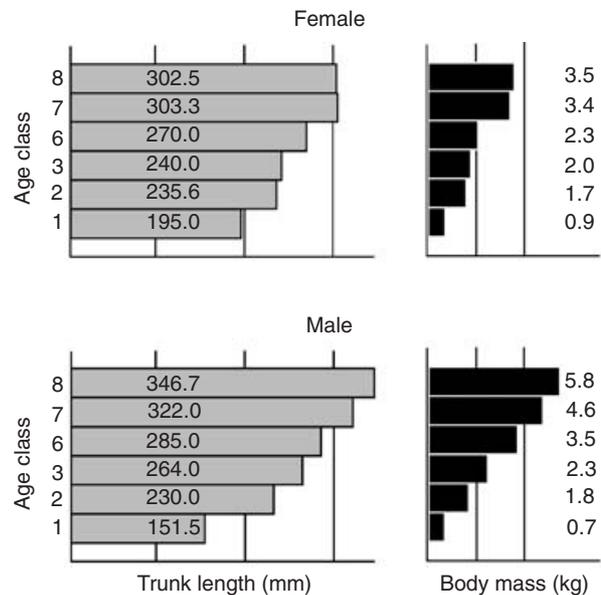

Fig. 2. Means of trunk length (mm) and body mass (kg) by sex and age class in vervet monkeys.

(ANOVA: $F_{1,28} = 86.895$, $P < 0.001$ for hand and $F_{1,28} = 187.913$, $P < 0.001$ for foot). Tails did not show a significant sex difference in lengths in juveniles (ANOVA: $F_{1,14} = 3.231$, $P = 0.092$, NS), but do in adults (ANOVA: $F_{1,25} = 17.744$, $P < 0.001$).

Adult vervets showed sexual dimorphism in chest circumference (ANOVA: $F_{1,27} = 52.915$, $P < 0.001$). This chest difference was only barely significant in female and male juveniles (ANOVA: $F_{1,16} = 4.295$, $P = 0.054$), but not apparent in infants or young juveniles (up to c. 2 years).

At 1 year of age, females and males have comparable trunk lengths, and in juveniles, sex differences in trunk length are not significant (ANOVA: $F_{1,17} = 2.271$, $P = 0.149$, NS). As adults, sex differences in trunk length are significant ($F_{1,34} = 70.214$, $P < 0.001$).

Age class 1 females and males were comparable in body mass. Adult females average 3526.7 g ($n = 15$, SE = 134.2 g, 95% CI: 3238.8–3814.5 g) and adult males 5767.0 g ($n = 21$, SE = 150.6 g, 95% CI: 5453.0–6081.1 g). Our data suggest that female and male mass differences appear during the second year, or age class 3 (see Fig. 2). Age class 6 (third year) females were 65% of the body mass of their male age classmates. When all juveniles are lumped together, sex differences in body mass barely reach significance (ANOVA: $F_{1,17} = 4.466$, $P = 0.049$). Adult female and male body mass means are significantly different (ANOVA: $F_{1,33} = 112.231$, $P < 0.001$).

Soft tissue and body composition

Adult female cranial capacities average 58.9 ml ($n = 11$, SE = 1.2, 95% CI: 54.8–63.1 ml) and adult males 68.7 ml ($n = 14$, SE = 1.4, 95% CI: 63.5–73.8 ml).
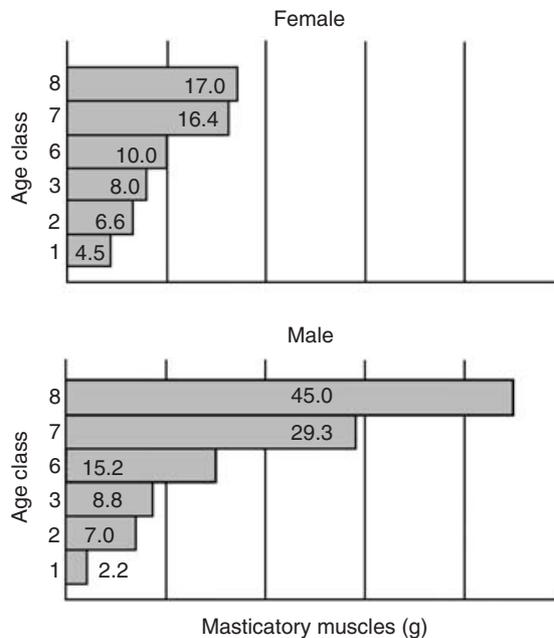
Female

Male

Masticatory muscles (g)

Fig. 3. Means of masticatory muscles (g) by sex and age class in vervet monkeys.

