



Ontogeny of limb mass distribution in infant baboons (*Papio cynocephalus*)

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Received 6 October 2004; accepted 26 May 2005

Abstract

Primates have more distally distributed limb muscle mass compared to most nonprimate mammals. The heavy distal limbs of primates are likely related to their strong manual and pedal grasping abilities, and interspecific differences in limb mass distributions among primates are correlated with the amount of time spent on arboreal supports. Within primate species, individuals at different developmental stages appear to differ in limb mass distribution patterns. For example infant macaques have more distally distributed limb mass at young ages. A shift from distal to proximal limb mass concentrations coincides with a shift from dependent travel (grasping their mother's hair) to independent locomotion. Because the functional demands placed on limbs may differ between taxa, understanding the ontogeny of limb mass distribution patterns is likely an essential element in interpreting the diversity of limb mass distribution patterns present in adult primates. This study examines changes in limb inertial properties during ontogeny in a longitudinal sample of infant baboons (*Papio cynocephalus*). The results of this study show that infant baboons undergo a transition from distal to proximal limb mass distribution patterns. This transition in limb mass distribution coincides with the transition from dependent to independent locomotion during infant development. Compared to more arboreal macaques, infant baboons undergo a faster transition to more proximal limb mass distribution patterns. These results suggest that functional demands placed on the limbs during ontogeny have a strong impact on the development of limb mass distribution patterns.

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Keywords: Inertial properties; Biomechanics; Development; Grasping hands and feet

Introduction

Previous researchers have highlighted important differences in the limb muscle mass distribution

patterns of primates compared to nonprimate mammals (Grand, 1977a; Vilensky, 1979; Preuschoft and Gunther, 1994; Raichlen, 2004). Primates in general have mass concentrated relatively distally on their limbs, corresponding to muscles that control manual and pedal grasping (Grand, 1977a;

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Preuschoft and Gunther, 1994; Raichlen, 2004), a trait considered to be a hallmark of the order (Cartmill, 1972, 1974, 1992).

Limb mass distribution patterns differ among taxa within broad mammalian groups depending on differences in limb muscular adaptations. For example, primates that spend a large proportion of time in arboreal settings (climbing, suspensory behaviors, and arboreal quadrupedalism) have relatively more distal limb muscle mass than do more terrestrial primates (Preuschoft and Gunther, 1994; Raichlen, 2004). Among quadrupedal mammals, cursors tend to have more proximal concentrations of muscle mass compared with non-cursors (Hildebrand, 1985; Myers and Steudel, 1997), which may be adaptation for reducing the energy costs of swinging distally heavy limbs (Hildebrand, 1985; Lieberman et al., 2003; but see Taylor et al., 1974). Finally, differences among dog breeds offer another example of how closely related taxa may differ in limb mass distribution depending on limb functions. Breeds that are considered fighting specialists have greater distal muscle mass compared to more cursorial dog breeds because they rely on their fore and hind paws for combat (Pasi and Carrier, 2003). Although the differences among dogs are the result of artificial selection, they demonstrate how limb mass distribution reflects variation in the functional demands placed on distal limb elements.

Interestingly, within a species, individuals at different developmental stages also appear to differ in limb mass distribution patterns (Grand, 1977b, 1981; Turnquist and Wells, 1994). For example, infant macaques have more distally concentrated limb mass compared to adults (see Grand, 1977b, 1981; Turnquist and Wells, 1994). A shift from more distal to more proximal limb mass concentrations occurs as macaques shift from dorsal and ventral riding on their mothers to independent locomotion (Turnquist and Wells, 1994). This shift from riding to independent locomotion changes the functional demands on the limbs from primarily grasping to locomotor propulsion. Because these functional demands may differ between taxa, understanding the ontogeny of limb mass distribution patterns is likely an essential element

in interpreting the diversity of limb mass distribution patterns present in adult primates.

This study documents changes in limb mass distribution during the development of *Papio cynocephalus*, providing the first longitudinal description of limb inertial properties (mass, center of mass, radius of gyration and mass moment of inertia) in an ontogenetic sample of primate quadrupeds. Limb inertial properties have been described for adult primate taxa (see Reynolds, 1974; Vilensky, 1979; Wells and DeMenthon, 1987; Raichlen, 2004), but the ontogeny of limb masses and centers of mass has been described cross-sectionally for only one genus, *Macaca* (Grand, 1977b, 1981; Turnquist and Wells, 1994).

Baboons are one of the most terrestrial primates (Napier and Napier, 1967; Fleagle, 1998) and therefore likely undergo drastic changes in the functional roles of their distal limb elements during ontogeny. Previous research examining morphological growth and development in baboons has focused mainly on changes in body mass and limb lengths over the entire developmental period (birth to 7 years; see Coelho, 1985; Glassman and Coelho, 1987, 1988; Ruttenberg and Coelho, 1988). Because these studies generally focus on long term patterns, they may miss correlations between morphological development and important behavioral transitions during infancy. For example, Altmann (1980) found that the transition from dependant (riding on their mothers) to independent locomotion in *Papio cynocephalus* occurs between approximately four and six months of age. Because of the likely importance of the timing of locomotor independence on the changing functional roles of the limbs, this study focuses on the morphological development of *Papio cynocephalus* between one and nine months of age.

In addition to documenting the ontogeny of all limb inertial properties in a primate taxon for the first time, this study considers whether interspecific differences in the development of limb mass distribution patterns exist. Turnquist and Wells (1994) reported ontogenetic changes in the limb segment masses of rhesus macaques (*Macaca mulatta*) and correlated morphological development with locomotor development (see also Wells and Turnquist, 2001). Because adult macaques are

slightly more arboreal than adult baboons (see Rose, 1973; Fleagle, 1998), it is possible that the functional demands on the limbs in these taxa will differ during ontogeny. To examine possible interspecific differences, the ontogeny of limb segment masses in the baboon sample are compared with segment masses in a cross-sectional sample of rhesus macaques (*Macaca mulatta*; data from Turnquist and Wells, 1994).

Methods

Geometric model

This study employs a geometric modeling technique based on one developed by Crompton et al. (1996) and Raichlen (2004) to determine the inertial properties of limb segments (segment mass, position of the segment center of mass, segment mass moment of inertia). This method allows collection of inertial property data from live subjects. Crompton et al. (1996) developed a geometric model that takes into account the irregularity of limb shape. Their model is based on columns with elliptical cross-sections. Raichlen (2004) made a small improvement on the Crompton et al. (1996) model by allowing the shape of the limb to vary in all directions. The limb of a living animal may then be modeled by taking external measurements along the length of the limb segments (Crompton et al., 1996; Raichlen, 2004).

The model used for this study is based on the geometric models developed by Crompton et al. (1996) and Raichlen (2004) with the exception of the fact that, in living infant baboons, major and minor axis measurements are exceedingly difficult to obtain due to small body sizes and time constraints on collecting data from non-anesthetized subjects (subjects were not anesthetized due to safety issues associated with repeatedly anesthetizing infant animals). Therefore, the body segments of the infant baboons were modeled as cylindrical columns (Fig. 1) where the radius of the column model was allowed to vary along its length.

