



# Ontogenetic adaptation to bipedalism: age changes in femoral to humeral length and strength proportions in humans, with a comparison to baboons

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## Abstract

The increase in lower/upper limb bone length and strength proportions in adult humans compared to most other anthropoid primates is commonly viewed as an adaptation to bipedalism. The ontogenetic development of femoral to humeral proportions is examined here using a longitudinal sample of 20 individuals measured radiographically at semiannual or annual intervals from 6 months of age to late adolescence (a subset of the Denver Growth Study sample). Anthropometric data (body weights, muscle breadths) were also available at each examination age. Results show that while femoral/humeral length proportions close to those of adults are already present in human infants, characteristically human femoral/humeral diaphyseal strength proportions only develop after the adoption of bipedalism at about 1 year of age. A rapid increase in femoral/humeral strength occurs between 1 and 3 years, followed by a slow increase until mid-late adolescence, when adult proportions are reached. When age changes in material properties are factored in, femoral strength shows an almost constant relationship to body size (body mass·bone length) after 5 years of age, while humeral strength shows a progressive decline relative to body size. Femoral/humeral length proportions increase slightly throughout growth, with no apparent change in growth trajectory at the initiation of walking, and with a small decline in late adolescence due to later growth in length of the humerus. A sex difference in femoral/humeral strength proportions (females greater) but not length proportions, develops early in childhood. Thus, growth trajectories in length and strength proportions are largely independent, with strength proportions more responsive to actual changes in mechanical loading. A cross-sectional ontogenetic sample of baboons (n=30) illustrates contrasting patterns of growth, with much smaller age changes in proportions, particularly strength proportions, although there is some indication of an adaptation to altered limb loadings early in baboon development.

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## Introduction

An association within primates between locomotor mode and the relative lengths of the fore and hindlimb bones has long been recognized (Schultz, 1937; Erikson, 1963; Napier and Napier, 1967; Jungers, 1985). Intermembral differences in limb bone circumferences (Schultz, 1953) and strengths (Schaffler et al., 1985; Demes and Jungers, 1993; Connour et al., 2000; Ruff, 2002) have also been related to locomotion. Within this context, it is natural that changes within the hominin lineage in the relative size of the upper and lower limb bones have been viewed as key markers in the evolution of bipedalism (McHenry, 1978; Johanson et al., 1982; Jungers, 1982; Wolpoff, 1983; Hartwig-Scherer and Martin, 1991; McHenry and Berger, 1998; Asfaw et al., 1999; Richmond et al., 2002). However, despite some recent advances in developmental genetics (Hamrick, 2001; Hallgrímsson et al., 2002), relatively little is known about the specific mechanical or other factors that contribute to differentiation of upper and lower (or fore and hind) limb bone dimensions during growth in humans or other

primates. Such information is critical for functional and phylogenetic interpretations of fossil limb bone proportions (Ward, 2002).

Modern human adults are distinct from most other primates in having relatively very long and strong lower limb bones compared to upper limb bones (Schultz, 1953; Jungers, 1985). Fig. 1 compares femoral to humeral proportions in maximum length and section modulus (a measure of bone strength—see below) in a sample of 100 modern humans and 179 nonhuman catarrhines (all adults). Species in the nonhuman sample include all of the great and lesser apes, three cercopithecines, and four colobines (Ruff, 2002); humans are a mixed Amerindian/East African sample representing a diversity of body shapes (Ruff, 1995, 2000). Confirming earlier studies, human adults have longer femora relative to humeri than the great majority of other catarrhines (Fig. 1A), overlapping in proportions only with some colobines (*Presbytis rubicunda*, *Trachypithecus cristata*, and *Colobus guereza*) who engage in frequent leaping behavior (Ruff, 2002) (*P. rubicunda*, the most specialized leaper, actually exceeds humans in femoral/humeral length proportions). Human

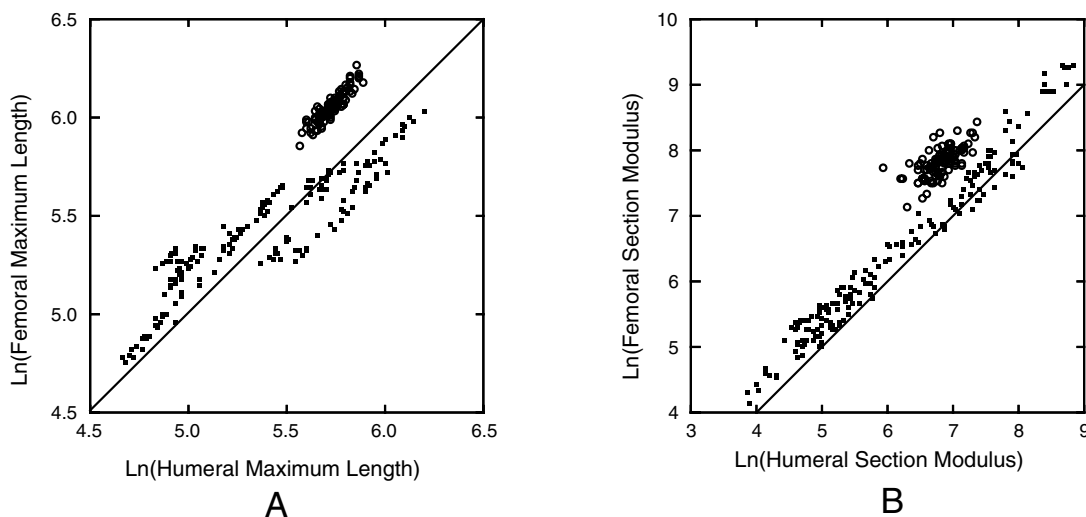


Fig. 1. Femoral to humeral length (A) and strength (B) proportions in 100 modern humans (open circles) and 179 nonhuman catarrhines (filled squares). Human sample from Ruff (1995); nonhuman primates from Ruff (2002). Femoral polar section modulus determined at midshaft, humeral polar section modulus at 40% of bone length from the distal end (see text and Ruff, 2002, for definitions). All data natural log-transformed. An isometric line of equivalence between femoral and humeral dimensions is plotted for reference. Note that data overlap obscures some individual points in both human and nonhuman samples.

adults also have stronger femora relative to humeri than almost all other nonhuman primates in this sample (Fig. 1B), again overlapping slightly only with some colobines (*P. rubicunda* and *C. guereza*) as well as mountain gorillas (*Gorilla gorilla beringei*), the least “forelimb dominant” of the apes (Ruff, 2002). Interestingly, while there are many significant interspecific differences in intermembral proportions between primate species (e.g., see Jungers, 1985; Ruff, 2002), *within* all of the species included here both length and strength proportions are isometric, i.e., the log–log reduced major axis slopes within species are nonsignificantly different from 1.0.

While comparisons such as those shown in Fig. 1 can delineate patterns of variation in adult individuals and suggest possible locomotor correlates, more information on the determinants of such differences can be obtained by examining ontogenetic trajectories. For example, in terms of bone lengths, it is known that interspecific differences in intermembral proportions develop prior to birth, presumably before any direct locomotor-related mechanical effects (Scammon and Calkins, 1929; Lumer, 1939; Schultz, 1973; Buschang, 1982b) (although differential muscular action can affect long bone growth even in utero [Hall and Herring, 1990]). However, some intermembral proportional differences between species are increased or exaggerated via differential postnatal growth of the limbs, during which they are used for locomotion (Lumer, 1939; Schultz, 1973; Buschang, 1982b; Jungers and Hartmann, 1988). Thus, it is possible that development of adult intermembral length proportions is in part dependent on normal mechanical usage of the limbs. (Additional studies bearing on this issue are reviewed in the Discussion.) Characterization of ontogenetic trajectories is also important for interpreting juvenile fossil remains, especially when those remains are evaluated within the context of adult comparative samples (Ruff and Walker, 1993; Richmond et al., 2002; Ruff, 2002; Ruff et al., 2002). More generally, analysis of ontogenetic data can give important insights into the timing of life history events and their evolution (Smith, 1993; Leigh, 1996; Bogin, 1999).

While limb bone length proportions have been included in a number of ontogenetic studies (Lumer, 1939; Gavan, 1971; Schultz, 1973; Jungers and Fleagle, 1980; Shea, 1981; Buschang, 1982a,b; Jungers and Susman, 1984; Jungers and Hartmann, 1988), other limb bone dimensions have received relatively little attention. Growth in bone breadths of individual long bones has been documented radiographically in living humans (Maresh, 1961, 1966; Johnston and Malina, 1966; Malina and Johnston, 1967; Tanner et al., 1981); however, none of these studies specifically examined proportional changes in upper to lower limb dimensions. In addition, none included actual bone strength measures (i.e., section moduli). Only one study to date has examined intermembral proportional changes in such properties (Sumner and Andriacchi, 1996), and it was of an archaeological sample. While this study produced some very interesting results, discussed later in this paper, it was by necessity limited in several respects—relatively small sample sizes within age groups, especially in adolescence, possible bias due to differential survival, imprecise age estimates, no sex assessments prior to adolescence, and no soft tissue measurements for comparison (e.g., muscle breadths, body mass). In addition, of course, like almost all of the in-vivo studies (with the exception of Tanner et al., 1981), this study was cross-sectional rather than longitudinal in design, further increasing chances for nonrandom sampling of different age group categories.

The present study employs a longitudinal sampling of children derived from the Denver Growth Study sample (McCammon, 1970) to examine ontogenetic changes in femoral to humeral length and strength proportions in humans from infancy to late adolescence. The Denver sample has been used for a number of skeletal growth studies (Maresh, 1970, and references therein; Pritchett, 1988, 1992), although, aside from Buschang's brief analyses (Buschang, 1982a,b), not for the study of upper to lower limb bone proportions per se. Bone dimensional data were obtained from radiographs taken as part of the original study. In addition, muscle breadths and body weights for the same individuals were obtained from the study archives. Because dimensions were available both prior to

the initiation of walking as well as during the early period of bipedal support, they can be used in a kind of “natural experiment” to study the effects of a relatively abrupt change in locomotor patterns on intermembral proportions. The use of the same individuals throughout the entire age range also largely eliminates the problem of nonrandom sampling within age groups. Correlations between individual growth velocities in bone, muscle, and body size parameters in this sample have been reported elsewhere (Ruff, 2003). The present study is mainly concerned with mean trends in intermembral proportions throughout growth, although comparisons between males and females are also carried out. In addition, comparisons are carried out between this sample and an ontogenetic sample of baboons, which can be taken as a quadrupedal “baseline” against which to compare the effects of bipedalism. Some preliminary analyses of this latter sample have been presented previously (Ruff, 2002, 2003).

## Materials and methods

### *Samples*

The Denver Growth Study was carried out between 1927 and 1967 (McCammon, 1970), although all of the individuals included here were measured after 1940. Subjects in the study were of European ancestry and of middle to upper middle-class socioeconomic status. They were examined from two months of age until late adolescence/early adulthood, at 2-month intervals to six months, semiannually from six months to mid-adolescence, and annually thereafter. As part of the examination, a battery of anthropometric measurements were taken, as well as radiographs of the chest and extremities (Hansman, 1970; Maresh, 1970). Twenty individuals—10 males and 10 females—with relatively complete radiographic records for the extremities were identified from among the archived radiographs housed at the Lifespan Health Research Center of the Wright State University School of Medicine (Dayton, Ohio). All individuals had at least one measurable femoral and humeral radiograph at six months of

age or earlier, and a radiographic record through at least 17 years of age (in one case, a female, through 16.5 years).

Missing data—due either to a missing examination or an unusable radiograph (see below)—were estimated through linear interpolation (averaging) over adjacent examinations. This is justified given the close temporal spacing of the data and visual inspection of resulting individual age curves, which indicated approximate linearity over these short intervals. The total number of missing data estimated through interpolation was 7% for the femur, and 14% for the humerus. In no case were any data estimated through extrapolation, i.e., at the beginning or end of an individual’s age range. Because data prior to 6 months of age were some of the most frequently missing (and would usually necessitate extrapolation to estimate), only data from six months and older were used here. After 14 years of age progressively smaller subsets of the study sample had data available for semiannual examinations. Therefore, to avoid differential sampling within age intervals, only annual (i.e., 15, 16, and 17 year) data were included in this age range. As noted earlier, in one individual the last examination was at 16.5 years; this was used as the 17 year data point for this person. Fourteen of the 20 individuals in the sample, evenly divided by sex, had usable radiographs from examinations beyond 17 years, with the last examination ranging in age from 18 to 21.5 years (mean, 19.0 years). To include these older data in the comparisons, the mean difference in measurement values between the 17 year and oldest available examination was calculated for these 14 individuals, then used along with mean 17 year values for the total sample to estimate mean “19 year old” data values for the sample. For sex-specific analyses, sex-specific values were used in the same procedure. Thus, a total of 32 age points were included in the study, taken at 6 month intervals from 6 months to 14 years and at yearly intervals from 14 to 17 years, plus the 19 year old data point. All 20 individuals in the sample are represented at each age point (except 19 years).