Washburn autopsied two females from age class 2 and age class 6. The ovaries were described to be 'large' and 'mature' on both individuals. Washburn diagnosed the testes of all males through age class 6 (*c.* 3 to 3.5 years old) as 'tiny,' 'not descended,' and when weighed did not exceed 2 g. Age class 7 males (all dentition erupted but still skeletally immature) had descended testicles, weighing 6 g, 7 g, and 12.5 g, indicating an increase in mass by this age class. The adult male mean testes weight is 13.3 g ($n = 13$, SE = 0.73, 95% CI: 10.7–15.9 g).

Sex differences in masticatory muscle growth and development were marked in the vervets. When grouped and analysed as juveniles, female and male muscle mass did not show significant differences (masseter: ANOVA, $F_{1,17} = 4.172$, $P = 0.056$; temporalis: ANOVA, $F_{1,17} = 3.952$, $P = 0.062$). As adults, females are significantly less muscular than the males (masseter: ANOVA, $F_{1,29} = 92.95$, $P < 0.001$); temporalis: ANOVA, $F_{1,29} = 142.01$, $P < 0.001$). When considered by age class, the difference appears during age class 6 (see Fig. 3).

To illustrate the mosaic pattern of achieving maturity in body systems, scores were averaged from juvenile animals for a feature and calculated as a percentage of the average adult score. The systems are presented below in order of earliest maturation to latest.

DISCUSSION

Several points are elucidated by this study: (1) body systems develop at different rates within a species; (2) within this framework, females and males differ in the order and timing of development in bones, teeth, muscle and body mass, which further elaborates life-history markers for both sexes; (3) the socio-ecology of a species interacts with developmental patterns.

Body systems grow in a mosaic fashion

Body systems mature within a species at different rates and times as illustrated in Table 3. The brain matures earlier than other systems. The skeletal framework and dental complement mature, followed by muscle mass. During this juvenile phase, the body is under continuous reorganization to achieve adult proportion and composition.

Females and males differ in ordering and timing of development

This collection of vervets demonstrates a sex difference in the pathway to adulthood. Sex differences in females and males do not vary in the same way for all geographical regions, either between closely related species or within species (Washburn, 1942).

Cranial–dental growth

By the first molar eruption, both females and males achieved > 91% of the average adult cranial capacity. Similar findings were reported for 21 primates species (B. H. Smith, 1991). Sexual dimorphism in body mass is not evident at this time, and therefore young males with the same body mass as females have larger brain size-to-body size ratios. Muscle and body mass continue to increase without an increase in brain mass. Consequently, as adults, females have a larger brain size-to-body size ratio than do males.

Dental developmental sequences remain similar between females and males with the exception of the canines, and possibly the third molars. Male canines erupt to full occlusion after M3s are in place. Adult canine lengths exhibit sexual dimorphism with males averaging 7.3 mm and females 5.7 mm (McCown, 1978, measured on this collection).

The third molars may exhibit some sexual dimorphism in emergence in vervets (L. Fairbanks, pers. comm.). For a captive colony at the UCLA-VA Vervet Research Center (VRC), male third molars were present by 4.5 years. In many females, however, the third molars do not erupt before age 5. Up to this stage, eruption times of males and females did not differ. Many older females in the captive colony had impacted or missing third molars, which was not the case for the males. This suggests a possible anomalous condition for the M3 development in this captive population of female vervets. The VRC founders were collected from a genetically isolated, feral vervet population on St. Kitts Island, in the Caribbean, from which other population-distinct features occur, including vocalizations, displays, and physical attributes (McGuire, 1974; McGuire, Berg *et al*., 1974). The impacted or missing third molars may be a product of genetic drift in this inbred founder population (McGuire, Ervin *et al*., 1974).