The shape of the model described above was found by taking three measurements of segmental

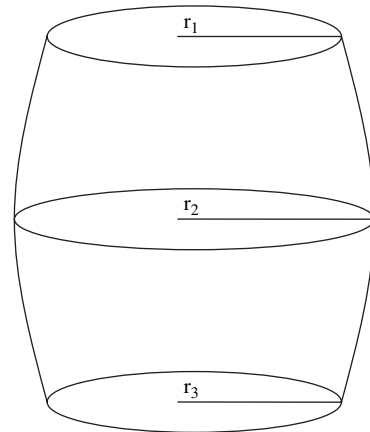


Fig. 1. Cylindrical column model (after Crompton et al., 1996). The height of the column is equal to the length of the segment, and r_1 , r_2 , and r_3 are the radius measurements taken from three locations along the segment. The model was used to generate segment inertial properties from equations developed in Raichlen (2004).

circumference along the length of each limb segment, as well as one measure of the length of the segment (see Measurement protocols and sample). The circumference was converted into a radius (radius = circumference/ 2π) and a second order polynomial was fit to these measurements to describe the change of the radius along the length of the segment. The inertial properties (mass, center of mass, mass moment of inertia) for these segments were then calculated using equations developed in Raichlen (2004).

Calculating inertial properties

Once the inertial properties of all limb segments are calculated, the whole limb inertial properties may be calculated. The center of mass of a limb (D) is found using the following equation (from Tipler, 1976):

$$D = \frac{\sum_{i=1}^n m_i r_i}{\sum_{i=1}^n m_i} \quad (1)$$

Where m_i is the mass of the i th segment and r_i is the distance of the center of mass of the i th segment from the proximal end of the limb. The

denominator is the calculation for the total mass of the limb (M). The mass moment of inertia describes a body's resistance to angular acceleration and is found using the following equations:

$$I_{cm} = \sum_{i=1}^n m_i r_i^2 + I_i \quad (2)$$

$$I_p = I_{cm} + M(D^2) \quad (3)$$

Where I_{cm} is the whole limb mass moment of inertia about a transverse axis through its D , I_i is the i th segment's mass moment of inertia about a transverse axis through its D , and I_p is the whole limb mass moment of inertia about a transverse axis through the proximal end of the segment (i.e., the resistance of the limb to angular acceleration during swing phase). Finally, the limb radius of gyration (R) about the proximal end is found using the equation (from Myers and Steudel, 1997):

$$R = \sqrt{\frac{I_p}{M}} \quad (4)$$

This variable is an important measure of overall limb mass distribution as it is the position on a body where a point mass would have an equal mass moment of inertia to the body itself. From Eqs. 1-4, it should be apparent that if limbs carry relatively distal mass, the D and R positions will be relatively distal, and I_p will be relatively large.

Measurement protocols and sample

Measurements were taken on four live infant baboons (*Papio cynocephalus*) throughout their early development. The sample included one male (Infant 1) and three females (Infants 2-4). Each individual was obtained from the Southwest Foundation for Biomedical Research (SFBR) from a population rejected by their mothers and placed in the SFBR nursery. Individuals were housed at the University of Texas Animal Resource Center using methods approved by both the University of Texas Institutional Animal Care and Use Committee (IACUC) and the SFBR IACUC.

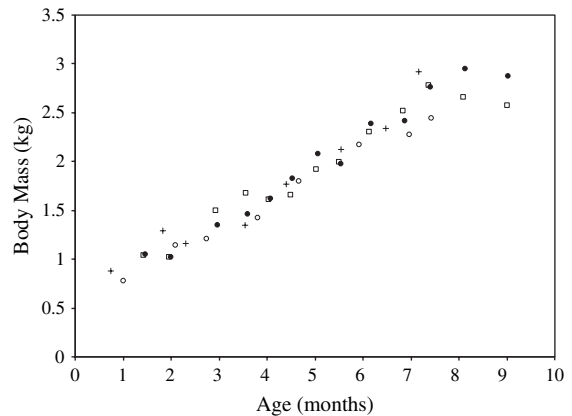


Fig. 2. Changes in body mass with age in the infant baboon sample. Increases in body mass are similar for all four infant baboons. Infant 1 is the male individual and is represented by open circles ($n = 8$). Infant 2 (open squares; $n = 13$), Infant 3 (closed circles; $n = 13$), and Infant 4 (crosses; $n = 8$) are all females.

The study period lasted from age one to eight months for Infants 1 and 4 and from one to nine months for Infants 2 and 3. The ages were selected to sample early development of infant baboons, including the time at which these individuals would have begun independent locomotion in the wild (approximately 4-6 months; see Altmann, 1980). The study was concluded when individuals could no longer be handled safely without administering anesthesia. This developmental period also allows males and females to be studied together, since sexual size dimorphism is not present in infant baboons at these ages (Fig. 2; see also Coelho, 1985). At regular intervals throughout ontogeny (approximately twice per month), each infant baboon was placed face down on a soft surface (e.g., towels on a top of a gurney). Segment lengths and circumferences were measured using measuring tape (to the nearest 1 mm). Segment circumferences were measured at three locations along each body segment (one proximal, one mid-segment, and one distal).

The following segment definitions were used to define the proximal and distal ends of the segments:

- a) The arm was defined proximally by a point in between the acromion process of the scapula

and the greater tubercle of the humerus and extended to the most proximal edge of the radial head.

- b) The forearm was defined proximally as the proximal edge of the radial head and distally as the styloid process of the radius.
- c) The hand extended from the styloid process of the distal radius to the end of the longest digit.
- d) The thigh was defined to be between the greater trochanter and the distal edge of the lateral condyle of the femur.
- e) The leg was defined to be between the proximal edge of the lateral tibial condyle and the lateral malleolus of the fibula.
- f) The foot extended from the posterior edge of the calcaneus to the tip of the longest digit.

Validity of the model

The validity of the geometric model has been previously tested for adult limbs and limb segments (see Raichlen, 2004). For the present study, the validity of the model when calculating infant baboon inertial properties was tested by comparing the total body mass of each individual at each age measured using an electronic scale (to the nearest 0.1 kg) with the total body mass calculated as the sum of all segment masses determined using the model. These values were compared using a paired t-test.

Data analysis

The ontogeny of limb mass distribution was analyzed using three methods. First, each limb inertial property was analyzed using the method of ontogenetic allometry. Limb inertial properties were regressed against limb length for the entire infant baboon sample. All values were log transformed prior to analysis. Each limb's length was calculated as the sum of all limb segments (arm, forearm, and hand; thigh, leg, and foot). The use of limb length is more appropriate than body mass in this analysis because inertial properties may be more sensitive to changes in limb length than to changes in body mass (see Myers and Steudel, 1997). Reduced major axis regressions were performed to obtain the slope, intercept, and estimates

of the 95% confidence limits of the slope and intercept for all regression equations. All infant baboons were analyzed together (combined-sample analysis) and individually (intra-individual analysis).