The sample of baboons (*Papio cynocephalus*) used for comparison was derived from the collections of the Department of Mammology, Kenya

National Museums. All were wild-shot, and originate from southern Kenya (near Kibwesi). A total of 40 individuals were measured (Ruff, 2002); of these, 30 were used here, including juveniles and young adults. Juveniles were aged using baboon dental eruption standards (Reed, 1967; Phillips-Conroy and Jolly, 1988; Kahumbu and Eley, 1991). Twenty individuals (10 males and 10 females) had at least one unfused long bone epiphysis and were used previously as a juvenile sample (Ruff, 2002); this sample ranged in age from 7 months to 7.5 years. Three additional individuals had fused epiphyses but not fully erupted dentitions, and could be aged to 6.7 years (a female), 8 and 10 years (males). Seven other individuals (4 males and 3 females), had fully erupted dentitions but very little dental wear (similar to that of the oldest “dental juveniles”); these were assigned an arbitrary age of 10 years. Body weights were available for all individuals. All long bone epiphyses were present and were used to reconstruct maximum bone lengths. Bone structural properties were determined from direct and computed tomographic measurements, as described previously (Ruff, 2002).

### *Measurements*

As described in the original reports for the Denver Growth Study (Maresh, 1943, 1955), A-P radiographs of the limbs were taken using a long tube-film distance (2.3 meters) to minimize radiographic distortion. Remaining radiographic enlargement of bone (and muscle—see below) breadths was estimated using information presented in Green et al. (1946), adjusted for differences in tube-film distance, as described in detail elsewhere (Ruff et al., 2002). Proper (A-P) orientation of radiographs was ascertained by observing the position of bony landmarks such as the medial and lateral humeral epicondyles; films with evidence of significant rotation were not measured.

The location of bone cross sections for measurement were based on percentages of bone length and are the same as those described previously for the samples shown in Fig. 1 (Ruff, 2000, 2002): at 50% (midshaft) of bone length for the femur, and at 40% of bone length from the distal end of the

humerus. “Bone length” here refers to the distances parallel to the diaphyseal longitudinal axis from the average distal projection of the femoral condyle surfaces to the superior surface of the femoral neck, and from the lateral lip of the trochlea to the superior surface of the humeral head (see Ruff, 2002 for illustrations). Given the individual rate of development of femoral and humeral epiphyses, these dimensions could be directly determined (with some slight estimation of missing contours) beginning between 3 and 6 years of age. Prior to this age, section locations were located relative to diaphyseal length. To find homologous positions for these bones, locations relative to both diaphyseal length and bone length were first determined in radiographs of 3–6 year old children. The 50% and 40% of bone length locations were found to correspond to an average of 45.5% and 41% of diaphyseal length (from the distal end) for the femur and humerus, respectively, with a relatively narrow ( $\pm 1\%$ ) range of variation. These locations were then used for measuring the youngest children. Maximum bone lengths, measured analogously to in-vitro measurements of dry bones, i.e., not necessarily parallel to the diaphyseal long axis, were also taken when possible given epiphyseal development. For younger individuals, maximum lengths were estimated from diaphyseal lengths using the mean ratio between the two in individuals where both could be measured: for the femur, 1.10 ( $\pm 0.01$  SD), and for the humerus, 1.08 ( $\pm 0.01$  SD). All length measurements were taken to the nearest mm using a clear ruler.

A clear acetate template with marked longitudinal and transverse lines was placed over each radiograph, aligned with the long axis of the diaphysis, and positioned so that the transverse line corresponded to the correct location as described above. Total subperiosteal and cortical breadths were then measured along the transverse line with sharp-tipped digital calipers to the nearest 0.01 mm. Medullary breadth (M) was calculated as the total subperiosteal (T) minus summed cortical breadths.

Mechanical loading of limb bone diaphyses is dominated by bending (Rubin and Lanyon, 1982); thus, structural properties that reflect average

bending strength are the most appropriate for evaluating mechanical adaptations during growth and development. The polar moment of inertia,  $J$ , is proportional to (twice) average bending rigidity (and also torsional rigidity in sections that do not depart too radically from circularity), and can be calculated as  $\pi/32 \cdot (T^4 - M^4)$  (Timoshenko and Gere, 1972), assuming circularity in shape. The polar section modulus,  $Z_p$ , a measure of (twice) average bending strength, (or torsional strength) can then be calculated as  $J/(T/2)$ . While bone cross sections are not perfectly circular, violation of this assumption for the femoral 50% and humeral 40% locations is not too severe, at least on average. Comparison of section moduli calculated about A-P and M-L axes in these regions of the femur and humerus in two archaeological juvenile samples where they could be directly measured (Ruff et al., 1994; Sumner and Andriacchi, 1996) give mean A-P/M-L ratios between 0.95 and 1.03 (a ratio of 1.0 would indicate equivalent A-P and M-L bending strength) (Ruff, 2003). This issue is addressed again later in the Discussion, where a comparison of results with those of Sumner and Andriacchi (1996) is given.

Bending and torsional loads should be proportional to the product of a force and a distance (moment arm), which for the mid-regions of long bone diaphyses can provisionally be estimated to be proportional to body weight·bone length (Selker and Carter, 1989; Polk et al., 2000; Ruff, 2000). This was used as an index of body “size” in analyses of bone strength relative to size.

Measurement error was assessed through remeasurement of two individuals at ten age intervals from infancy to adolescence, several weeks after the first measurement. The mean difference between measurements was <0.5% for bone lengths, <1% for subperiosteal breadths, <5% for cortical breadths (except <7.5% for medial humeral cortical breadth), and about 3% for the calculated section moduli.

Body weight (mass) and limb tissue breadths, the latter measured from radiographs by the original investigators (Maresh, 1961, 1970), were obtained from the Denver Growth Study computer archives (Siervogel, pers. comm.). Limb tissue breadths had been taken at mid-femur level

and at maximum external breadth of the forearm. No comparable measurements of the (upper) arm were available. However, correlations between muscle areas at maximum forearm breadth and in the mid-arm in children are high ( $r=0.72-0.91$ ) (Boye et al., 2002); thus, the forearm measurement here will be taken to be representative of arm muscularity as well. From total limb, fat, muscle, and external bone breadths measured in the same planes, muscle cross-sectional areas could be calculated, again assuming a cylindrical geometry. While this assumption is certainly questionable, especially for the forearm (no equivalent arm measurements were available), the general shape, and thus departure from circularity, of soft tissue in these regions is probably reasonably consistent between individuals and age groups. All bone and muscle measurements are reported in mm (areas in  $\text{mm}^2$ , section moduli in  $\text{mm}^3$ ), and body mass in kg.

#### *Statistical analysis*

The great majority of previous studies have used log–log bivariate linear regressions of one limb against another to examine and compare ontogenetic trajectories in proportions (Lumer, 1939; Gavan, 1971; Jungers and Fleagle, 1980; Shea, 1981; Buschang, 1982a,b; Jungers and Susman, 1984; Jungers and Hartmann, 1988). Fig. 2 shows such bivariate plots for femoral and humeral lengths (A) and femoral and humeral section moduli (B) in the Denver sample, using the means (of individual log-transformed data) for each age point as input. An isometric line of equivalence (femur=humerus) is also given in each plot for reference. Both trajectories show significant positive allometry (reduced major axis slopes of  $1.089 \pm 0.005$  and  $1.330 \pm 0.015$  for lengths and section moduli, respectively, both  $p < 0.0001$  relative to 1.0), indicating greater overall growth of the femur than the humerus, consistent with human bone length data reported previously (Buschang, 1982a,b; Jungers and Hartmann, 1988) (Buschang, in fact, used bone lengths derived from the Denver Growth Study sample for his analyses.) The age trend for length proportions (Fig. 2A) appears approximately linear, except for the uppermost

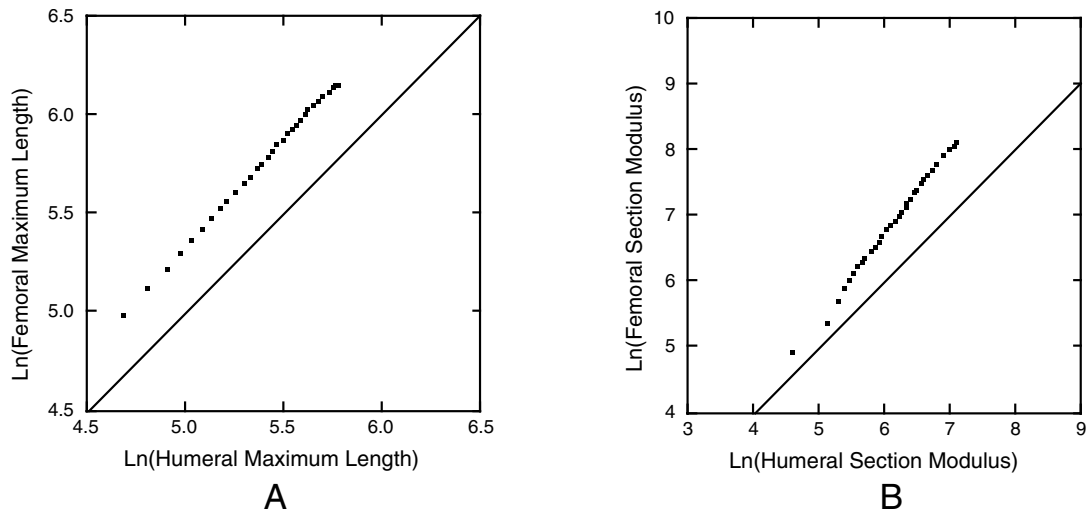


Fig. 2. Femoral to humeral maximum length (A) and section modulus (B) in the Denver Growth Study sample. Each point represents a mean age group value from 6 months to 19 years of age. Lines indicate (isometric) equivalence between femur and humerus.

data points (but see below). However, the age trend for strength proportions (Fig. 2B) is obviously non-linear, with an especially strong deviation from linearity between the first two data points (6 months and 1 year of age) and the subsequent four points (1.5 to 3 years). This, in combination with a higher slope thereafter (RMA slope for 3–19 years =  $1.291 \pm 0.011$ ), accounts for the relatively much greater age change in section modulus proportions than in bone length proportions from infancy through adolescence. The distributions in Fig. 2 make an interesting comparison to those in Fig. 1, suggesting that the distinctive bone strength proportion in human adults is not present in infants and only develops during growth, while bone length proportional differences between humans and most nonhuman catarrhines are always present to some degree (this contrast is addressed again below in the comparisons to the ontogenetic baboon sample). Again, the result for bone lengths here is consistent with previous observations (Schultz, 1973; Buschang, 1982a,b; Jungers and Hartmann, 1988).

While bivariate linear regression analyses can thus provide some insights into ontogenetic trajectories, a more detailed and interpretable description of proportional age changes, including irregular, nonlinear changes, can be obtained by

examining age trends in individual properties and in ratios between properties. This is the approach used in the remainder of this study. Because the principal aim here is to investigate the ontogenetic development of the relatively larger human lower limb, log ratios of femoral to humeral properties are calculated. Log ratios (i.e.,  $\log$  [femur/humerus]) are appropriate for examining proportional differences where the baseline for comparison is isometry (Ruff, 2002); this approach is supported by the intraspecific results for adults shown earlier (see above). Use of logged data also preserves proportionality over different size ranges. For example, in both functional and morphological senses, change in a ratio from 0.7 to 0.8 is much more significant than change in a ratio from 1.7 to 1.8. This is reflected in the log ratios, where the former change is more than twice that of the latter change, but not in the raw ratios, where the two changes are viewed as equivalent. In terms of individual properties (not ratios), plots of log-transformed data provide a visual assessment of the specific (percentage) as opposed to absolute growth rate for each property (see Shea, 1985).

In the following analyses, (natural) logged values are calculated for each individual in the sample, and means of these values for each of the 32 age groups are then plotted against

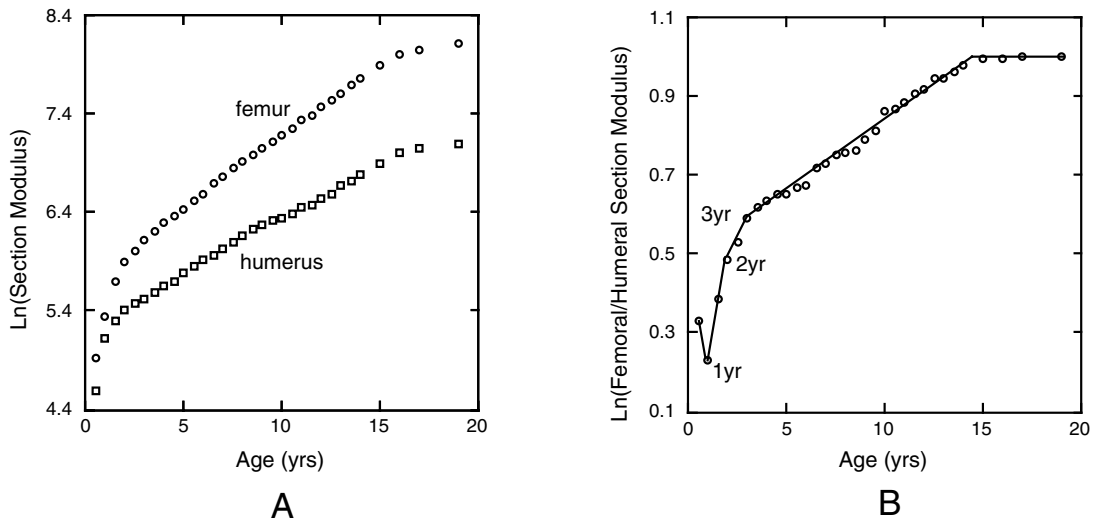


Fig. 3. Femoral and humeral section modulus changes with age in the total combined sex sample: A) age changes in each bone (circles: femur; squares: humerus); B) age changes in femoral/humeral ratio. Lines in B indicate approximately linear regions of change (ages of inflection points in early development indicated). See Table 1a for regression statistics.

chronological age. This provides a convenient method to examine proportional changes relative to developmental landmarks, such as the initiation of walking or the onset of adolescence. As shown in these plots, age changes in many proportions are approximately linear over particular age ranges, with clearly defined inflection points. To better visualize results graphically, linear trend lines (fit by eye) are included in the plots where appropriate. For statistical comparison of growth changes in proportions, least squares linear regressions<sup>1</sup> of lower to upper limb ratios against age are also calculated for each of these age regions (those including at least three age points), in two ways. First, lines are fit through the means for each age group. Second, lines are fit through the data points for each individual, and the mean of the resulting 20 slopes is calculated. As shown below, the two methods yield almost identical results. ANCOVA, using individual data, is used to compare the sexes across multiple age groups while controlling for age. Because they were derived from a reduced data set, the 19 year old data

<sup>1</sup> Use of least squares rather than a model II regression method (such as reduced major axis) is justified here, since: a) the independent variable (age) is measured without error, and b) proportions are clearly dependent on age, i.e., growth.

points are not included in regression analyses or ANCOVAs.