Table 3. Traits of juvenile vervets (nine females and nine males between 12 and 67 months) as a percentage of adult values

	Juvenile mean	Adult mean	Percent growth completed	Order of body growth
Cranial capacity (cc)	62.8	63.8	98	1
Tail (mm)	540.6	586.8	92	2
Foot (mm)	119.5	130.1	92	2
Hand (mm)	75.2	83.9	90	3
Femur (mm)	124.8	144.1	87	4
Trunk (mm)	274.0	327.7	84	5
Dentition[a]	28.8	48.0	60	6
Body mass (g)	2861.1	4833.6	59	7
Skeleton[b]	30.0	54.0	56	8
Masseter (g)	3.2	7.3	44	9
Testes (g)	5.7	13.3	43	10
Temporalis (g)	10.0	27.1	37	11

[a] The eruption scores were added together and divided by the added scores for adults. Specimens missing teeth were removed from sample (one female age class 3 and one female age class 7).
[b] The following epiphyseal union scores were added together and divided by the added scores for adults: proximal (p), medial, and distal (d) humerus; p and d radius, ulna, tibia, fibula, femur; greater and less trochanter of femur; three borders of the acetabulum and the ischio-pubic ramus.

Table 4. Descriptive statistics for juvenile and adult vervet monkeys

		Juveniles Age class 2–7			Adults Age class 8		
		n	Mean	SD	*n*	Mean	SD
TBM (g)	F	11	2422.70	854.97	15	3526.67	519.83
	M	9	3396.80	1205.47	21	5767.05	690.00
	Total	20	2861.10	1115.26	36	4833.56	1278.66
Trunk (mm)	F	11	263.72	34.06	15	302.47	15.98
	M	9	286.55	33.26	20	346.65	15.03
	Total	20	274.00	34.81	35	327.71	26.90
Chest circumference (mm)	F	10	272.50	37.14	13	312.69	25.05
	M	9	311.66	45.21	16	384.06	27.22
	Total	19	291.05	44.74	29	352.07	44.39
Chest breadth (mm)	F	10	71.30	9.58	13	82.00	7.20
	M	9	79.77	11.75	17	101.94	16.68
	Total	19	75.31	11.23	30	93.30	16.61
Temporalis (g)	F	11	7.50	3.72	12	12.79	2.47
	M	9	13.11	8.45	20	35.70	6.34
	Total	20	10.02	6.75	32	27.11	12.40
Masseter (g)	F	11	3.09	1.16	13	4.23	0.78
	M	9	4.44	1.79	19	9.32	1.78
	Total	20	3.70	1.59	32	7.25	2.92
Humerus (mm)	F	8	96.87	11.87	13	108.39	6.89
	M	9	110.00	13.56	17	127.24	4.18
	Total	17	103.82	14.11	30	119.08	10.93
Femur (mm)	F	11	115.90	14.86	15	130.47	7.44
	M	9	135.66	18.42	17	156.12	4.62
	Total	20	124.80	18.99	32	144.09	14.32
Tail (mm)	F	10	519.50	50.74	13	551.92	30.99
	M	7	570.71	67.05	15	617.00	47.58
	Total	17	540.58	61.72	28	586.79	51.89
Hand (mm)	F	10	70.50	5.48	14	77.00	3.04
	M	9	80.44	8.23	17	89.53	4.20
	Total	19	75.21	8.44	31	83.87	7.32
Foot (mm)	F	9	111.77	5.40	14	118.29	4.32
	M	9	127.22	11.11	17	139.88	4.40
	Total	18	119.50	11.62	31	130.13	11.74

Table 5. Order (from top of each column down) of initiation of epiphyseal fusions[a] before and after full eruption of M3, in females and males of three primate species. Data from Cheverud, 1981; Kimura & Hamada, 1990; Y. Hamada, pers. comm.

Vervets *Cercopithecus aethiops*		Rhesus macaques *Macaca mulatta*		Japanese macaques mulatta *Macaca fuscata*	
Females	Males	Females	Males	Females	Males
Elbow	Elbow	Elbow	Elbow	Elbow	Elbow
Hip	Hip	Hip	Hip	Hip	Hip
Ankle	FULL M3	Ankle/knee	Ankle	Ankle/knee	Ankle
Knee	Ankle		FULL M3		Knee
FULL M3	Wrist	Shoulder	Knee	Shoulder	FULL M3
Wrist	Shoulder	Wrist	Wrist	FULL M3	Wrist
Shoulder	Knee	FULL M3	Shoulder	Wrist	Shoulder

[a] Elbow: distal (*d*) humerus, proximal (*p*) ulna; Hip: *p* femur, three borders of acetabulum; Ankle: *d* tibia, *d* fibula; Knee: *d* femur, *p* tibia; Wrist: *d* ulna, *d* radius; Shoulder: *p* humerus.