Second, limb inertial properties were normalized using dimensional analyses (see also Raichlen, 2004) and compared as the individuals aged. Inertial properties were made dimensionless by dividing each value by a fundamental quantity (or combination of quantities) of the same dimension that is constant in size and biologically relevant (see Hof, 1996). If inertial properties in baboons remain geometrically similar during ontogeny, then larger body masses and longer limb lengths should be associated with larger limb inertial property values. Therefore, the use of body mass and limb length as fundamental quantities removes differences in inertial properties among baboons of different sizes due simply to geometric scaling.

The dimensionless set of inertial properties were constructed after Hof (1996) as follows: limb masses (unit: kg) were divided by body mass; length variables (D and R; unit: m) were divided by limb length; and mass moments of inertia (unit: $\text{kg}\cdot\text{m}^2$) were divided by the product of body mass and the square of limb length. For all inertial properties, Pearson product-moment correlations were calculated for the relationship between dimensionless limb inertial properties and age. A significant correlation indicates a deviation from geometric scaling during ontogeny. The lack of a correlation between a given dimensionless quantity and age indicates geometric scaling.

The dimensionless analysis was performed for two reasons. First, the analysis provides a confirmation of the ontogenetic allometry analysis. Second, the use of dimensionless inertial properties may be the only way to compare these values among individuals who differ in body size (see Raichlen, 2004). Thus, the use of dimensionless inertial properties is the only way to compare infant baboons with adults.

Although changes in whole limb inertial properties with age describe changes in whole limb mass distribution, it is important to examine how changes in dimensionless limb segment masses contribute to these overall limb mass distribution changes. For all segments, dimensionless segment

masses were calculated at each age in two ways. First, segment masses were calculated as a percentage of body mass. Second, segment masses were calculated as a percentage of limb mass. This second method provides a more direct measure of how limb mass is distributed on a limb regardless of changes in body mass due to changes in either trunk or head mass. Additionally, changes in segment lengths were analyzed to determine the influence of length of changes on segment mass. This analysis provides an indication of how much of the change in segment mass is due simply to a change in segment length. All segment lengths were divided by the cube root of body mass to make them dimensionless.

Results

Model validity

Body masses measured on a scale and those calculated from the model for the infant baboon sample do not differ significantly (Table 1). Measured and calculated body masses are highly correlated ($r = 0.974$; Fig. 3) and the regression line relating these variables does not differ significantly from the line of identity ($y = x$; Fig. 3). The relatively high maximum percent error is likely due to the fact that any small errors in predicting segment masses are summed when total body mass is predicted. These results, combined with the model validation from Raichlen (2004), support the use of the model for calculating inertial properties and making comparisons of these properties with published values for other taxa.

Ontogenetic allometry

If limb mass distribution becomes more proximally concentrated with age, as predicted, then

centers of mass, radii of gyration, and mass moments of inertia should all increase negatively allometrically with limb length. Limb length is an appropriate size variable to use since it increases isometrically with body size in this sample (Table 2). These predictions are met by all limb inertial properties (Table 2). In fact, hind limb D, R, I increase with negative allometry despite the fact that hind limb mass increases with positive allometry (Table 2).

An intra-individual analysis of ontogenetic allometry for each individual infant baboon generally confirms the combined-sample analysis described above (Table 3). Instances where there is a discrepancy between the individual analysis and the combined-sample analysis are shown in bold in Table 3. In nine out of the ten instances where an inconsistency occurs, the individual's inertial property increases isometrically, while the whole sample shows either a positive or a negative allometric increase. In these cases, the slope of the intra-individual allometric increase agrees with the combined-sample analysis, but the 95% confidence limits overlap with isometry (see Table 3). These discrepancies with the combined-sample analyses may be due to small intra-individual sample sizes ($n = 8$ for Infants 1 and 4; $n = 13$ for Infants 2 and 3). Only one case (forelimb mass in Infant 1) disagrees in both slope and 95% confidence interval with the whole sample analysis. In this case, the forelimb of Infant 1 becomes relatively more massive as the limb increases in length.

Dimensionless inertial properties

The analysis of dimensionless inertial properties confirms the allometric results and supports the use of dimensionless inertial properties for inter-specific comparisons. Dimensionless limb lengths and forelimb mass are not significantly correlated with age, consistent with their isometric increases

Table 1
Comparison of measured body mass with body mass predicted from the geometric model

Property	Mean measured	Mean predicted	Mean % difference	Max % difference	Min % difference	Paired t-test sig.
Body mass	1.69	1.71	0.53	−23.20	−0.03	0.29

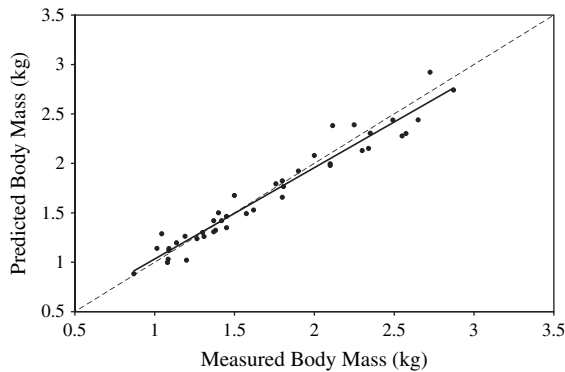


Fig. 3. Predicted vs. measured body masses in the infant baboon sample. Dotted line is the line of identity ($y = x$; slope is equal to 1.0 and line passes through the origin); solid line is a least squares regression line through the infant baboon sample [$r = 0.974$, Slope (95% C.I.) = 0.92 (0.08), Intercept (95% C.I.) = 0.11 (0.12), $p < 0.0001$].

with increasing size (Fig. 4a,b; Table 4). Hind limb mass is positively correlated with age, agreeing with the positively allometric increase in hind limb mass with limb length (Fig. 4b; Table 4). Forelimb and hind limb Ds, Rs, and mass moments of inertia are all negatively correlated with age, consistent with their negative allometric increases with length (Fig. 4c-e; Table 4). In general, dimensionless inertial properties are larger in the infant baboons compared to adult baboons (Figs. 4a-e). Infant baboons therefore have more distally distributed limb mass at young ages (larger dimensionless Ds, Rs, and mass moments of

inertia) and have more distal limb mass distributions than adult baboons.

Intra-individual analyses of the changes in dimensionless limb inertial properties with age generally agree with the whole sample analysis (Table 5). In three out of the four infant baboons, when a difference occurs (shown in bold), it is because the individual's sample does not show a significant correlation, but the general trend does not differ (the correlation coefficients have the same signs in the individual analysis compared to the whole sample analysis). Infant 1 shows four discrepancies (shown in bold-italics) where the sign of the correlation coefficient differs from those of the whole sample analysis, but only two of these are significant correlations. Dimensionless hind limb length and forelimb mass in Infant 1 increase significantly with age.