Paired *t*-tests are used for comparisons of individual data involving only two age points, or for comparisons between the upper and lower limbs within a single age group. Two sample *t*-tests are used to compare the sexes within single age groups. Means and standard deviations of properties for each age group are also given in tabular form in the Appendix for the total sample and by sex. All statistical analyses and data plotting were carried out using SYSTAT (SYSTAT: Statistics, 1990).

## Results

### *Section moduli*

Age trends in femoral and humeral section moduli for the total combined sample are shown in Fig. 3, both separately by bone (A) and as a femoral/humeral ratio (B). Regression statistics are given in Table 1a. Between 6 months and 1 year of age the humerus increases in strength faster than the femur, resulting in a significant decline in the femoral/humeral ratio ( $p < 0.05$ , paired *t*-test). This trend abruptly reverses after 1 year of age, the approximate average age of onset of unassisted

Table 1a

Least-squares linear regression slopes, lower to upper limb section modulus proportions on age

Age range (yrs)	Femoral/Humeral Section Modulus			
	Means <sup>a</sup>		Individuals <sup>b</sup>	
	slope	SE	slope	SE
1.0–2.0	0.2526	0.0328	0.2511	0.0314
2.0–3.0	0.1069	0.0115	0.1044	0.0222
3.0–15.0	0.0356	0.0008	0.0358	0.0038
15.0–17.0	0.0005*	0.0010	0.0026*	0.0133

<sup>a</sup>Calculated from age group means. SE=standard error of slope through age group means.<sup>b</sup>Mean of individual slope values (n=20). SE=standard error of individual slope values.

\*Non-significantly different from 0 (p&gt;0.05).

Table 1b

Least-squares linear regression slopes, lower to upper limb maximum length proportions on age

Age range (yrs)	Femoral/Humeral Maximum Length			
	Means <sup>a</sup>		Individuals <sup>b</sup>	
	slope	SE	slope	SE
0.5–5.0	0.0137	0.0007	0.0146	0.0018
5.0–12.5	0.0062	0.0002	0.0062	0.0007
12.5–17.0	–0.0038	0.0004	–0.0038	0.0011

<sup>a</sup>Calculated from age group means. SE=standard error of slope through age group means.<sup>b</sup>Mean of individual slope values (n=20). SE=standard error of individual slope values.

walking (Burnett and Johnson, 1971; Hensinger, 1986; Stanitski et al., 2000). The pace at which growth in femoral strength outstrips that in humeral strength is highest just after this, between 1 and 2 years of age (see Table 1a), and is due to a large reduction in the rate of humeral growth (Fig. 3A). The ratio of femoral/humeral strength increases at a somewhat reduced rate between 2 and 3 years of age, and then continues to increase, but at a still further reduced rate between 3 and 15 years of age (Fig. 3B, Table 1a). After 15 years of age there is no change, on average, in femoral/humeral strength proportions. As shown in Table 1a these general trends are very similar whether mean age group or individual data are used.

Table 1c

Least-squares linear regression slopes, lower to upper limb diaphyseal length proportions on age

Age range (yrs)	Femoral/Humeral Diaphyseal Length			
	Means <sup>a</sup>		Individuals <sup>b</sup>	
	slope	SE	slope	SE
0.5–5.0	0.0135	0.0003	0.0142	0.0020
5.0–12.5	0.0061	0.0003	0.0067	0.0008

<sup>a</sup>Calculated from age group means. SE=standard error of slope through age group means.<sup>b</sup>Mean of individual slope values (n=20). SE=standard error of individual slope values.

Table 1d

Least-squares linear regression slopes, lower to upper limb muscle area proportions on age

Age range (yrs)	Thigh/Forearm Muscle Area			
	Means <sup>a</sup>		Individuals <sup>b</sup>	
	Slope	SE	slope	SE
0.5–1.5	0.0058*	0.0146	0.0058*	0.0508
1.5–3.5	0.1250	0.0135	0.1250	0.0298
3.5–10.5	0.0196	0.0026	0.0196	0.0063
10.5–12.0	0.0686	0.0115	0.0686	0.0157
12.0–17.0	–0.0219	0.0039	–0.0219	0.0084

<sup>a</sup>Calculated from age group means. SE=standard error of slope through age group means.<sup>b</sup>Mean of individual slope values (n=20). SE=standard error of individual slope values.

\*Non-significantly different from 0 (p&gt;0.05).

In Fig. 4 the same data are plotted by sex. The general age patterns within sex are similar to those described above for the pooled sample, although there are also some significant sex-related differences. First, there is no significant change in femoral/humeral strength between 6 months and 1 year of age in females (p>0.90, paired *t*-test), while there is a highly significant decline in males (p<0.0001, paired *t*-test). Thus, the decline in the ratio observed in the total sample (Fig. 3B) is due entirely to a change in males, although females also show no *increase* in femoral/humeral strength proportions until after age 1. Age trends from 1 to 14 years are very similar in the two sexes—all slopes within 1–2, 2–3, and 3–14 year old age

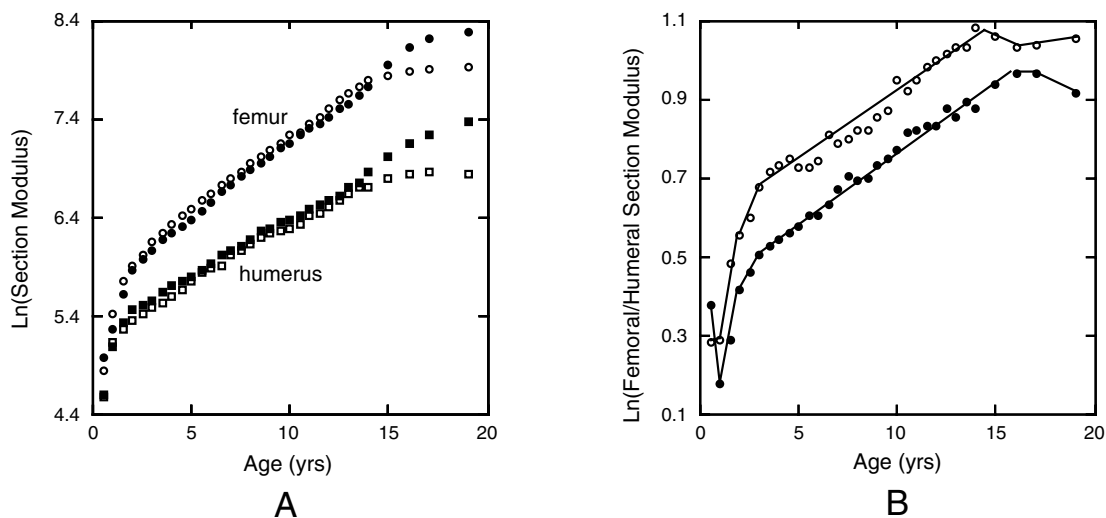


Fig. 4. Femoral and humeral section modulus changes with age, by sex: A) age changes in each bone (circles: femur; squares: humerus); B) age changes in femoral/humeral ratio. Open symbols: females; filled symbols: males.

ranges are nonsignificantly different between the sexes ( $p > 0.70$ , ANCOVA, age-sex interactions). However, females have consistently higher femoral/humeral ratios throughout this entire age range ( $p < 0.001$ , ANCOVA within each of the three age ranges, effect of sex with age as a covariate). This sex-related difference is caused by both a stronger femur among females as well as a stronger humerus among males (Fig. 4A) ( $p < 0.05$ , all comparisons, ANCOVA within 1–3 and 3–14 year age ranges). After 14 years in females, and 16 years in males, there is some fluctuation in the ratio, probably due in part to fluctuations in body weight and thigh muscle size in the sample (both of which preferentially affect femoral strength [Ruff, 2003]). This may have been a result of dieting: four females had weight losses of 4–9% and thigh muscle area losses of 8–31% between 15 and 17 years; one male had a weight loss of 8% and a thigh muscle area loss of 44% between 17 and 19 years. Due to continuing growth in body size, males develop stronger femora as well as humeri after 14 years of age (Fig. 4A); however, females maintain a higher femoral/humeral ratio ( $p < 0.01$ , ANCOVA).

#### Bone lengths

Bone length data for the pooled sample are shown in Fig. 5. As described above, maximum bone lengths (including the epiphyses) were calculated from diaphyseal lengths in the younger children. Femoral/humeral ratios are shown for both maximum and diaphyseal lengths in Fig. 5B, and regression statistics for both lengths are given in Tables 1b and 1c. Only maximum bone lengths are plotted in the individual bone curves (Fig. 5A); diaphyseal lengths show almost identical trends (displaced downwards, of course) over their corresponding age ranges. Both types of bone lengths give very similar results in terms of age changes in femoral/humeral proportions (Fig. 5, Tables 1b,c), although the results for very young children (under 3 years of age), where no maximum lengths could be directly measured, are probably slightly more accurate using diaphyseal lengths.

Although there is a general similarity in the age curves for section moduli (Fig. 3) and bone lengths (Fig. 5)—an increase in femoral/humeral proportions throughout growth, with the greatest increase occurring early in development—there are also

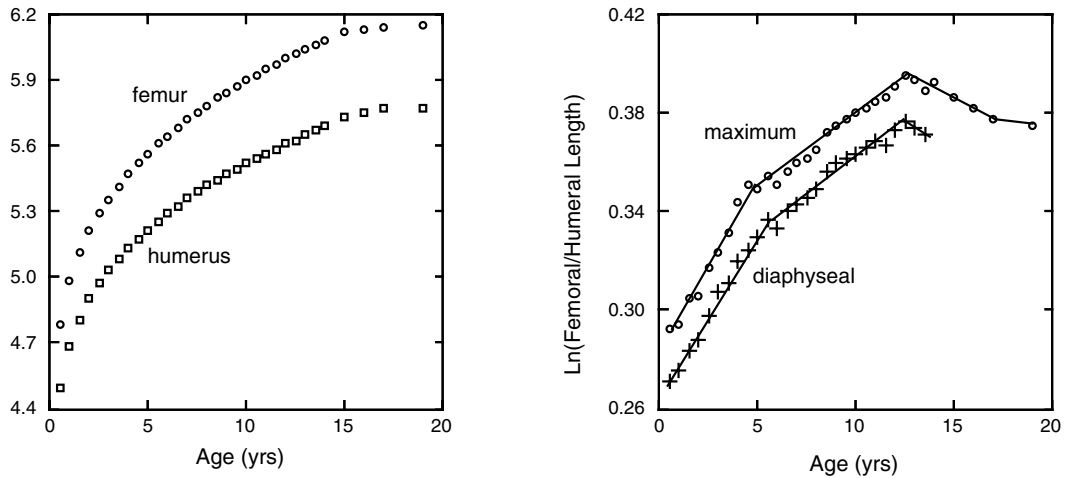


Fig. 5. Femoral and humeral length changes with age in the total combined sex sample: A) age changes in maximum length of each bone (circles: femur; squares: humerus); B) age changes in femoral/humeral ratio for maximum (circles) and diaphyseal (crosses) lengths. Lines in B indicate approximately linear regions of change. See Tables 1b,c for regression statistics.

some major differences. Unlike section moduli, bone lengths show no evidence for a reduction in femoral/humeral proportions between 6 months and 1 year of age or a change in slope at 1 year of age, or again at 2 or 3 years of age. Rather, femoral/humeral length proportions show a constant log-linear increase from 6 months to about 5 years of age. This is due largely to the absence of an abrupt reduction in growth rate of humeral length during the second year of life (compare Fig. 5A with Fig. 3A). Thus, the transition to walking at about a year of age has no discernable effect on relative femoral/humeral growth in length.