However, this pattern of slightly delayed female M3 emergence is evident in other sexually dimorphic catarrhines, such as the rhesus macaques on Cayo Santiago, although this is also an inbred, captive colony (Cheverud, 1981), but not in others, e.g. the Japanese macaques *Macaca fuscata* (Y. Hamada, pers. comm.). In chimpanzees, sex differences in tooth eruption times of the M3 exist, but are less pronounced (Nissen & Riesen, 1964). More data are needed to determine the significance of what seems to be a slightly delayed female M3 eruption in some catarrhines.

Skeletal growth

Females and males differed in the sequence of long bone fusion (see Table 5). Some sex difference in the wrist/shoulder fusion sequence has been reported in several macaque species (van Wagenen & Asling, 1958; Cheverud, 1981; Kimura & Hamada, 1990), but not in langurs (Washburn, 1943). Sex differences in skeletal–dental development have also been reported for seven catarrhine species (King, 2002). The sex difference at the knee joint in the Ugandan vervets may be a product of species and population variation, or the distal femur and proximal tibia may be the bones that can most optimally add length. Future studies on locomotor development may point to functional differences between females and males in knee joint maturation and other postcranial differences observed in this collection.

External measurements

Schultz (1956) reported measurements of chest girth for 13 anthropoid primate species by sex. In all species, male chest girth exceeded that of females both relative to body mass and absolutely for body size, even when females and males overlap in body mass. Hip breadths of females, in contrast, are either about the same as or larger than their male counterparts. Our sample also demonstrates a larger chest in males compared to females, and this sex difference increases with age.

Hand and foot lengths followed a similar pattern in that significant sex differences increased with adulthood. Adult males have significantly longer tails than females, but not during the juvenile phase.

These sex differences in time to maturity are consistent with those on vervets from Kenya (Turner *et al.*, 1997). Before M3 eruption, during the third year of life, the Kenyan females reached adult size for external measurements and body mass. The Uganda sample suggests that females reached the adult dimensions later, after M3 eruption (after *c.* 4 years). Our findings on males are consistent with the Kenyan study, which found that males from four populations had not completed growth in several physical dimensions by full M3 eruption. In other dimensions such as muscularity and overall body mass, substantial growth in males continues after all teeth are fully erupted.

Trunk length

Relatively little is known about the growth of skeletal length across primates (Leigh, 1996). Limited evidence from Japanese macaques suggests that males have slow, continued growth of trunk length after dental maturity through to senility (Matsubayashi & Mochizuki, 1982; Hamada *et al.*, 1986). In a longitudinal study, female and male mandrills, like vervet monkeys, were born with comparable crown-to-rump lengths, and females reached mature lengths before males (Setchell *et al.*, 2001). Adult males reach 1.3 times the length of females, and did so through longer period of growth rather than increased growth rates. Vervets may follow this pattern of longer trunk growth in males.

Hip fusion

In age class 1, only the female has a fused ischio-pubic ramus, while the five males have no fusion (see Fig. 4). This trend in bimaturation of the pelvis continues through development, with female pelvic fusion always advanced compared to the males in the same age group. By age
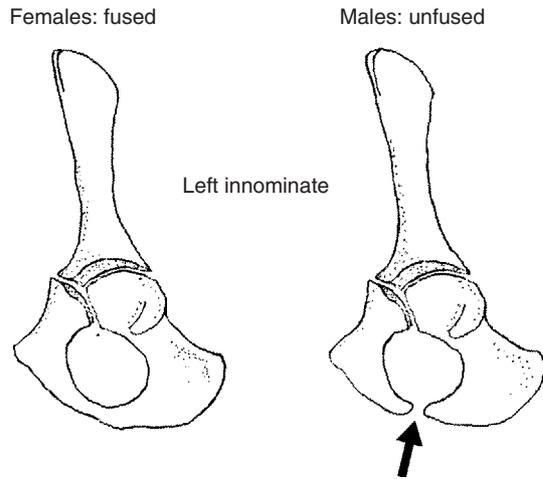
Females: fused   Males: unfused

Left innominate

Fig. 4. Ischio-pubic ramus fusion by sex at full deciduous tooth eruption (age class 1) in vervet monkeys.

class 6, the eruption of the canines (during the third year of age), the female has completed pelvic growth while the males have not. Bimaturation of the pelvis at the ischio-pubic ramus and the acetabulum also characterizes other species of sexually dimorphic macaques (van Wagenen & Asling, 1958; Cheverud, 1981; Hamada *et al*., 1986; Kimura & Hamada, 1990).