Dimensionless segment masses and lengths

Based on the results showing a proximal shift in limb mass during development, dimensionless proximal segment masses should increase with age, while dimensionless masses of distal segments should either decrease with age, or remain constant. All dimensionless forelimb and hind limb masses confirm these predictions (Figs. 5a-d; Table 6). The proximal segments become relatively more massive, the middle segments generally remain consistent in their dimensionless masses, and the distal segments become relatively less

Table 2

Ontogenetic allometry in infant *Papio* ($n = 42$)

Variable	Isometric slope	Slope	95% CI slope	Intercept	95% CI intercept	r^2
Forelimb Length	0.33	0.319	± 0.029	0.374	± 0.095	0.926
Hind limb Length	0.33	0.363	± 0.037	0.289	± 0.111	0.910
Forelimb Mass	3.00	3.217	± 0.228	-2.410	± 0.353	0.937
Hind limb Mass	3.00	3.606	± 0.305	-3.010	± 0.548	0.926
Forelimb D	1.00	0.439	± 0.041	0.674	± 1.015	0.921
Hind limb D	1.00	0.311	± 0.028	2.852	± 0.801	0.875
Forelimb R	1.00	0.517	± 0.050	0.695	± 1.215	0.927
Hind limb R	1.00	0.364	± 0.038	3.671	± 1.133	0.891
Forelimb Inertia	5.00	4.596	± 0.282	-2.086	± 0.487	0.949
Hind limb Inertia	5.00	4.467	± 0.251	-1.999	± 0.521	0.958

Note: These data represent the regression statistics for the combined-sample of four infants. Isometric slope is the slope expected if the variable increases isometrically. Length is regressed on body mass; all other forelimb and hind limb variables are regressed on either forelimb or hind limb length, respectively. 95% CI is the 95% confidence limit of the slope and intercept.

Table 3
Intra-individual ontogenetic allometry

Variable (subject)	Isometric slope	Slope	95% CI slope	Intercept	95% CI intercept	r ²	n
Fore Length (1)	0.33	0.328	±0.055	0.348	±0.175	0.973	8
Hind Length (1)	0.33	0.398	±0.051	0.166	±0.163	0.984	8
Fore Mass (1)	3.0	3.404	±0.267	−2.654	±0.372	0.994	8
Hind Mass (1)	3.0	3.528	±0.310	−2.835	±0.444	0.992	8
Fore D (1)	1.0	0.495	±0.099	−0.705	±2.487	0.962	8
Hind D (1)	1.0	0.309	±0.046	2.703	±1.287	0.978	8
Fore R (1)	1.0	0.375	±0.062	4.236	±1.539	0.974	8
Hind R (1)	1.0	0.163	±0.144	8.408	±3.969	0.562	8
Fore Inertia (1)	5.0	4.866	±0.223	−2.427	±0.311	0.998	8
Hind Inertia (1)	5.0	4.719	±0.788	−2.294	±1.129	0.973	8
Fore Length (2)	0.33	0.269	±0.110	0.536	±0.242	0.882	13
Hind Length (2)	0.33	0.332	±0.086	0.399	±0.280	0.895	13
Fore Mass (2)	3.0	2.973	±0.519	−2.095	±0.734	0.949	13
Hind Mass (2)	3.0	3.276	±0.572	−2.547	±0.846	0.949	13
Fore D (2)	1.0	0.368	±0.079	2.611	±2.056	0.925	13
Hind D (2)	1.0	0.263	±0.121	4.324	±3.682	0.73	13
Fore R (2)	1.0	0.351	±0.131	4.489	±3.401	0.897	13
Hind R (2)	1.0	0.221	±0.180	7.036	±5.494	0.679	13
Fore Inertia (2)	5.0	4.294	±0.808	−1.695	±1.142	0.941	13
Hind Inertia (2)	5.0	4.236	±0.486	−1.694	±0.720	0.977	13
Fore Length (3)	0.33	0.337	±0.056	0.307	±0.180	0.955	13
Hind Length (3)	0.33	0.321	±0.074	0.423	±0.241	0.915	13
Fore Mass (3)	3.0	2.814	±0.436	−1.814	±0.613	0.960	13
Hind Mass (3)	3.0	3.665	±0.768	−3.090	±1.130	0.928	13
Fore D (3)	1.0	0.428	±0.114	0.880	±2.962	0.889	13
Hind D (3)	1.0	0.275	±0.056	3.936	±1.665	0.933	13
Fore R (3)	1.0	0.436	±0.135	2.083	±3.488	0.857	13
Hind R (3)	1.0	0.207	±0.088	7.291	±2.650	0.757	13
Fore Inertia (3)	5.0	4.418	±0.707	−1.829	±0.997	0.957	13
Hind Inertia (3)	5.0	4.562	±0.477	−2.154	±0.702	0.981	13
Fore Length (4)	0.33	0.300	±0.085	0.436	±0.272	0.926	8
Hind Length (4)	0.33	0.326	±0.100	0.409	±0.323	0.913	8
Fore Mass (4)	3.0	3.028	±0.534	−2.913	±0.747	0.978	8
Hind Mass (4)	3.0	4.706	±1.588	−3.718	±1.396	0.948	8
Fore D (4)	1.0	0.395	±0.066	1.840	±1.679	0.973	8
Hind D (4)	1.0	0.270	±0.134	4.131	±3.888	0.802	8
Fore R (4)	1.0	0.361	±0.218	4.898	±5.539	0.731	8
Hind R (4)	1.0	0.109	±0.152	10.828	±4.416	0.338	8
Fore Inertia (4)	5.0	4.789	±0.994	−2.337	±1.390	0.959	8
Hind Inertia (4)	5.0	4.675	±0.393	−2.296	±0.573	0.993	8

Note: Values shown in bold differ in their slope compared to the combined-sample analysis. Isometric slope is the slope expected if the variable increases isometrically. Length is regressed on body mass, all other forelimb and hind limb variables are regressed on either forelimb or hind limb length respectively. 95% CI is the 95% confidence limit of the slope and intercept.

massive with age. The only difference between the use of body mass or limb mass as the denominator in the dimensional analysis was in the lower leg (Fig. 5c,d; Table 6). When made dimensionless using limb mass as the denominator, dimensionless leg mass decreases significantly with age.