From about 5 to 12.5 years of age femoral/humeral length proportions continue to increase, but at a slower rate (Tables 1b,c). After 12.5 years there is a significant *reduction* in femoral/humeral length due to an overall greater increase in humeral length (16%, versus 13.6% in the femur). Thus, again, changes in femoral/humeral length proportions do not parallel changes in section moduli proportions. Overall, changes during growth in femoral/humeral length proportions are much less than those in femoral/humeral strength proportions: the total change from 6 months to 17 years of age in section moduli is about 8 times greater (in log units) than that in lengths. This is

true even when allowance is made for different units of measurement (section moduli in  $\text{mm}^3$ , lengths in mm), which would predict only a  $3 \times$  greater change in section moduli.

Sex-specific analyses of bone lengths are shown in Fig. 6. No linear trend lines are included on Fig. 6B due to increased noise in the smaller sex-specific samples, but the same general trends (to about 10–11 years) are apparent in both sexes as were noted for the pooled sample (Fig. 5B). Unlike section moduli (Fig. 4), prior to adolescence there is no consistent difference between the sexes in femoral/humeral length proportions ( $p > 0.10$ , ANCOVA, 6 months–5 years, 5 years–11 years, and 6 months–11 years). Females level off in length proportions at about 10 years of age, and then decline after 12.5 years. Males follow the same general pattern, but about 2 years later. This age disjunction is very likely due to the earlier skeletal maturation of adolescent females, apparent in the approximately 2 year difference in peak growth velocities characteristic of many body dimensions in this sample (Ruff, 2003), as well as other samples (e.g., Tanner et al., 1966; Bailey et al., 2000), coupled with the later growth in length of the humerus relative to the femur noted above. Thus, there is a transient sex difference in proportions between 11 and 16 years ( $p < 0.01$ ,

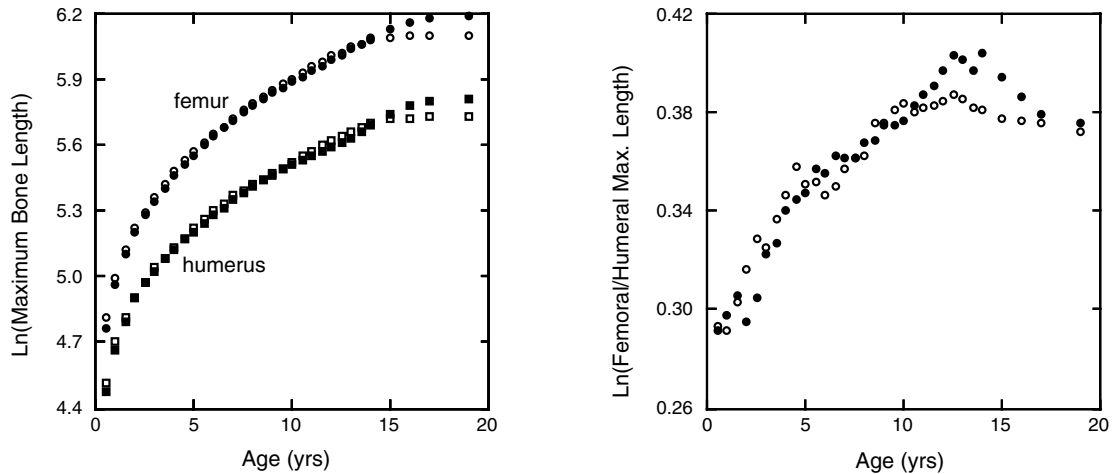


Fig. 6. Femoral and humeral maximum length changes with age, by sex: A) age changes in each bone (circles: femur; squares: humerus); B) age changes in femoral/humeral ratio. Open symbols: females; filled symbols: males.

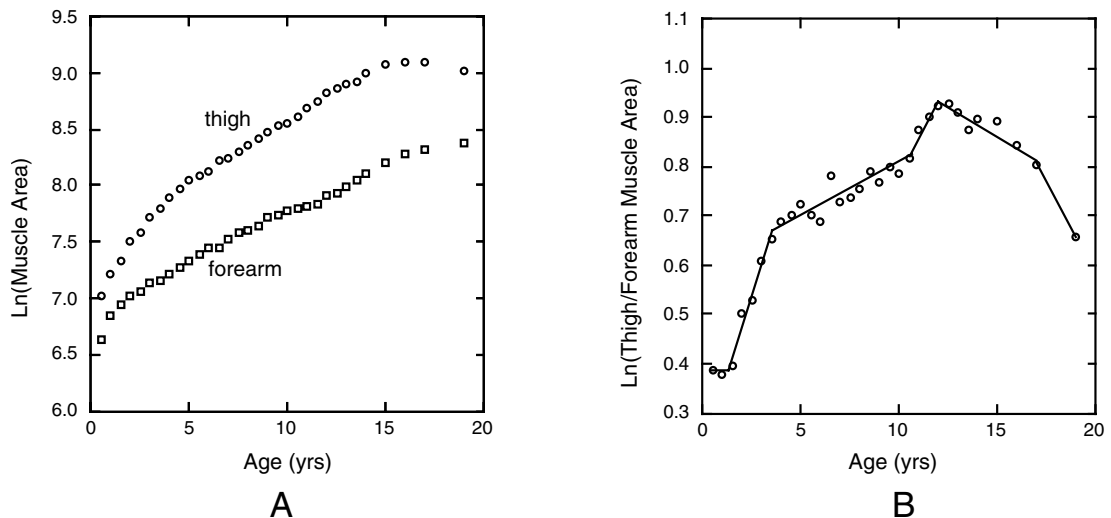


Fig. 7. Thigh and forearm muscle area changes with age in the total combined sex sample: A) age changes in each muscle region (circles: thigh; squares: forearm); B) age changes in thigh/forearm muscle ratio. Lines in B indicate approximately linear regions of change. See Table 1d for regression statistics.

ANCOVA). By 17–19 years of age, the sexes are again nonsignificantly different in length proportions ( $p > 0.60$ , two sample  $t$ -tests at each age).

#### Muscle areas

Thigh and forearm muscle areas for the pooled sex sample are shown in Fig. 7, with regression

statistics given in Table 1d. In terms of general patterns, pre-adolescent age changes in upper and lower limb muscle areas—both separately and as a ratio—are more similar to those for corresponding section moduli than those for bone lengths (compare with Figs. 3 and 5). Thigh/forearm muscle proportions show no increase between 6 months and 1.5 years, followed by a very rapid increase to

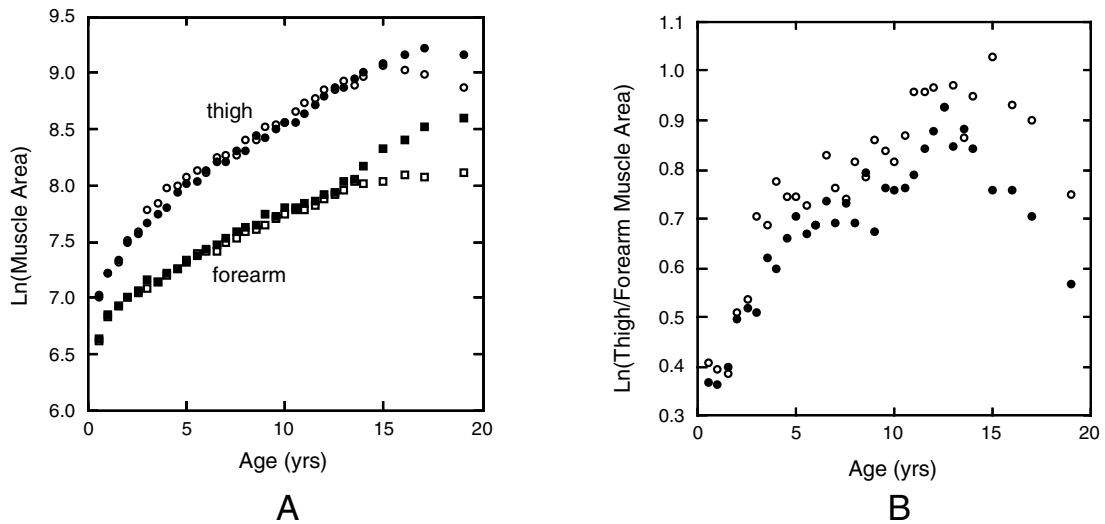


Fig. 8. Thigh and forearm muscle area changes with age, by sex: A) age changes in each muscle region (circles: thigh; squares: forearm); B) age changes in thigh/forearm muscle ratio. Open symbols: females; filled symbols: males.

about 3.5 years, and then a more gradual increase to about 10.5 years (Fig. 7B, Table 1d). The rapid increase in thigh to forearm strength in the second and third years of life is due to a sharp decrease in the rate of growth in forearm muscle area (Fig. 7A), similar to the pattern observed for humeral strength (Fig. 3A), but not length (Fig. 5A). Thus, changes in muscle area proportions, like those in bone section moduli, appear to be correlated with the adoption of bipedal locomotion, albeit it with a slight (6 month) delay.

Between 10.5 and 12–12.5 years, muscle area of the thigh increases more rapidly than that of the forearm. This pattern is then reversed through the rest of adolescence, as forearm muscle area continues to increase while thigh muscle area levels off, and may even decrease slightly from 17 to 19 years ( $p=0.09$ , paired  $t$ -test), resulting in a large decline in thigh/forearm muscle area between the last two age points ( $p<0.05$ , paired  $t$ -test). The general pattern in adolescence is superficially similar to that for bone lengths (Fig. 5B), although the large decrease in lower/upper limb muscle between 17 and 19 years is not paralleled in femoral/humeral length.

Muscle area age trends within sex are shown in Fig. 8. Again, as with bone lengths, due to

increased noise in these smaller samples, no linear trend lines are plotted. However, the general patterns of age changes in each sex are similar to each other and to the pattern described above for the pooled sample. As with section moduli, the major difference between the sexes is the development of relatively greater lower/upper limb muscle areas in females. This difference is apparent as early as 3 years of age (Fig. 8A) and persists throughout development ( $p<0.0001$ , ANCOVA, 3–12 years, 12–17 years). Prior to adolescence, the difference is caused mainly by greater thigh muscle area in females ( $p<0.002$ , ANCOVA, 3–12 years), although males have slightly greater forearm muscle area as well ( $p<0.05$ , ANCOVA, 3–12 years), beginning at about 6.5 years (Fig. 8A). During later adolescence, males increase greatly in forearm muscle area while females level off, contributing to a large increase in the sex proportional difference (the average sex difference in muscle area proportions to age 14 years is 9%, from 15 years on, 26%). As noted earlier, there is some decline in thigh muscle area in later adolescence, greater in females ( $p=0.001$ , paired  $t$ -test, 17 to 19 years), associated with significant weight loss in some individuals.

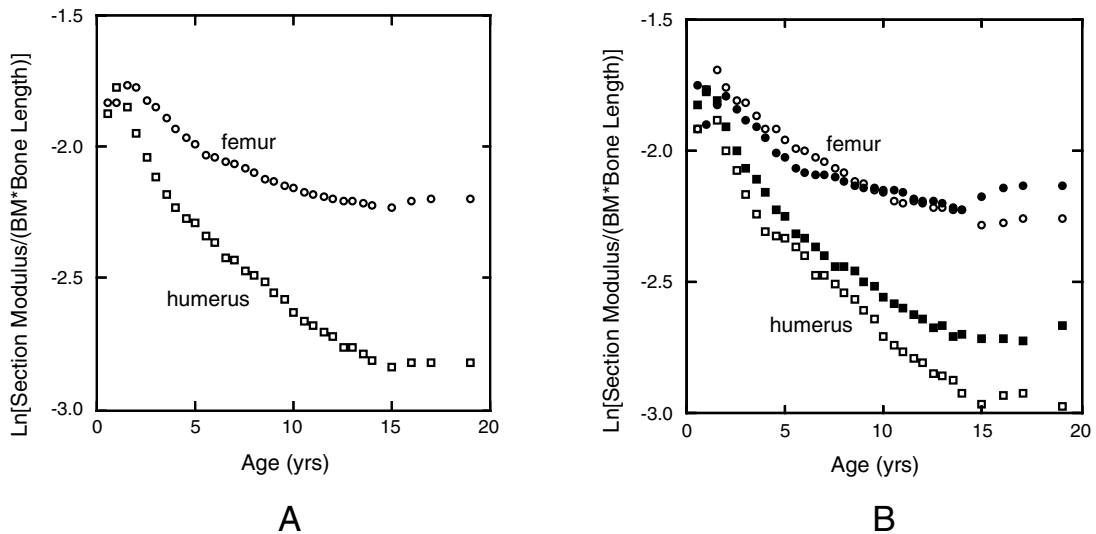


Fig. 9. Age changes in bone section moduli relative to body size (body mass-bone length): A) combined sex; B) sexes separate. Circles: femur; squares: humerus; open symbols: females; filled symbols: males.

#### *Bone strength relative to body size*

Fig. 9 shows (log-transformed) femoral and humeral section moduli divided by the product of body mass (and the corresponding bone length) for the pooled sample (A) and by sex (B). Differences between relative femoral and humeral strengths at particular ages are evaluated using paired *t*-tests.