In vervets, acetabular fusion in females occurs around the time of mean age of first birth in captive colonies at 41 months (Bramblett *et al*., 1975), although in the wild first reproduction occurs at 5 years, and more rarely, 4-year-olds have been observed to give birth (Cheney *et al*., 1988). Age at first birth represents a flexible life-history variable, particularly under plentiful food conditions as found in captivity (J. Altmann, 1987). This study suggests that parturition may be constrained by the completion of pelvic growth.

Body mass

The mean adult female mass was 61% of the adult male's mean. By age class 7, while skeletally immature, females had attained 97% of the female adult average body mass in the sample. Age class 7 males (erupted third molars and skeletally immature) only reached 80% of the adult male average body mass. In contrast to the females, males continue to add soft tissue after skeletal-dental maturity, which is probably mostly muscle (Grand, 1983).

Other studies of vervet populations (Horrocks, 1986; Turner *et al*., 1997; R. J. Smith & Leigh, 1998) have also found that body mass does not exhibit sex differences in the early stages of life. Slight differences emerge by second molar eruption in Turner's study, or *c*. 2 years for known-aged wild vervets (Horrocks, 1986).

Body composition and soft tissue

The masticatory muscles (temporalis and masseter) illustrate well the mosaic nature of growth. Among our

variables, they are the last regional-functional trait to reach mature proportions. The mass of adult masticatory muscle is not simply a correlate of canine eruption, but may be a capstone of all muscularity. For example, relative to total body mass, muscle tissue is only 25% in newborn macaques, but is 40–45% in adults (Grand, 1977).

Reproduction

Potentially, yearling female vervets have well-developed, 'mature' reproductive organs. They may not be fully functioning, because in captivity first oestrus does not occur until a mean age of 30 months (Bramblett, Pejaver & Drickman, 1975). The ability of females to shorten the time of first reproduction, before the maturity in other body systems, characterizes some 'food-enriched' primate species (J. Altmann, 1987; Setchell *et al*., 2002). The maturation of the primate female reproductive system represents a plastic life-history variable, but the effects on other maturational variables, e.g., skeletal, behavioural, etc. remains unclear (J. Altmann, 1987).

In contrast, male vervets have a delayed reproductive development, with testes descending during age class 7. Longitudinal studies report rapid testicular growth in wild yellow baboons (J. Altmann, Altmann & Hausfater, 1981), and vervet males may follow a comparable course of growth. This attainment of testes maturity represents what Dixson (1998) refers to as 'age of pubertal onset,' which is often accompanied by higher levels of circulating testosterone. Sperm production most likely begins before pubertal onset. Male macaques can produce sperm before testes size reach mature proportions (Matsubayashi & Mochizuki, 1982), also found in male humans (Short, 1976).

Smaller and less experienced males cannot successfully compete and participate in the adult male dominance system, although they may mate surreptitiously and may even sire offspring. Males change groups at smaller sizes, (Cheney & Seyfarth, 1983), a factor that reduces their threat potential (Rowell, 1989). Males can maintain immature proportions longer because their growth spurts are not constrained by the energetics of pregnancy and lactation, as in females (Leigh, 1996). Adult-sized testes camouflaged with immature body mass and canines might facilitate the integration of males into the new group. Learning social skills, including male migration strategies, communication skills, and adeptness at solitary living may also favour postponing male somatic growth (J. Altmann, 1987; Rowell, 1989).

Socio-ecology and body maturation

The pattern of growth and development reflects modifications for the habitat niche. For example, vervets and savanna baboons diverged from a common monkey ancestor *c*. 8 million years ago (Cronin, Cann & Sarich, 1980); they are sympatric, although they differ in their developmental schedules: vervets reach about one-fourth

the body size of the baboons. These differences in growth and development in vervets have affects on their behaviour, diet and eco-space.