It is important to consider changes in dimensionless segment masses within the context of changes in segment lengths. Dimensionless arm, forearm, and thigh lengths do not change significantly with age in the infant baboon sample (Table 7). Dimensionless leg length increases significantly with age, while

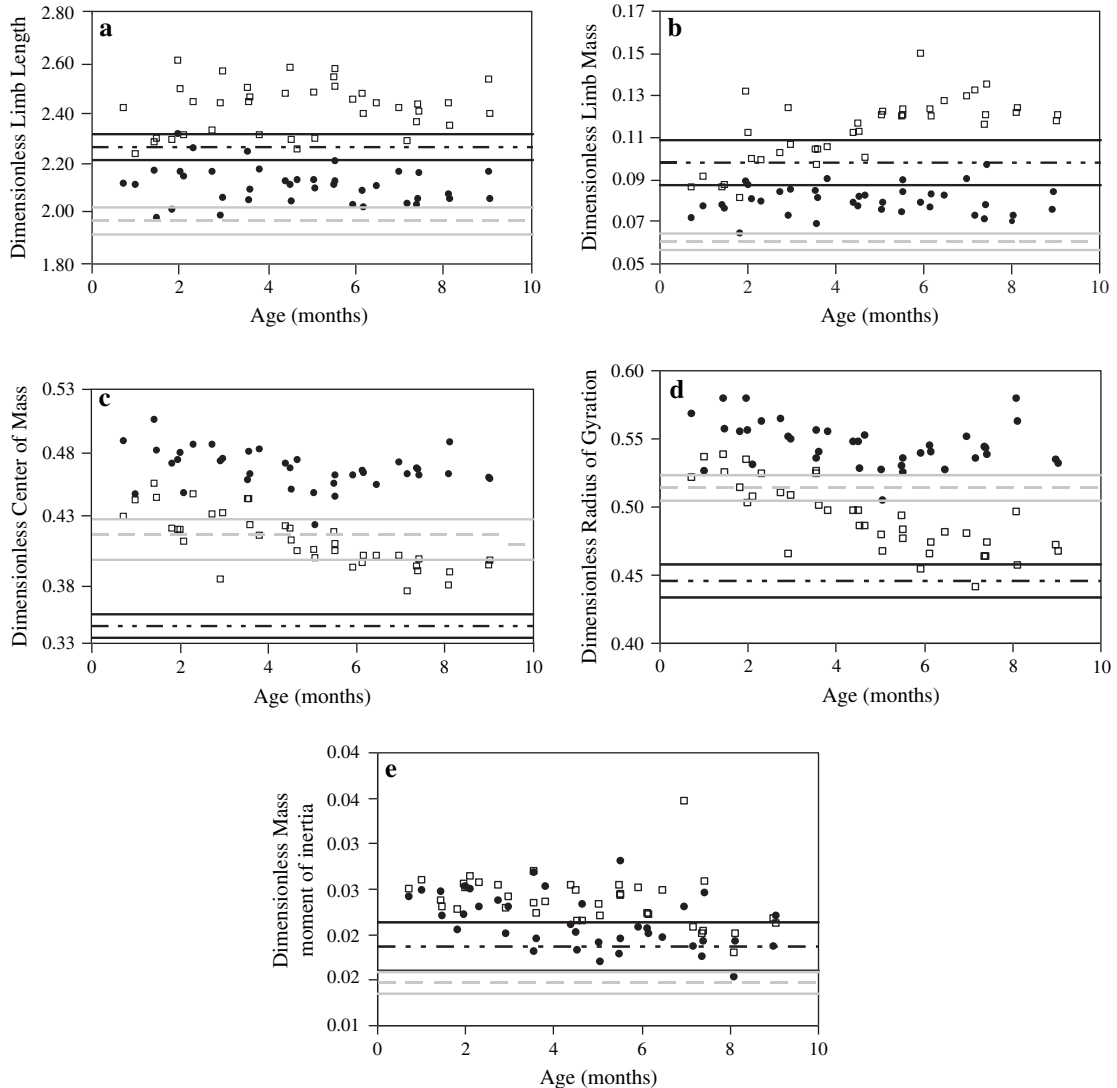


Fig. 4. Dimensionless inertial property changes with age in the infant baboon sample. (a) Dimensionless limb lengths are not correlated with age (see Table 4); (b) dimensionless hind limb mass is positively correlated with age, while forelimb mass is not significantly correlated with age (see Table 4); (c) dimensionless limb center of mass is negatively correlated with age (see Table 4); (d) dimensionless limb radius of gyration is negatively correlated with age (see Table 4); and (e) dimensionless limb mass moments of inertia are negatively correlated with age (see Table 4) in the infant baboon sample. Infant baboon forelimbs are closed circles and infant baboon hind limbs are open squares. Adult baboon values from Raichlen (2004) are shown for comparison. Mean adult hind limb values are indicated by the black dot-dashed line and the 95% confidence limits of the means are indicated by the solid lines above and below it. Mean adult forelimb values are indicated by the grey dashed line and the 95% confidence limits of the means are indicated by the solid lines above and below it. Infant baboons generally have larger limb inertial properties than adults.

dimensionless foot and hand lengths decrease significantly with age (Table 7).

The increase in dimensionless arm and thigh mass with increasing age is therefore not due to

a change in dimensionless segment length. The decrease in dimensionless hand and foot mass may, however, be due to a decrease in dimensionless segment length with increasing age. The

Table 4
Dimensionless inertial property changes with age in infant *Papio* (n = 42)

Variable	Slope	95% CI slope	Intercept	95% CI intercept	r ²	p-value
Forelimb Length	−0.006	±0.010	2.148	±0.050	0.037	0.220
Hind limb Length	0.006	±0.013	2.394	±0.069	0.019	0.388
Forelimb Mass	0.0001	±0.001	0.074	±0.005	0.001	0.816
Hind limb Mass	0.005	±0.001	0.087	±0.008	0.489	<0.0001
Forelimb D	−0.002	±0.002	0.476	±0.010	0.115	0.028
Hind limb D	−0.007	±0.002	0.443	±0.010	0.598	<0.0001
Forelimb R	−0.003	±0.002	0.556	±0.013	0.111	0.031
Hind limb R	−0.009	±0.002	0.532	±0.012	0.606	<0.0001
Forelimb Inertia	−0.001	±0.0004	0.024	±0.002	0.229	0.001
Hind limb Inertia	−0.0004	±0.0004	0.025	±0.002	0.104	0.038

Note: These data represent the regression statistics for the combined-sample of four infants. 95% CI is the 95% confidence limit of the slope and intercept.

decrease in dimensionless leg mass occurs despite an increase in dimensionless leg length with age.

Comparison with *Macaca mulatta* during ontogeny

The comparison of mass distribution changes in the infant baboons with those of *Macaca mulatta* are complicated by the difference in samples. Turnquist and Wells (1994) performed their analysis on a large cross-sectional sample of free-ranging macaques at Cayo Santiago, Puerto Rico, while the baboon sample is longitudinal and captive born and raised. Additionally, because Turnquist and Wells (1994) provided only means and ranges for macaque segment masses, the significance of any interspecific differences cannot be tested. Therefore, the following analyses should be interpreted with caution.

Segment masses as a percentage of limb mass in infant baboons over the sampled developmental period were compared with values from a cross-sectional sample of *Macaca mulatta* from one day to one year of age (data from Turnquist and Wells, 1994). Forelimb segment masses are quite similar in the two samples. Dimensionless arm and forearm masses for infant baboons are within the range of variation found in infant macaques at similar ages (Figs. 6a,b). Dimensionless hand mass appears to drop more steeply in infant baboons compared to infant rhesus macaques, although the baboon values generally fall within the range of variation of the macaque sample (Fig. 6c).