Body size-standardized femoral and humeral strengths are nonsignificantly different at 6 months of age in the pooled sample and within sex ( $p > 0.10$ ). At 1 year of age, males have significantly stronger humeri than femora relative to body size ( $p < 0.05$ ), and by 1.5 years females have significantly stronger femora than humeri ( $p < 0.05$ ). From 2 years of age onward, both sexes have much stronger femora than humeri relative to body size ( $p < 0.01$ ), with the difference progressively increasing until 15 years of age. These results confirm those shown earlier for section moduli (Figs. 3 and 4).

Females have relatively stronger femora than males between 1.5 and 9 years of age ( $p < 0.001$ , ANCOVA), and males have relatively stronger humeri than females at all ages from 6 months onwards ( $p < 0.05$ , two sample *t*-test at 6 months;  $p < 0.0001$ , ANCOVA, entire age range) (Fig. 9B).

From 15 years of age onwards, males also have relatively stronger femora than females ( $p < 0.0001$ , ANCOVA, ages 15–17 years;  $p < 0.05$ , *t*-test in 19 year-olds). These patterns of sex differences are very similar to those observed for muscle areas (Fig. 8A), and suggest that differences in bone strength relative to body size are strongly influenced by muscular development.

The peak in relative humeral strength prior to age 1 and its steep reduction thereafter is not unexpected given the changing role of the upper limb in weight support in this age range. However, by the same reasoning, the high values for relative femoral strength in infancy and the less steep but still highly significant ( $p < 0.0001$ , regressions through either age group means or individual data) decline in relative femoral strength after 1.5 years (Fig. 9) are somewhat counterintuitive. This apparent anomaly can be largely explained by considering changes in bone material properties that occur during ontogeny, which are not incorporated into purely geometric models of bone strength (i.e., section moduli) alone.

It is well known (e.g., Currey and Butler, 1975) that compact bone in young children is less stiff and strong (i.e., has a lower modulus of elasticity and lower ultimate stress) than that of adults. Two

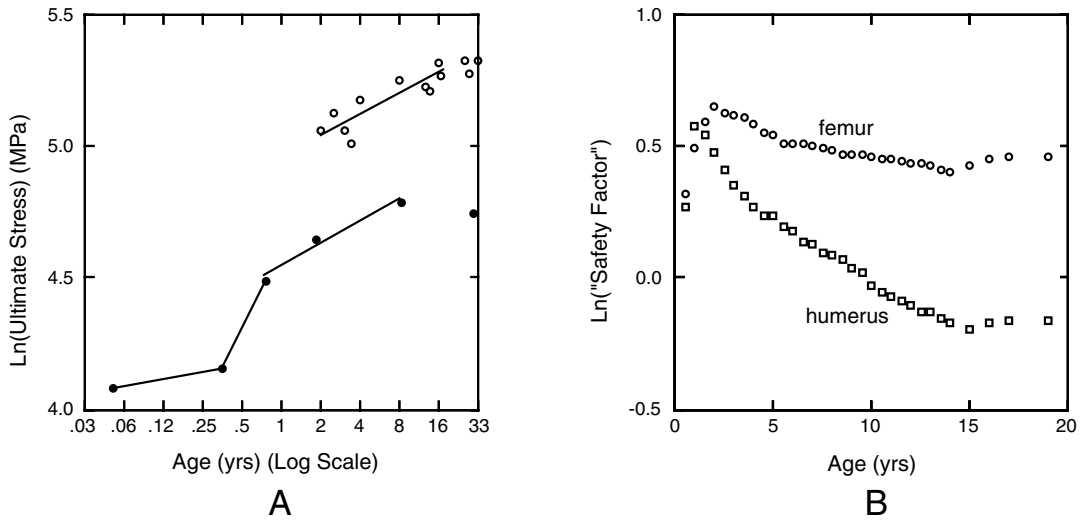


Fig. 10. A. Ultimate bone stress (i.e., bone material strength) changes with age. Open circles: Currey and Butler, 1975; filled circles: Vinz, 1970. Regression lines through 17 years of age plotted (see text for equations). B. Femoral and humeral “safety factors”—section moduli multiplied by estimated ultimate stress and divided by body size (body mass·bone length)—at different ages. Circles: femur; squares: humerus.

previous studies have reported age changes in bone material properties of femoral midshaft specimens (Vinz, 1970; Currey and Butler, 1975).<sup>2</sup> A plot of ultimate stress against age for these two studies is shown in Fig. 10A. Because the two studies used different testing procedures and measured somewhat different properties—ultimate tensile stress in Vinz, ultimate bending stress in Currey and Butler—absolute values cannot be compared (bending tests give higher values than tensile tests; see Currey, 1999). Also, different age ranges were included in the two studies and the data were reported differently (as age group means in Vinz and as individuals in Currey and Butler) (see Fig. 10A). However, the changes in values over time, within overlapping age ranges, are quite similar in the two studies. It was found that a log–log plot of ultimate stress against age produced an approximately linear change in ultimate

<sup>2</sup> A third study (Hirsch and Evans, 1965) also examined bone material properties in infants and one adolescent, but otherwise did not document age changes per se. Their results were consistent with those of Currey and Vinz, however. One subject in the Currey study—a 6 year-old girl suffering from diabetes—was not included in the analysis, since this disease may affect bone material properties and the individual was an outlier for her age.

stress between 0.75 and 17 years of age, with an average slope over both studies of 0.11. This was used together with a widely accepted value of compact bone ultimate tensile stress for young adults (20–29 years) of 140 MPa (Burstein et al., 1976) to determine the y-intercept in a log–log linear regression on age between 0.75 and 17 years (no change in ultimate stress is apparent between 17 years and young adulthood):  $\log(140) = 0.11 \cdot \log(17) + 4.63$ . Exponentiating yields: ultimate stress =  $e^{0.11 \cdot \log(\text{age}) + 4.63}$ . For the 6 month old data point, a similar procedure using the slope obtained from Vinz’s data in this age range (0.32–0.75 years, see Fig. 10A) yields the following equation: ultimate stress =  $e^{0.433 \cdot \log(\text{age}) + 4.72}$ .

The “safety factor” for bone can be defined as the ultimate stress/maximum stress incurred under loading (Biewener, 1992).<sup>3</sup> As described above, bending/torsional loads are taken here to be proportional to body mass·bone length; thus, maximum stress = (body mass·bone length)/section modulus (see Ruff, 2000), and “safety factor” = (ultimate stress·section modulus)/(body mass·bone

<sup>3</sup> Ultimate rather than yield stress is used here since Currey and Butler (1975) reported only the former property in their study.

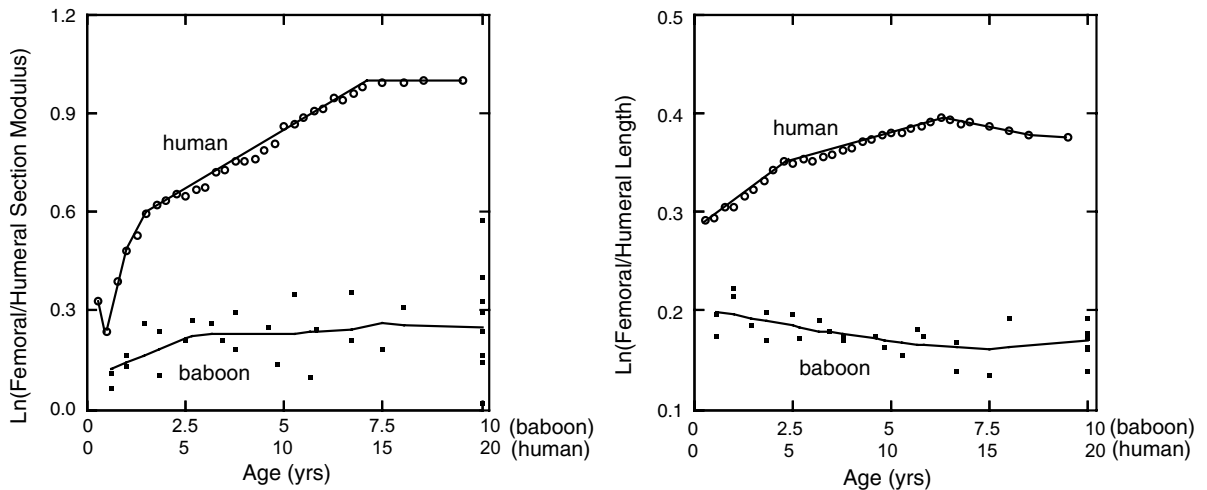


Fig. 11. Changes with age in femoral/humeral section moduli and maximum lengths in humans (open circles) and baboons (filled squares): A) section moduli; B) lengths. Human data from Figs. 3 and 5; baboon data fit with LOWESS nonparametric curves.

length). So, in effect, “safety factor” is equivalent to the body-size-standardized section modulus values shown in Fig. 9, multiplied by the age-specific ultimate stress for bone. It reflects the overall strength of bone under loading taking into account both geometric and material properties.

An age plot of safety factors for the femur and humerus (log-transformed) is shown in Fig. 10B. The addition of age changes in bone material properties modifies the curves shown in Fig. 9A in several ways. (Note that the relative scales on Fig. 10B and Fig. 9 are the same so that direct comparisons can be made.) First, the overall relative strength of the femur, including material properties, is lowest at 6 months of age. It then shows a very marked increase (almost 40%), peaking at 2 years of age, after which it shows a moderate decline (about 15%) to 5.5 years, followed by a very slow decline to 14 years, and then a slight increase to 17 years. The average index at 5.5 years is within 5% of that at 17–19 years, i.e., essentially “adult” values are reached in the femur by mid-childhood. The humerus shows an extremely rapid increase in overall relative strength between 6 months and a year, increasing by 36% over this short interval. It then undergoes a precipitous decline, dropping below 6 month values by 5 years, and continues to decline to age 15 years, when it

reaches values more than 50% below the 1 year old peak. Thus, these age trends are more in line with expectations based on mechanical/locomotor changes during development.

#### *Comparisons to baboons*

Age changes in femoral/humeral section moduli and maximum lengths for the human and baboon samples are shown together in Fig. 11. The y-axes are scaled here to reflect equivalent relative changes in section moduli and bone lengths: since section moduli are expressed in linear dimensions to the third power, a change in logarithmic units of 1.2 for section moduli is equivalent to a change of 0.4 units for bone lengths. Similarly, age ranges for baboons and humans are adjusted to reflect the shorter developmental period of baboons. Epiphyseal union of baboon long bones occurs roughly two to three times faster than in humans (Krogman, 1962; Bramblett, 1969); a 1:2 ratio of baboon to human years is used in Fig. 11. This age scale adjustment is not meant to imply a direct correspondence between developmental events in humans and baboons occurring at any particular age, but rather a more a general equivalence in terms of overall duration of growth from infancy to adulthood. The same linear trend lines are

plotted for the human data as in previous figures (Figs. 3 and 5). Because of the greater scatter of the baboon data (representing individuals rather than age group means and cross-sectional rather than longitudinal sampling), nonparametric LOWESS lines, with a window smoothing width of 0.5 (Cleveland, 1979), are used to illustrate general age trends in the baboons. The significance of apparent age trends indicated in the LOWESS plots is tested by linear regression analysis and two-sample *t*-tests between age groups, as appropriate.

Femoral/humeral section moduli proportions are similar in infant baboons and infant humans, with baboons slightly lower (Fig. 11A). Baboons increase slightly in this ratio from 7 months to 2.5 years ( $r=0.70$ ,  $p<0.05$ , regression on age); individuals under 2.5 years are significantly lower in section moduli proportions than all other age groups ( $p<0.05$ , *t*-tests with all older baboons, 2.5–8 year-olds, and 2.5–5 year-olds). From 2.5 years to adulthood section moduli proportions do not change in baboons (all regressions and age group comparisons non-significant). Human 1 year-olds have proportions virtually identical to those of baboons 2.5 years of age or older ( $p>0.70$ , *t*-test). After 1 year of age in humans, the two species diverge dramatically: human 3 year-olds are already more than 40% greater in femoral/humeral strength than older baboons, and by 15 years of age humans have strength ratios more than twice those of older baboons. The total age change in strength proportions is about six times greater in humans than in baboons.

Age-related divergence of human and baboon bone length proportions is much less pronounced (Fig. 11B). Baboons show a slight but significant decline in femoral/humeral length that extends throughout the whole growth period, from infants through subadults (6–8 years) ( $r=0.614$ ,  $p<0.01$ ), i.e., unlike section moduli there is no rapid change in proportions during the first three years of life followed by a leveling off. As a result of the opposite changes in humans and baboons during growth, femoral/humeral length proportions are maximally different between species among “adolescents” and adults. However, humans never approach baboons in length proportions at any age.

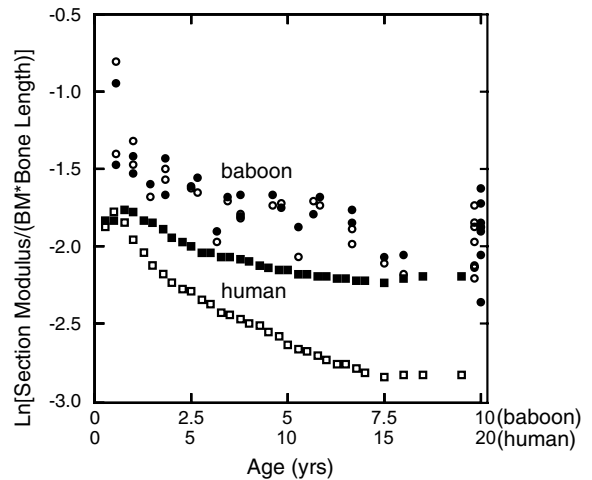


Fig. 12. Age changes in bone section moduli relative to body size (body mass  $\times$  bone length) in humans (squares) and baboons (circles). Filled symbols: femora; open symbols: humeri.