S. Altmann (1998) contrasts the strategies of vervets and baboons *Papio cynocephalus* that live together in the Amboseli Reserve in Kenya. These two closely related cercopithecines have similar morphologies, sexual dimorphism, social systems and ecologies; however, baboons exploit 200 more food items than the vervets. Their foods group into two categories: vertebrates, eggs and snails; and corms and bulbs. The latter group requires digging strength to exploit, whereas vervets are better at 'microextraction.' Only an adult male vervet had the comparable strength of a young yearling baboon. Thus juvenile and adult female vervets lacked the strength to exploit the kinds of resources that baboons of all ages do. Because of the shorter time to vervet adulthood (*c.* 2 years ahead of the baboons), vervets may also have fewer opportunities to learn foraging strategies. Variability in foraging choices and quality selections among yearling baboons had long-term effects on individual survival and later reproductive success (S. Altmann, 1998).

The larger body size of the baboons permits them to forage more widely (24.1 km² home range, travelling on average 6.1 km/day), which S. Altmann (1998) attributes in part to the baboons' ability to ward off predators better than the vervets. The vervets clustered around the woodlands, with their home range averaging 1.2 km² and daily travel of 0.42 km/day (Klein, 1978 as cited in S. Altmann, 1998). With less mobility, the vervets had a decreased access to patchy and widely distributed resources, including wide-range, seasonally occurring food items. Rather than a large menu, vervets concentrate on one local food item for extensive periods (weeks). This feeding pattern was also observed in sympatric vervets and baboons of Ethiopia (Dunbar & Dunbar, 1974).

This restricted mobility, S. Altmann argues, makes vervets more vulnerable to seasonal fluctuations in food, which may be why vervets have a defined breeding season in Amboseli while baboons do not. This susceptibility may also explain the earlier reproductive and body size maturation of vervets compared to baboons as an adaptation to unpredictable food resources, or marginal environments (Rowell, 1977). That vervets develop sooner than baboons may explain or be explained by their exploitation of locally and seasonally available foodstuffs (Lee & Hauser, 1988).

SUMMARY AND CONCLUSION

Primate studies help to discriminate which developmental elements humans share with our close relations, and which are novel adaptations (Washburn, 1951; Washburn & Avis, 1958; McCown, 1982; Morbeck, 1997*b*). Insight into the growth rates in living primates, and the role of nutrition, diet, locomotion and reproduction in the maturation of body systems (Lee & Hauser, 1988) will better position researchers to interpret fossil species, their life-history stages and associated behaviours. With this framework, it becomes possible to reconstruct selective socio-ecological factors that shaped human growth patterns, for example, the addition of a unique human childhood stage (Bogin & Smith, 1996; Leigh & Park, 1998; Bogin, 1999).

A detailed analysis of growth and development requires the examination of several body regions and systems. However, the mosaic pattern also leads to difficulties in age classifications because terms, e.g. infant, juvenile, sub-adult, adult, may be based on assessments of different body systems. We maintain that hard tissue standards should be applied in assessing age classes whenever possible. Hard tissues, particularly teeth, are conservative life-history features, and eruptions can be recorded from field and captive observations, and can be correlated with skeletal and fossil specimens (e.g. Schultz, 1940, 1941, 1942; Randall, 1943; Pusey, 1978; Turner *et al.*, 1997). Teeth and bones provide a common framework for identifying life stages within a species, and also as a standard for cross-species comparisons, that can be further elaborated with behavioural data and external development.

Furthermore, we propose that catarrhines share a similar pattern of growth and development in the following ways that can be refined or modified with additional data:
(1) adult females have a greater brain size to body size ratio than adult males;
(2) males attain full canine growth later than females;
(3) females provide the baseline of the species growth and development, while males modulate this pattern by a later 'bulking up' period.
(4) pelvis/hip joints fuse earlier in females than in males;
(5) males grow trunk length for a longer period, not faster, than do females;
(6) females have broader hips than chests; males have broader chests than hips;
(7) females are fully mature in all dimensions before males, with the possible exception of the third molar;
(8) ovaries mature (in size) much earlier than testes;
(9) males initiate sperm production before testicles reach adult size.

Catarrhine females express development of adult body size, musculature, skeletal fusion, and sex organ maturity earlier than males of comparable dental age. Schultz recognized this and therefore used the male growth pattern as the standard for the species (e.g. 1969: 148).

The dimorphic growth pattern in total body systems fits a theoretical model in which females stop growing earlier and thereby increase the energy available for reproduction and survival, including nutritional transfer, infant transport, gestation, pregnancy mobility, heat transfer, and grooming (J. Altmann 1980, 1986; Lee, 1987).

Because natural selection operates at all life stages, the study of whole body growth and development provides a key element in evolutionary studies and life-history theory.

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