Dimensionless hind limb masses show much greater differences than those of the forelimb. Dimensionless thigh mass rises at a higher rate in the infant baboon sample compared to the infant macaque sample, while both dimensionless leg and foot masses fall at steeper rates in infant baboons compared to infant macaques (Figs. 6e & f).

These differences that begin to appear during ontogeny are reflected in differences in the dimensionless segment masses of adults of these species. Adult *Papio* have significantly heavier arms and thighs compared to adult *Macaca* (95% confidence limits do not overlap; Fig. 7). Adult *Papio* also have significantly lighter forearms, hands and feet (95% confidence limits do not overlap; Fig. 7). *Papio*'s dimensionless leg masses do not differ from those of *Macaca*, although their mean is lower (Fig. 7).

Discussion

The results of this study highlight a proximal migration of limb mass with age in this sample of infant baboons. At older ages, the infant baboons have relatively more proximal centers of mass and radii of gyration and have relatively lower limb mass moments of inertia compared to younger ages. There are, however some minor discrepancies when ontogenetic allometry and the dimensionless inertial properties are examined within each individual. These discrepancies may be attributed to the small intra-individual sample sizes (n = 8 for Infants 1 and 4; n = 13 for Infants 2 and 3). While

Table 5
Intra-individual changes in dimensionless inertial properties with age

Variable (subject)	r	p value	n
Fore Length (1)	0.15	0.73	8
Hind Length (1)	0.73	0.04	8
Fore Mass (1)	0.79	0.02	8
Hind Mass (1)	0.93	<0.0001	8
Fore D (1)	0.34	0.41	8
Hind D (1)	-0.80	0.02	8
Fore R (1)	-0.96	<0.0001	8
Hind R (1)	-0.94	<0.0001	8
Fore Inertia (1)	-0.45	0.26	8
Hind Inertia (1)	0.34	0.42	8
Fore Length (2)	-0.28	0.40	13
Hind Length (2)	-0.12	0.71	13
Fore Mass (2)	-0.45	0.14	13
Hind Mass (2)	0.34	0.27	13
Fore D (2)	-0.59	0.04	13
Hind D (2)	-0.67	0.02	13
Fore R (2)	-0.32	0.31	13
Hind R (2)	-0.61	0.04	13
Fore Inertia (2)	-0.56	0.00	13
Hind Inertia (2)	-0.40	0.02	13
Fore Length (3)	-0.07	0.84	13
Hind Length (3)	-0.14	0.66	13
Fore Mass (3)	-0.27	0.39	13
Hind Mass (3)	0.79	0.002	13
Fore D (3)	-0.14	0.65	13
Hind D (3)	-0.89	0.0001	13
Fore R (3)	-0.16	0.61	13
Hind R (3)	-0.85	0.0005	13
Fore Inertia (3)	-0.17	0.16	13
Hind Inertia (3)	-0.47	0.009	13
Fore Length (4)	0.22	0.59	8
Hind Length (4)	0.05	0.91	8
Fore Mass (4)	0.44	0.27	8
Hind Mass (4)	0.97	<0.0001	8
Fore D (4)	-0.79	0.02	8
Hind D (4)	-0.79	0.02	8
Fore R (4)	-0.70	0.05	8
Hind R (4)	-0.97	<0.0001	8
Fore Inertia (4)	-0.27	0.52	8
Hind Inertia (4)	-0.37	0.36	8

Note: Boldfaced values do not agree with the combined-sample analysis in significance, but do agree in the sign of the correlation coefficient. Values in italics do not agree with the combined-sample analysis in the sign of the correlation coefficients.

some intra-individual trends did not achieve statistical significance, the direction of these trends generally conformed to the combined-sample results. It is also possible that individuals vary in

the development of limb inertial properties. A larger sample of individuals is necessary to examine the amount of individual variation within a taxon.

Although a causal explanation for the proximal shift in limb mass distributions is difficult to determine, the changing functional roles of the limbs during ontogeny may play a role in the development of limb inertial properties. Most of an infant baboon's travel at young ages is performed while riding on its mother (Altmann, 1980). This form of travel likely requires strong manual and pedal grasping abilities. Infant *Papio cynocephalus* are able to climb onto the mother's chest under their own power by their second week of life for ventral riding (Altmann, 1980). During their first few months, infant baboons are, however, able to locomote independently (Altmann, 1980). By three months of age, infant baboons are generally able to cling to their mothers' backs, and do so for any amount of travel (Altmann, 1980). This form of travel presumably reduces an infant's grasping needs, since gravity helps the infant remain on its mother's back.

The third and fourth months of an infant baboon's life are characterized by increasing independence from its mother (Altmann, 1980). Infant *Papio* are able to play, walk, and run in both terrestrial and arboreal settings by this developmental stage (Altmann, 1980). By the fourth month, infant baboons ride on their mothers only for rapid or long journeys, using independent locomotion for all other travel needs (Altmann, 1980). At this same time, however, manual foraging becomes an increasingly important source of nutrients (Altmann, 1998). Baboons' ability to use their hands for fine manipulation of food items is an essential element of their foraging success (Altmann, 1998). Altmann (1998) showed that early foraging success was the best predictor of both survivability to adulthood and reproductive success. Therefore, despite their changing locomotor needs, and the reduced reliance on pedal grasping for transport, infant baboons must maintain fine grasping abilities in their hands.

Based on this discussion, it is likely that the changes in limb mass distribution in the infant baboon sample reflect the changing functional demands placed on the limbs during ontogeny. In