Fig. 12 shows femoral and humeral section moduli standardized over body mass  $\times$  bone length for humans and baboons. Age changes in relative strength of the baboon femur and humerus are similar to each other, and generally parallel the age pattern of the human femur: highest values early in development, followed by a gradual decline, with near-adult values reached in “late childhood” in both species (about 8–10 years in humans, 3–4 years in baboons). There is a subsequent transient decline in the index in baboon subadults (7.5–8 years) as well as a large positive spike in baboon one year-olds, although because of the small number of specimens and cross-sectional design it is difficult to say how much random sampling error may have contributed to these deviations. The baboon femur is slightly relatively stronger than the humerus from 2.5 years of age onwards ( $p<0.01$ , paired *t*-test between bones, average difference 9%). However, the real deviant in both age pattern and magnitude of relative strength is the human humerus, which after infancy declines to values far below those of the human femur and both bones in the baboon.

Unfortunately there are no data adequate to incorporate bone material properties into this comparison, as in Fig. 10, for baboons. Based

on several ontogenetic studies of bone material properties in a number of nonhuman mammalian species (Torzilli et al., 1981, 1982; Keller et al., 1985; Currey and Pond, 1989; Brear et al., 1990), it seems certain that bone material stiffness and strength also increases after infancy in baboons. The only study to date that actually measured such properties in immature baboons (or nonhuman primates, as far as I am aware) did in fact find evidence for such an age trend, although the data are too limited (three individuals, youngest 3 years of age) to derive any kind of equation that could be applied to the present sample. Of the studies of nonhuman species that included younger individuals (Torzilli et al., 1981, 1982; Currey and Pond, 1989; Brear et al., 1990), ultimate tensile stress about doubled from near birth to adulthood, which is similar to that found here for humans (Fig. 10A). Thus, it is likely that the apparent age-related decline in relative femoral and humeral strengths for baboons shown in Fig. 12, like that of the human femur, is largely compensated by an increase in bone material strength.

## Discussion

### *Development of femoral to humeral proportions in humans*

Adult human limb proportions are clearly distinctive: the adult human femur is both longer and stronger relative to the humerus than in the great majority of anthropoid primates. However, the ontogenetic trajectories by which adult human skeletal proportions are reached are different for bone length and bone strength. Humans are born with relatively long lower limbs: human infants already have length proportions similar to those of adult anthropoid specialized leapers and different from more generalized quadrupeds. This length disproportion gradually increases throughout post-natal growth, and appears to be a continuation of a trend observed in utero. Fig. 13 is a plot of thigh and arm lengths against gestational age in a large sample of human fetuses measured by Scammon and Calkins (1929). While not strictly comparable to the femoral and humeral length

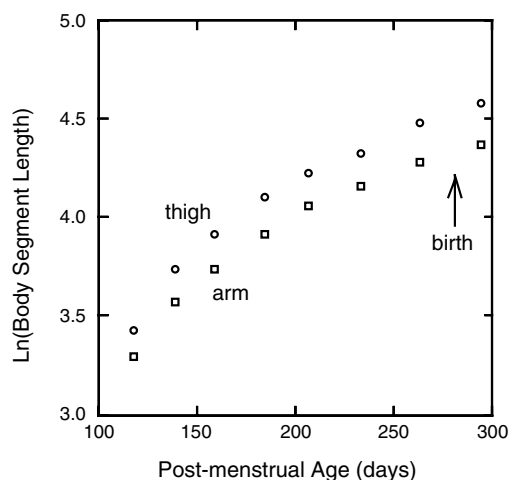


Fig. 13. Mean thigh (greater trochanter to knee) and arm (acromion to elbow) segment lengths in human fetuses measured by Scammon and Calkins (1929); Tables 126 and 147;  $n=17-47$  individuals per age group. Post-menstrual ages determined from mean crown-heel lengths using their formula (Table 9). Values from first three age groups reported in original study not used because only one individual included in first age group and next two age groups not matched (i.e., different  $n$ 's). Average age at birth (280 days) shown for reference; although not stated by authors, last age group must include some post-term neonates.

measurements used here, the fetal data do demonstrate a small but progressive increase in lower to upper limb segment length proportions from the fourth month post-conception through the neonatal period ( $r=0.79$ ,  $p<0.05$ , regression of  $\ln$  [thigh length/arm length] on gestational age). Thus, as also noted by Schultz (1973), human limb length proportions develop very early, well prior to any known specific mechanical stimuli and certainly prior to conferring any functional advantage. This is consistent with findings from recent experimental developmental studies, which indicate a high developmental penetrance, or early ontogenetic appearance of interspecific differences in relative limb segment lengths (Hamrick, 2001).

In contrast, humans are born with femoral/humeral bone strength proportions that are quite different from those of adults. In fact, in terms of relative lower/upper limb strength, human infants are much closer to older juvenile and adult baboons and (nonspecialized) quadrupedal primates in general than they are to human adults.

The adoption of unassisted bipedality at about 1 year of age (Burnett and Johnson, 1971; Hensinger, 1986; Stanitski et al., 2000) corresponds to a major shift in growth trajectories in bone strengths: between 6 months and a year of age, when the upper limb is an integral weight-bearing element in crawling and “cruising” (Burnett and Johnson, 1971; Hensinger, 1986), femoral and humeral strengths increase at either the same rate (females) or faster in the humerus (males); after one year of age femoral strength increases much faster than humeral strength. The steepest change in proportions occurs between 1 and 2 years, when femoral strength increases almost three times as fast as humeral strength, due to a large decline in growth velocity of the humerus coupled with a continued high growth rate in the femur (Ruff, 2003). This is the only time during development when there is a clear disjunction between growth velocity in body size and growth velocities in femoral and humeral strength (Ruff, 2003), which is not surprising given the profound changes in mechanical loading relative to body size that occur in this age range.

Femoral/humeral strength proportions continue to rise rapidly between 2 and 3 years, and then settle into a much slower increase that extends to mid-late adolescence, when adult proportions are reached. Children do not acquire a “mature” gait pattern, including a narrow mediolateral base of support, greater limb stability and normal step cadence, until about 2.5–3 years of age (Sutherland et al., 1980). Age trends in bone structural data thus closely match behavioral changes, with an initial very rapid increase in femoral strength as the femur adapts to its new role in (sole) weight support, probably exacerbated by the extra demands produced by an inefficient gait pattern, followed by a slow and constant change in proportions that characterizes most of childhood and early adolescence, during which walking patterns are also stable. In this latter period increases in femoral strength are closely tied to increases in body size (body mass:bone length); increases in humeral strength are also correlated with increases in body size, but at a lower level (Ruff, 2003). During childhood and early adolescence the humerus continues to decline markedly in strength

relative to body size, while femoral strength (including material properties) relative to body size remains almost constant. Thus, the slight positive allometry observed in femoral/humeral strength between 3 and about 15 years of age (sexes averaged) is due to continuing adaptation of the femur to increases in body size, coupled with a continuing decline in humeral strength relative to body size. (Sumner and Andriacchi [1996] have presented a similar argument based on estimated strains in the femur and humerus during growth.) When the rate of growth in body size declines in mid-late adolescence (Ruff, 2003), femoral/humeral strength proportions also stabilize.

Consideration of bone material properties in addition to geometry is important in evaluating changes in relative bone strength, especially during the first few years of life when material properties are changing rapidly. It should be noted that the material property values that were used for the humerus are based on mechanical tests of femoral specimens (there are apparently no similar data available for upper limb bones) and thus could be erroneous. However, it seems likely that if the humerus and femur were to differ in their material property changes with age, the humerus would exhibit less of an increase in stiffness and strength than the femur (if such changes are mechanically adaptive—see Currey, 1979). Thus, overall relative strength of the maturing humerus could be overestimated here, and the widening difference between femur and humerus during development could be even greater. A similar phenomenon was reported by Carrier and Leon (1990) in an ontogenetic study of the California gull, in which dramatic increases in both geometric and material properties of the wing bones occurred at the initiation of flying, leading to large increases in breaking strength relative to body mass and to that of the hindlimb bones. Muscle mass for the wings relative to the hindlimb also increased greatly at the same ontogenetic stage. Thus, this species provides another example of a “natural experiment” of the effects on bone (and muscle) structural properties of pronounced change in limb function during growth, paralleling that in human limbs, but reversed in direction. Interestingly, the one exception to this general pattern in the gull was limb

bone length, which was always greater in the wing than in the hindlimb throughout development, and showed only a modest increase in rate of growth at the inception of flying. Again this is similar to results of the present study, indicating a much less tight coupling between actual mechanical function (loads) and limb bone length proportions.

The safety factors obtained here incorporating material properties appear smaller than expected—a log (safety factor) of 0.5, for example, about the average value obtained for the femur, indicates a (raw) safety factor of 1.65. Since this is derived using the polar section modulus, which is about twice the section modulus for bending, safety factors in bending would actually be about one-half of this, or about 0.8, which is obviously unreasonable. The reason for the apparent discrepancy is that bone length was taken here to be *proportional*, not *equal* to relevant moment arms. In fact, the true M-L bending moment arm of body mass at femoral midshaft during single-legged stance in adults is about 1/8 femoral length (Ruff, 1995; also see McLeish and Charnley, 1970). Multiplying 0.8 by 8 results in a true average safety factor of about 6–7, which is reasonable compared to estimates derived from in-vivo limb bone measurements in mammals. These generally range between 2 and 4 during strenuous activities (Alexander, 1981), when loadings would be higher (and safety factors lower) than in the static support of body weight considered here. Of course, true in-vivo mechanical loadings, including relevant moment arms, will be much more complex than this (e.g., see Thorpe et al., 1999). However, the general correspondence between the present estimates of relative bone strength and those based on in-vivo measurements is reassuring, and supports the validity of the approach.

There are several possible explanations for the slight apparent decline in femoral strength relative to body size after 2 years of age that persists even after age changes in bone material properties have been factored in. First, due to the relative inefficiency of gait during the initial period of walking (see above), mechanical loads on the femur, relative to body size, may be greatest at about 1–2 years of age and decline somewhat thereafter, leading to slight declines in relative strength.

Second, the method for evaluating body size here, i.e., body mass·bone length, may also contribute to the apparent decrease in relative strength. Although this appears to be a mechanically appropriate index for evaluating bending/torsional loading in adults of fairly diverse body shape (Ruff, 2000), children undergo even more extreme changes in body shape from infancy through adolescence. In particular, during growth relative limb length (especially lower limb length) increases greatly, while relative body breadth decreases (see Hansman, 1970; Maresch, 1970). Thus, use of bone length may systematically overestimate true moment arms (of body mass and muscles) in older children and adults relative to young children, resulting in declines in strength relative to body mass·bone length.

The final factor that may contribute to this apparent age trend is inaccuracy in use of one-dimensional (radiographic) bone breadths to reconstruct two-dimensional cross sections. As mentioned above, two studies of archaeological samples have measured true cross-sectional properties of the femur and humerus in juveniles (Ruff et al., 1994, and unpublished data; Sumner and Andriacchi, 1996, and Sumner, pers. comm.). Of these studies, that by Sumner and Andriacchi of the Grasshopper Pueblo sample makes the more informative comparison because they included infants and very young children, while the other study did not. Fig. 14 shows age changes in femoral/humeral section moduli measured in the Grasshopper sample and in the present study. Two section moduli are plotted for Grasshopper:  $Z_p$ , the true polar section modulus, and  $Z_y$ , the M-L section modulus (i.e., measured about the A-P axis). The latter is closer to what was actually measured in the present study (from A-P radiographs). The two section moduli ratios give similar results in terms of age trends, although there is more of an age increase in the true polar section modulus ratio than in the M-L section modulus ratio. A closer examination of Sumner and Andriacchi's original data (not shown here) reveals that this is a result of greater age increases in A-P section moduli of the femur and M-L section moduli of the humerus than in their corresponding perpendicular section moduli. Thus, measurement

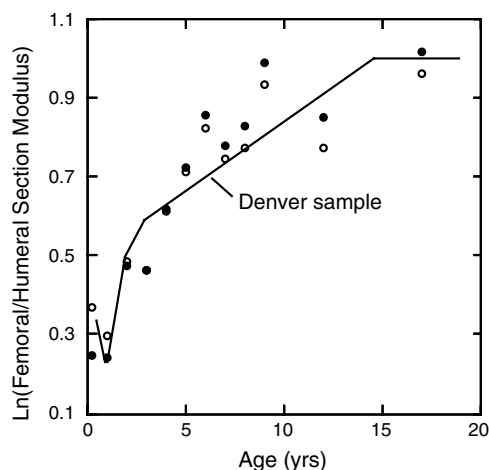


Fig. 14. Comparison of age trends in femoral/humeral section moduli in the present study (Denver sample) and in the Grasshopper Pueblo sample (Sumner and Andriacchi, 1996; Sumner, pers. comm.). Line plotted is for Denver sample (from Fig. 3). Individual data points are age class means for Grasshopper sample: filled circles:  $Z_p$  (polar section modulus); open circles:  $Z_y$  (M-L section modulus).

of only M-L properties, as was done in the present study, slightly underestimates increases in overall femoral strength, and slightly overestimates increases in overall humeral strength during growth, which together leads to a slight underestimation of the increase in femoral/humeral strength. (This assumes that growth changes in bone shape in the two samples are similar, which may not be true.) The age changes in femoral/humeral strength proportions documented here are thus probably slightly conservative, with the femur gaining even more in overall strength relative to the humerus.