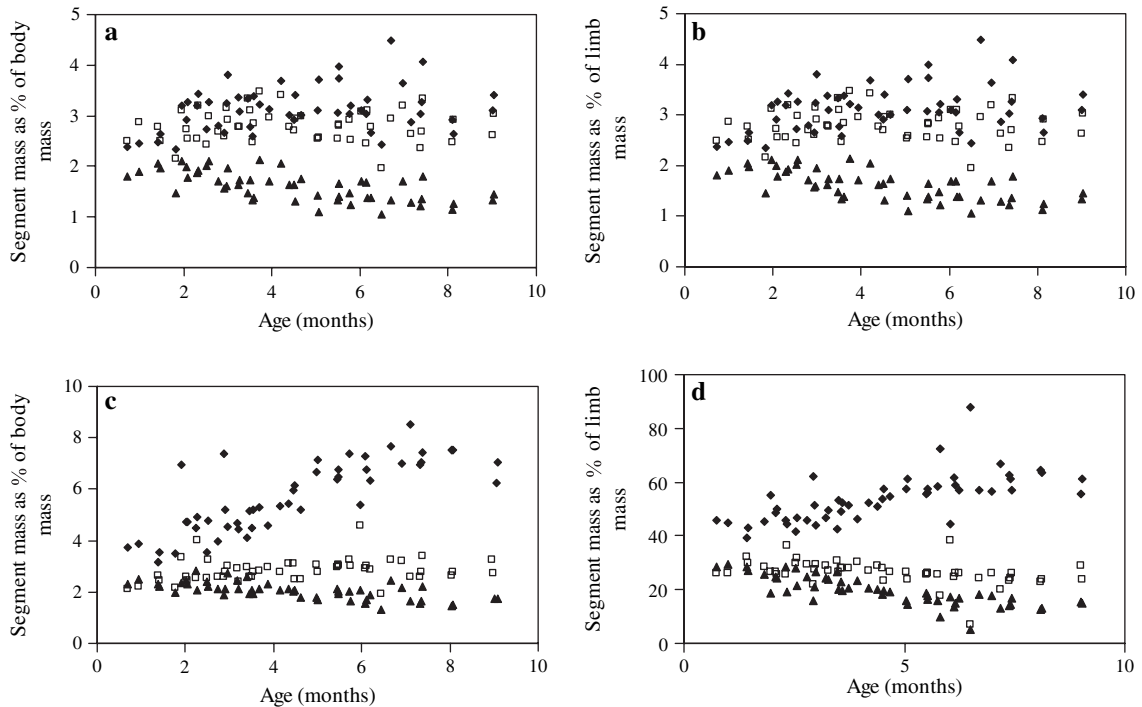


Fig. 5. (a) Forelimb segment masses as a percentage of body mass in the infant baboon sample. (b) Forelimb segment masses as a percentage of forelimb mass in the infant baboon sample. (c) Hind limb segment masses as a percentage of body mass in the infant baboon sample. (d) Hind limb segment masses as a percentage of hind limb mass in the infant baboon sample. In all figures, proximal segments (arm and thigh) are closed diamonds, middle segments (forearm and leg) are open squares, and distal segments (hand and foot) are closed triangles. Correlation coefficients and significance can be found in Table 6. In general, proximal segments are positively correlated with age, middle segments are not correlated with age, and distal segments are negatively correlated with age. The only exception is leg mass as a percentage of hind limb mass, which decreases significantly with age.

previous studies of the ontogeny of limb mass distribution in macaques, it has been shown that limb mass is concentrated most distally at ages when travel is dependent on grasping their mothers' hair (Grand, 1977b, 1981; Turnquist and Wells, 1994). It is during the transition from dependent to independent locomotion that limb mass distributions appear to change drastically (Turnquist and Wells, 1994). Independent quadrupedal locomotion requires strong musculature in the proximal segments of both the hind limbs and forelimbs, and the ontogeny of limb mass distribution in the baboon sample reflects these locomotor needs. Additionally, terrestrial mammals generally maintain light distal limb elements, possibly to reduce the energetic costs of limb swing (see Hildebrand, 1985; Lieberman et al., 2003). The reduction in

infant baboon distal limb mass as locomotor independence increases may also be related to this general mammalian trend.

Comparison of ontogeny in Papio and Macaca

The comparison of dimensionless segment masses in infant baboons and macaques highlights interspecific differences in the ontogeny of limb muscle mass distribution patterns. There are some differences between this study and that of Turnquist and Wells (1994) that do imply caution in interpreting these results. First, the macaque sample in Turnquist and Wells (1994) was larger and cross-sectional, precluding a direct comparison with the data reported here. Second, the macaque sample was free-ranging, while the sample in this

Table 6
Correlations between dimensionless segment masses and age in infant *Papio* (n = 42)

Variable	r	p
Arm/BM	0.31	0.03
FA/BM	0.01	0.93
Hand/BM	-0.66	<0.0001
Thigh/BM	0.80	<0.0001
Leg/BM	0.27	0.06
Foot/BM	-0.67	<0.0001
Arm/FM	0.59	<0.0001
FA/FM	0.15	0.30
Hand/FM	-0.75	<0.0001
Thigh/HM	0.69	<0.0001
Leg/HM	-0.39	0.005
Foot/HM	-0.80	<0.0001

Note: BM refers to body mass; FA refers to forearm; FM refers to forelimb mass; HM refers to hind limb mass.

study was captive born and raised. The differences in rearing environment may have some impacts on growth and development (see Suzuki et al., 2001). The rearing environment for the infant baboons did, however, include simulated arboreal supports and surrogates to cling to, allowing them to utilize locomotor behaviors similar to those used in the wild. Despite these sample differences, the comparison between taxa suggests that there are fundamental differences in the development of limb mass distribution patterns that may, in part, be related to differences in substrate use.

Although dimensionless forelimb segment masses are similar across the sampled ages, the proximal hind limb becomes relatively more massive in infant baboons, and the distal hind limb segments become relatively lighter compared to macaques. Because detailed data on the

Table 7
Correlations between dimensionless segment lengths and age in the infant *Papio* sample (n = 42)

Variable	r	p
Arm	0.02	0.87
Forearm	-0.21	0.12
Hand	-0.50	<0.0001
Thigh	0.20	0.14
Leg	0.33	0.01
Foot	-0.40	0.002

Note: Length variables were made dimensionless by dividing them by the cube root of body mass.

ontogeny of positional behavior do not exist for *Papio cynocephalus*, it is difficult to draw strong conclusions on how the changing functional demands on the limbs of these taxa could lead to divergent ontogenetic trajectories. Because the timing of the transition to independent locomotion is similar in macaques and baboons (approximately 4–6 months; Altmann, 1980; Turnquist and Wells, 1994), inter-specific differences in the ontogeny of limb inertial properties may simply be necessary to achieve adult mass distributions. Adult baboons have heavier proximal segments, and generally lighter distal segments compared to adult macaques that are likely related to slight differences in substrate use (Rose, 1973; Fleagle, 1998). Differences in the rates of change of segment masses during ontogeny may therefore lead to the diversity of adult primate limb mass distribution patterns in taxa that differ widely in substrate preference. The fact that differences in growth rates are apparent in taxa that show only slight variation in their use of arboreal supports suggests that larger differences should be apparent in taxa that are mostly or fully arboreal compared to the species sampled here.

Conclusions

The hypothesis that infant baboons will have a proximal shift in the mass distributions of both the forelimb and hind limb is strongly supported by the results of this study. Changes in limb mass distributions in infant baboons appear to be associated with changes in functional demands placed on their limbs. Comparisons between the infant baboon sample and adult baboons indicate that by 9 months of age, infants have not yet reached an adult limb mass distribution pattern. The trends for all inertial properties are, however, leading the infant baboons to adult patterns. Even though infant baboons are locomoting independently very early in life, their locomotor musculature is still developing into their late infancy.