However, despite differences in technique and the study samples themselves, the general magnitudes and patterns of change in femoral/humeral strength in the Grasshopper and Denver samples are remarkably similar (Fig. 14), including the initial decline or lack of change in infancy, the very rapid increase in the second and third years of life, and the more gradual increase thereafter. This lends some confidence both in the methods used here, and in the generality of growth patterns observed in the Denver sample.

Because the Grasshopper sample was cross-sectional in design, the original authors grouped

data by yearly intervals prior to age 10, and by five-year intervals between 10 and 14, and 15–19, with five individuals in each age group. Fig. 14 shows that even using these age group means, there is apparent nonrandom sampling and thus fairly substantial fluctuations in ratios between successive age groups, particularly after age 5 years, which is not atypical of cross-sectional samples. The inevitable inaccuracies in age estimation in archaeological samples also likely added to data scatter. This, plus the coarser sampling during adolescence, does not allow precise identification of the age at which adult proportions are reached. The present longitudinal analysis makes it clear that adult femoral/humeral strength proportions are not attained until mid-late adolescence, not late childhood or early adolescence as has been concluded based on the Grasshopper study results (Richmond et al., 2002). In the Denver sample, femoral/humeral strength increases by an average of 16.2% between 10 and 17 years, by 13.1% between 11 and 17 years, and by 9.0% between 12 and 17 years, all highly significant ( $p \leq 0.01$ , paired  $t$ -tests). Thus, strength proportions of fossil juvenile specimens such as KNM-WT 15000 (a 10–12 year-old) can not be directly compared to those of adults.<sup>4</sup>

Sumner and Andriacchi (1996) also noted the potential importance of growth in muscular strength as a stimulus to bone growth (also see Schönau et al., 1996; Frost, 1997); this is supported here through analysis of muscle area data. Age changes in lower/upper limb muscle area proportions largely parallel those in corresponding bone strengths, with some deviations in adolescence. Comparison of sex differences in relative bone strengths and muscle areas, discussed below, also support the importance of muscular loadings as a factor in stimulating bone cross-sectional growth. Controlling for growth in body size, growth in muscle area is a significant predictor of

<sup>4</sup> In terms of skeletal (as opposed to dental) age, KNM-WT 15000 may have been closer to a 13–13.5 year-old modern human (Smith, 1993), however, he was also a male. Within Denver males, femoral/humeral strength increases an average of 13.5% between 13 and 17 years, and 11.3% between 14 and 17 years, both statistically significant ( $p < 0.05$ , paired  $t$ -tests).

growth in bone strength (Ruff, 2003). Furthermore, this effect is stronger for the humerus than for the femur, highlighting the importance of muscular loadings (versus support of body weight) in the upper limb, as would be expected.

It is conceivable, of course, that both muscle and bone parameters respond to a third factor, such as a general growth stimulus (e.g., growth hormone levels). However, if this were true then one might expect coordination in the timing of muscular growth and overall bone growth, including growth in bone length, which is not the case in the present sample (Ruff, 2003). In any event, as with bone cross-sectional parameters, the specificity of muscular growth in the lower versus upper limb at different stages of development argues for the importance of localized mechanical effects rather than (or in addition to) systemic factors in controlling such growth.

#### *Developmental mechanisms*

These findings have more general implications regarding long bone developmental mechanisms, specifically, the relative importance of direct mechanical versus systemic (genetic, hormonal) effects on bone growth. On balance, results from experimental animal studies indicate little effect of moderate changes in mechanical loading (short of traumatic injury) on growth in long bone length (Lanyon, 1980; Biewener and Bertram, 1993). Clinical studies of human children indicate that some limb shortening may occur with partial limb paralysis (Stinchfield et al., 1949; Staheli et al., 1968; McDaid et al., 2002), although effects of this kind are generally relatively minor compared to those on bone cross-sectional dimensions (see below). These results are consistent with the present study findings: growth trajectories in femoral/humeral length proportions are seemingly unaffected by the major change in mechanical loadings occurring at about 1 year of age. Furthermore, the characteristically longer human femur begins to develop even prior to birth and femoral/humeral proportions are already not far from adult proportions (within 10%) in infancy. Thus, it seems likely that long bone length proportions are highly

heritable, although partially environmentally modifiable.

Conversely, development of normal long bone cross-sectional morphology appears to be strongly dependent upon mechanical stimuli. Characteristic human femoral/humeral strength proportions do not develop until after the adoption of bipedal gait. Subsequent changes in strength proportions are closely tied to mechanical factors as well—behavioral events occurring during early childhood and later changes in body size. With regard to the latter, it is important to recognize that growth in bone strength is not simply a function of the linear growth of long bones: correlations between growth velocities for stature and bone strength (humeral and femoral) are extremely low (Ruff, 2003). Many other studies have demonstrated the environmental (mechanical) sensitivity of long bone cross-sectional diaphyseal morphology during growth (Lanyon, 1980; Woo et al., 1981; Biewener and Bertram, 1994, and references therein; Ruff et al., 1994; Trinkaus et al., 1994), although there is also a genetic component to cross-sectional growth (Volkman et al., 2003).

Thus, while both genetics and environment (and their interaction) undoubtedly play a role in all aspects of long bone growth, growth in length appears to be less responsive to changes in actual mechanical loadings during life than growth in cross-sectional dimensions. In terms of interpreting fossil long bone morphology, this suggests that individuals/species undergoing a behavioral transition, e.g., to bipedalism, might first express this transition through alterations in bone cross-sectional structure, prior to longer-term genetic selection for a change in limb length proportions.

The results of the present study also have implications regarding methods of analysis of ontogenetic data. Most previous studies of human and nonhuman primate long bone proportional changes during growth have employed relatively simple models involving fitting of single log-linear regressions over the entire growth period (Lumer, 1939; Shea, 1981; Buschang, 1982a,b; Jungers and Susman, 1984; Jungers and Hartmann, 1988). While such analyses can illuminate general allometric trends, they can also obscure

more subtle, but functionally critical, changes in proportions. All of the analyses here—of bone length, bone strength, and muscle area proportions—indicate that growth patterns are not unilinear. Growth trajectories for bone length proportions come the closest to approximating a simple log-linear trend (through mid-adolescence), but even they undergo a significant change in slope in mid-childhood. The cause for this change in trajectory is not clear, and merits further investigation at the level of proximate causes, i.e., changes in growth plate activity in different metaphyses (Kember and Sisson, 1976; Karrholm et al., 1984; Pritchett, 1991). (Interestingly, adult values for femoral bicondylar angle, also dependent on differential metaphyseal growth, are also reached at about mid-childhood (Salenius and Vankka, 1975; Tardieu and Trinkaus, 1994).) The reversal in the femoral/humeral length trajectory in late adolescence has not, to my knowledge, been described previously, but is consistent with the late epiphyseal union of the (proximal) humerus relative to femoral epiphyses (Krogman, 1962); the proximal humeral epiphysis contributes the majority of growth in length of the humerus throughout development (Pritchett, 1991). Growth trajectories for bone strength proportions are even more strongly nonlinear. One reason why such changes have not generally been observed is the difficulty in discerning relatively subtle shifts in trajectory utilizing cross-sectional samples, where sampling bias blurs true growth-related differences. Examining data as (log) ratios also aids in discriminating minor proportional changes. Finally, inclusion of known-aged individuals, spanning the entire developmental period, can be important in elucidating functional interrelationships (e.g., the inclusion of pre-ambulatory infants in the present study).

It should be noted that these analyses, even though based on longitudinal data, were not designed to capture growth velocity information per se. Averaging across individuals is well-known to obscure true growth velocities (e.g., Tanner, 1955), thus, the group averaged curves shown here for bone lengths and strengths, and muscle areas, are inadequate for reconstructing such parameters. Other analyses of the same data

(Ruff, 2003) demonstrate clear growth velocity changes, e.g., adolescent growth spurts, in all bone and muscle parameters, although the timing of such spurts varies between parameters, and also relative to stature and body mass growth velocities.

### *Sexual dimorphism*

Males and females share the same general patterns of change in skeletal proportions during growth, but also differ in certain aspects. These differences can be attributed to two factors: 1) the development of greater upper body strength in males/lower body strength in females, and 2) the earlier maturation of females during adolescence.

The development of a sex difference in lower/upper limb muscle area during growth has been previously documented (e.g., Tanner et al., 1981). While changes occurring during adolescence have often been emphasized in this context (Parker et al., 1990; Round et al., 1999), some data suggest that this pattern is established earlier in childhood and is accentuated in adolescence (Tanner et al., 1981). In the present study sample, greater thigh muscle area in females, and greater forearm muscle area in males, is evident by mid-childhood. The sex difference in proportions then increases during adolescence. Sex differences in relative femoral/humeral bone strength are evident even earlier, beginning at 1 year of age. When expressed relative to body size (body mass-bone length), differences between the sexes in femoral and humeral strength are quite similar to those in muscle areas of the corresponding limbs. Thus, differential development of muscle in the upper and lower limbs, beginning in childhood, may largely explain sex differences in relative bone strengths. Muscular growth is particularly highly correlated with bone strength growth in the upper limb in males (Ruff, 2003).

The very early appearance of a sex difference in femoral/humeral strength proportions is initiated by the decline in this proportion between 6 months and 1 year of age in males, and the lack of such a decline in females. This sex difference then increases to about 3 years of age, after which it is stable throughout the rest of growth (with some

minor fluctuations in later adolescence). This pattern suggests a difference between the sexes in lower/upper limb use as early as infancy. Despite anecdotal impressions that girls may start standing and walking before boys, controlled observations have found no evidence for a significant sex difference in the timing of onset of unassisted walking (Burnett and Johnson, 1971; Stanitski et al., 2000). Studies of the development of gait during childhood (e.g., McGraw, 1940; Burnett and Johnson, 1971; Sutherland et al., 1980) generally do not include specific comparisons between boys and girls. However, broader studies of motor coordination and neuromuscular development suggest that some gender differences in limb use may be present even in young infants (Touwen, 1976; Piek et al., 2002), and more pronounced differences are apparent in young children. In a meta-analysis of 64 studies of more than 30,000 subjects, Thomas and French (1985) found a highly significant difference between boys and girls as young as 3 years of age in throwing ability, which they attributed largely to biological rather than environmental (cultural) differences. Interestingly, other measures of motor performance that reflected mainly lower limb development/coordination (running, jumping, etc.) showed much less striking gender differences in young children, and were considered to be more culturally determined. Thus, there may indeed be sex-related differences in physical development and/or neurological control of the upper and lower limbs beginning at a very young age, which could be related to the differences in skeletal strength documented here. The fact that such differences have not (to my knowledge) previously been demonstrated may be a consequence of past studies relying on cross-sectional rather than longitudinal data and focusing mainly on older children.

Unlike bone strength, femoral/humeral length proportions do not show any sex-related differences in childhood. This again emphasizes the relative independence, or uncoupling, of growth in bone length and strength. There is a transient sex difference in length proportions in mid-adolescence, but this is caused by the second factor noted above—the earlier maturation of females during adolescence—combined with the

later growth in length of the humerus (in both sexes). By late adolescence the sexes are similar in length proportions, again unlike strength proportions.

### *Baboons*

Baboons show much less extreme changes in femoral/humeral proportions during growth than humans, which is consistent with their much less pronounced changes in locomotion. Young juvenile baboons do show a slight increase with growth in femoral/humeral strength, with adult strength proportions only reached at about 2.5 years of age. This age change is similar to that described for body segment masses in juvenile macaques, in which the relative mass of the hindlimb increases more than that of the forelimb during growth, resulting in a posterior shift in the body center of gravity (Grand, 1981; Turnquist and Wells, 1994). This redistribution of mass occurs between birth and about 2 years of age in *Macaca mulatta*, and has been proposed to be linked to the development of greater “hindlimb propulsive forces” during growth (Turnquist and Wells, 1994, p. 495), which would be concordant with the increase in relative femoral strength. However, experimental data collected on young infant macaques indicate no fundamental differences in fore to hindlimb ground reaction forces from those of adults (Kimura, 2000). Detailed quantitative information on juvenile baboon locomotion appear to be lacking, but qualitative observations in the wild indicate that *P. cynocephalus* infants are actively locomoting on the ground within the first several months of life, although they rely on their mothers for long distance transport until about 5–6 months of age (Altmann, 1980), which is still prior to the age of the youngest individuals in the present sample. More data are needed specifically on ontogenetic changes in baboon locomotion, experimentally and in the wild, over a period extending beyond early infancy, to better interpret the skeletal proportional changes observed here. It would also be interesting to examine bone strength proportions in very young (neonatal) baboon infants, before they begin to actively locomote.