Despite this discussion of the changing functional demands on the limbs during ontogeny, the exact reasons infants have large distal elements remain unclear. It is possible that mass is distal at

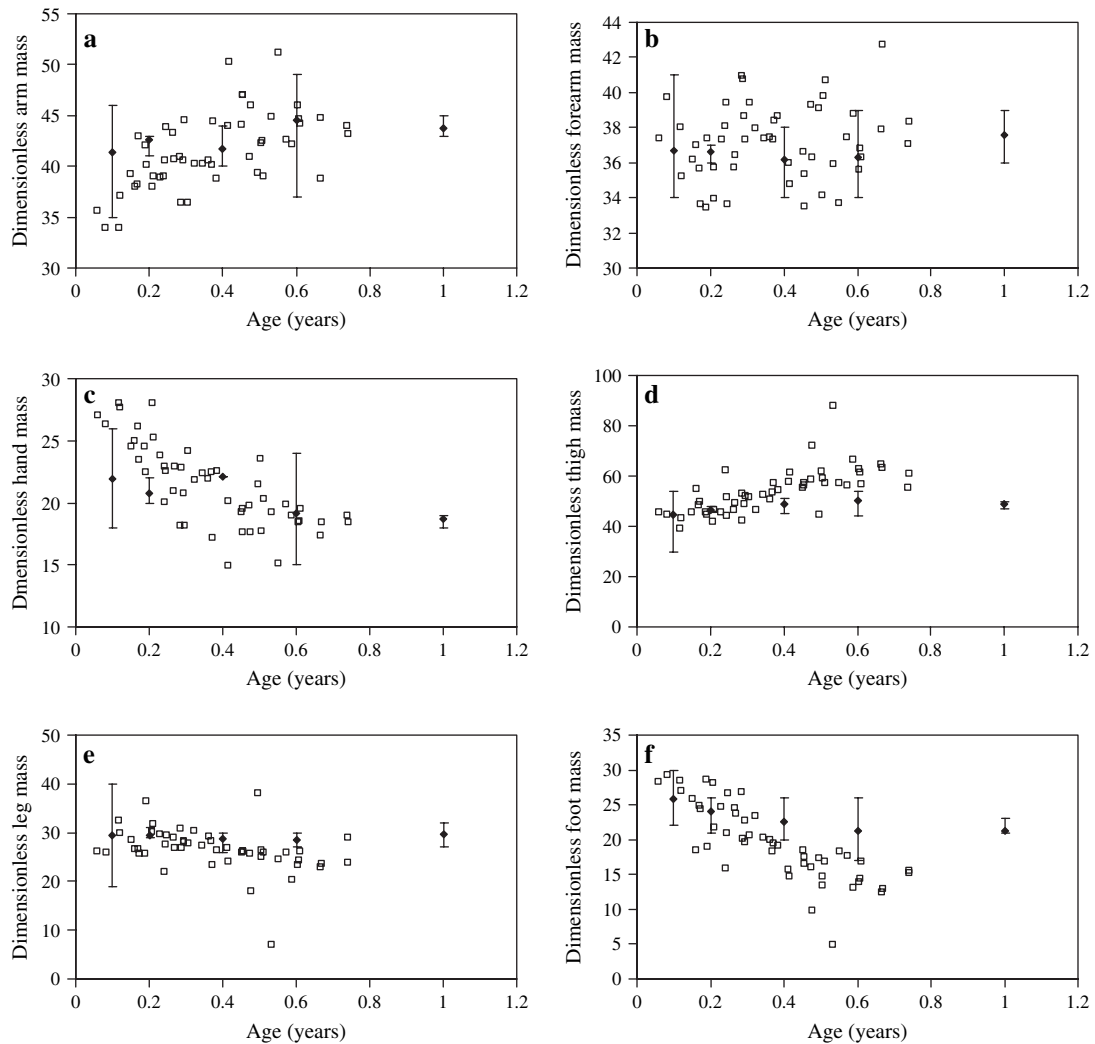


Fig. 6. Segment masses in infant baboons and infant macaques. (a) Comparison of infant baboon arm masses as a percentage of forelimb mass, (b) forearm masses as a percentage of forelimb mass, (c) hand masses as a percentage of forelimb mass, (d) thigh masses as a percentage of hind limb mass, (e) leg masses as a percentage of hind limb mass, and (f) foot masses as a percentage of hind limb mass with those of infant *Macaca* (data from Turnquist and Wells, 1994). Infant baboon values are open squares, mean values of *Macaca* at each age are closed diamonds, bars represent the range for infant *Macaca* at each age.

young ages to facilitate strong grasping of the mother's hair. It is also possible that these primates exhibit a primitive primate or mammalian developmental pattern. To further test the relationships between grasping hands and feet, limb mass distribution, and the ontogeny of locomotion, it is necessary to examine a broad comparative sample of infants that have a variety of functional

demands placed on their limbs during development. Especially important to include are primate taxa that do not cling to their mothers as infants (see Ross, 2001, for review). Many strepsirhines carry their infants orally and either park or nest them (e.g., *Daubentonia*, *Varecia*, *Cheirogaleus*, *Microcebus*, *Lepilemur*, *Galago*, *Otolemur*, *Tarsius*, *Hapalemur*; see Ross, 2001). A more complete test

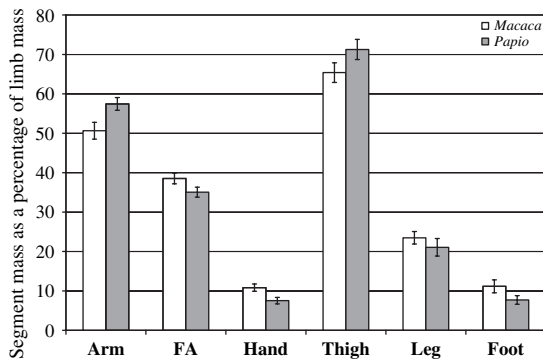


Fig. 7. Comparison of dimensionless segment masses in adult *Macaca* ($n = 8$) and *Papio* ($n = 9$). Segment masses as a percentage of limb mass are shown here for adult *Papio* in gray (from Raichlen, 2004) and for adult *Macaca* in white (from Grand, 1977a). Bars are 95% confidence limits of the means for each segment.

of the relationship between early grasping behaviors and muscle mass distribution would include an examination of these taxa.

This study provides comparative data suggesting that differences in adult primate limb mass distribution patterns associated with terrestrial and arboreal locomotion are the result of differences in growth trajectories. A greater understanding of the range of primate limb mass distribution patterns can be achieved by combining these data with more detailed behavioral studies of primate locomotor ontogeny. Linking morphological variation to life history patterns will provide a more complete representation of primate diversity.

Acknowledgements

I thank Liza Shapiro for her help and guidance during this project and in the preparation of this manuscript. Thanks also to John Kappelman, Susan Larson, Deborah Overdorff, Marcus Pandy, and Daniel Lieberman for their helpful discussions on this project and this manuscript. Thanks to Jerry Finig and the staff of the University of Texas at Austin Animal Resource Center for their help in caring for the baboon sample. Thanks to Karen Rice and Dee Carey for their help in facilitating the use of infant baboons for this study. Madgalena

Muchlinski and Katherine Whitcome provided help with animal care that was very appreciated. The comments of Adam Gordon, Robert Scott, Daniel Schmitt, Brian Richmond, and two anonymous reviewers greatly improved this manuscript. This project was supported by the L.S.B. Leakey Foundation and by NSF BCS-0313821.

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