The interpretation of bone strength proportions in baboons presented here is slightly different than that reported earlier for this sample (Ruff, 2002), in which the relative constancy of these proportions was emphasized (although a slight difference between juveniles and adults was noted). In fact, femoral/humeral strength proportions remain virtually constant during most of the growth period in baboons, and in particular in older juveniles, which are the appropriate comparative sample for the subadult fossil specimen previously analyzed (KNM-RU 2036, *Proconsul heseloni*). Thus, comparisons of interlimb bone strength proportions between the fossil specimen and adult catarrhines (Ruff, 2002) are valid. The identification of more subtle patterns of ontogenetic variation in baboons here is a result of the technique employed, i.e., detailed examination of age trends in log ratios.

Bone length proportions in baboons show a contrasting ontogenetic pattern to strength proportions, with the humerus gradually increasing in length relative to the femur until late adolescence, i.e., epiphyseal closure. The change is very close to log-linear over this entire time period, with no abrupt change in early development (similar to humans). Thus, both the direction and age-dependence of this trajectory are different from that for bone strength, once again demonstrating the relative independence of length and strength proportions. The pattern of change in length proportions is different than that described for *M. mulatta* by Lumer and Schultz (1941), in which hindlimb length dimensions increased slightly faster than forelimb length dimensions postnatally. Calculating reduced major axis slopes from their tabulated postnatal data, log-transformed, yields a value of  $1.0731 \pm 0.0311$  ( $n=10$ ,  $p<0.05$ ) for thigh length against arm length, while the same procedure for femur length against humerus length in the present sample of baboons gives a value of  $0.9662 \pm 0.0100$  ( $n=30$ ,  $p<0.01$ ). Jungers and Fleagle (1980), in a longitudinal study, also presented data consistent with greater growth in length of the femur than humerus in two species of *Cebus*. Among cercopithecines, *P. cynocephalus* adults do not have unusually long humeri relative to femora, in fact, the overall size trend in

cercopithecines appears to be one of negative rather than positive allometry, although adult *P. cynocephalus* are isometric (Ruff, 2002 and see above). Determining whether this growth trajectory is specific to baboons or this particular taxon awaits further ontogenetic data for other species.

Finally, it is apparent that baboons have stronger bones relative to body size than humans at all stages of development (Fig. 12). This is not surprising given previous demonstrations of the relative gracility of modern human long bones compared to those of other primates (Ruff, 2000). It is also consistent with the observed decline in robusticity of the hominin femur over the past 3 million years in both adults (Ruff et al., 1993, 1999; Ruff, 1998) and juveniles (Ruff et al., 1994; Trinkaus et al., 2002). The degree to which the relative strength of human long bones has declined can be appreciated by comparing relative femoral strength between humans and baboons: even though in humans the femur supports all of body weight during locomotion, as opposed to only partial body weight in baboons, on average over all ages shown in Fig. 12, it is still almost 40% weaker than the baboon femur. The human humerus, of course, is relatively even weaker than its corresponding bone in the baboon, although this greater difference progressively develops during life, as would be expected. As noted above, all of the juvenile baboons here were active quadrupeds engaging in a wide array of locomotor activities. Thus, even at an early age mechanical loadings on the femur and humerus were likely higher than those on developmentally comparable humans. Obtaining additional data on neonatal baboons would again be very interesting in this regard.

## Summary and conclusions

Detailed longitudinal analysis of a sample of human children reveals complex changes in human femoral to humeral proportions during growth that vary depending on the skeletal characteristic and age range examined. Growth trajectories for both bone length and bone strength proportions are not well described by simple log-linear models.

In infants the femur and humerus are nearly equal in strength relative to body size (body mass·bone length), and are similar in this respect to quadrupedal primates. There is a dramatic shift in the growth trajectories for femoral and humeral strength at 1 year of age, corresponding to the adoption of bipedality. This is followed by a two year period of rapid adaptation of the femur and humerus to their new mechanical environments (i.e., femoral strength increasing much faster than humeral strength), during which the child also acquires a mature gait pattern. The rest of childhood and early adolescence is characterized by a more gradual increase in femoral relative to humeral strength, with femoral strength paralleling growth in body size and humeral strength progressively declining relative to body size. Adult strength proportions are not reached until mid-late adolescence. Growth in upper and lower limb muscle size generally parallels that in bone strength. Femoral/humeral strength proportions are larger in females beginning at an early age, and are associated with corresponding sex-related differences in muscle size and possibly behavioral differences.

Bone length proportions undergo relatively much less change during growth and do not directly reflect known behavioral events. Human infants already possess relatively long femora/short humeri compared to generalized quadrupedal primates. Femoral/humeral length proportions gradually increase throughout childhood and adolescence, with a slight reduction in rate of increase at about 5 years of age. There is no change in length proportion trajectories at or near one year of age. Femoral/humeral length proportions actually decrease slightly in mid-late adolescence due to more prolonged growth of the humerus. Males and females show no differences in length proportions except for a transient difference in mid-adolescence due to the later growth of the humerus and later adolescent growth spurt in males. While sex differences in muscle areas in the lower and upper limbs are related to sex differences in bone strengths, no such relationship is apparent between sex differences in muscle area and bone lengths.

Thus, although both femoral/humeral strength and length proportions increase in humans during growth, the two types of characteristics appear to be largely independent in terms of specific physiological responses to their environments. Bone strengths appear to respond more to changes in actual mechanical loadings, and as a consequence interlimb strength proportions can vary dramatically with a change in behavior, i.e., the adoption of bipedal gait. In contrast, growth in bone length appears to be much less dependent on mechanical loadings and is more genetically or systemically determined. These findings have implications for the interpretation of morphological variation in fossil hominins. First, it is important to consider developmental status in assessing proportional differences between specimens, particularly bone strength proportions, which change dramatically and do not reach adult values until mid-late adolescence. Second, during locomotor behavioral transitions, mosaic patterns of variation in limb bone morphology might be expected, with strength proportions more directly reflecting current limb usage, prior to longer-term selection for changes in length proportions.

Comparisons with an ontogenetic baboon sample highlight the specific nature of the human developmental pattern. Baboons also show evidence of some developmental changes in proportions that may be indicative of anatomical and/or behavioral shifts during growth.

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Appendix Table 1  
Means and SD's of log-transformed data by age group, total sample (n=20)<sup>a</sup>

Age (yrs)	Ln (Section Modulus)						Ln (Maximum Length)						Ln (Muscle Area)					
	Femur		Humerus		Fem./Hum.		Femur		Humerus		Fem./Hum.		Thigh		Forearm		Thigh/Forearm	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
0.5	4.92	0.17	4.58	0.13	0.33	0.15	4.79	0.04	4.50	0.06	0.29	0.06	7.02	0.20	6.63	0.16	0.39	0.19
1.0	5.35	0.22	5.11	0.17	0.23	0.17	4.98	0.04	4.69	0.05	0.30	0.04	7.22	0.24	6.85	0.13	0.38	0.18
1.5	5.69	0.18	5.30	0.15	0.39	0.20	5.11	0.04	4.81	0.05	0.30	0.04	7.33	0.27	6.94	0.13	0.39	0.24
2.0	5.89	0.15	5.40	0.13	0.49	0.15	5.21	0.04	4.91	0.04	0.31	0.03	7.51	0.20	7.01	0.13	0.50	0.20
2.5	6.00	0.12	5.47	0.14	0.53	0.15	5.29	0.04	4.97	0.05	0.32	0.03	7.58	0.17	7.06	0.14	0.53	0.14
3.0	6.11	0.14	5.52	0.14	0.59	0.17	5.36	0.05	5.03	0.05	0.32	0.03	7.73	0.18	7.13	0.15	0.61	0.17
3.5	6.20	0.13	5.58	0.16	0.62	0.18	5.42	0.05	5.08	0.05	0.33	0.02	7.80	0.17	7.15	0.13	0.65	0.15
4.0	6.29	0.15	5.65	0.17	0.64	0.18	5.48	0.05	5.13	0.05	0.34	0.03	7.90	0.19	7.21	0.09	0.69	0.17
4.5	6.36	0.15	5.71	0.18	0.65	0.18	5.52	0.05	5.17	0.05	0.35	0.03	7.97	0.13	7.27	0.10	0.70	0.13
5.0	6.43	0.15	5.78	0.19	0.65	0.16	5.56	0.05	5.21	0.05	0.35	0.02	8.05	0.14	7.33	0.14	0.73	0.15
5.5	6.52	0.17	5.85	0.19	0.67	0.17	5.61	0.05	5.26	0.05	0.35	0.03	8.09	0.18	7.39	0.11	0.70	0.18
6.0	6.59	0.16	5.92	0.20	0.68	0.17	5.65	0.06	5.30	0.05	0.35	0.03	8.12	0.18	7.44	0.11	0.69	0.17
6.5	6.69	0.15	5.97	0.20	0.72	0.18	5.68	0.06	5.33	0.05	0.36	0.03	8.23	0.18	7.45	0.10	0.78	0.15
7.0	6.77	0.15	6.04	0.19	0.73	0.15	5.72	0.06	5.36	0.05	0.36	0.03	8.24	0.16	7.52	0.12	0.73	0.14
7.5	6.84	0.16	6.09	0.19	0.75	0.15	5.75	0.06	5.39	0.05	0.36	0.03	8.30	0.16	7.57	0.13	0.74	0.14
8.0	6.91	0.15	6.15	0.20	0.76	0.16	5.78	0.06	5.42	0.05	0.37	0.03	8.36	0.16	7.61	0.12	0.75	0.15
8.5	6.98	0.16	6.22	0.22	0.76	0.18	5.82	0.06	5.45	0.05	0.37	0.03	8.42	0.17	7.64	0.12	0.79	0.16
9.0	7.06	0.16	6.27	0.21	0.79	0.17	5.85	0.06	5.47	0.05	0.38	0.03	8.47	0.17	7.71	0.12	0.77	0.16
9.5	7.12	0.16	6.31	0.22	0.81	0.18	5.87	0.06	5.49	0.05	0.38	0.04	8.52	0.18	7.73	0.11	0.80	0.15
10.0	7.19	0.16	6.33	0.23	0.86	0.19	5.90	0.06	5.52	0.06	0.38	0.03	8.56	0.20	7.77	0.12	0.79	0.16
10.5	7.25	0.18	6.38	0.22	0.87	0.17	5.92	0.06	5.54	0.06	0.38	0.03	8.61	0.20	7.80	0.12	0.82	0.16
11.0	7.33	0.17	6.45	0.21	0.89	0.17	5.95	0.06	5.56	0.06	0.39	0.03	8.69	0.21	7.82	0.12	0.87	0.17
11.5	7.39	0.18	6.48	0.23	0.91	0.20	5.97	0.06	5.59	0.06	0.39	0.03	8.74	0.19	7.84	0.13	0.90	0.15
12.0	7.46	0.19	6.55	0.22	0.92	0.21	6.00	0.06	5.61	0.06	0.39	0.03	8.82	0.19	7.91	0.13	0.92	0.14
12.5	7.54	0.20	6.60	0.22	0.95	0.19	6.02	0.06	5.63	0.06	0.40	0.04	8.86	0.17	7.94	0.12	0.93	0.13
13.0	7.61	0.20	6.67	0.24	0.94	0.21	6.04	0.06	5.65	0.06	0.39	0.03	8.90	0.19	8.00	0.15	0.91	0.18
13.5	7.68	0.20	6.72	0.22	0.96	0.18	6.06	0.06	5.67	0.06	0.39	0.03	8.92	0.20	8.05	0.15	0.87	0.19
14.0	7.76	0.18	6.78	0.21	0.98	0.21	6.09	0.05	5.69	0.06	0.39	0.03	8.99	0.17	8.11	0.16	0.90	0.16
15.0	7.90	0.16	6.90	0.20	1.00	0.17	6.12	0.05	5.73	0.05	0.39	0.03	9.07	0.17	8.19	0.20	0.89	0.25
16.0	8.00	0.20	7.00	0.24	1.00	0.19	6.13	0.06	5.75	0.06	0.38	0.03	9.10	0.20	8.27	0.20	0.85	0.21
17.0	8.06	0.22	7.06	0.25	1.00	0.21	6.14	0.06	5.77	0.06	0.38	0.03	9.10	0.26	8.32	0.24	0.80	0.23
19.0	8.11	<sup>a</sup>	7.11	<sup>a</sup>	1.00	<sup>a</sup>	6.15	<sup>a</sup>	5.77	<sup>a</sup>	0.38	<sup>a</sup>	9.02	<sup>a</sup>	8.38	<sup>a</sup>	0.66	<sup>a</sup>

Section moduli in mm<sup>3</sup>, lengths in mm, areas in mm<sup>2</sup>.

<sup>a</sup>19 year-old mean calculated from 17-year mean as described in text (n=14). All data natural log-transformed prior to calculation of means.

Appendix Table 2  
Means and SD's of log-transformed data by age group, females (n=10)<sup>a</sup>

Age (yrs)	Ln (Section Modulus)						Ln (Maximum Length)						Ln (Muscle Area)					
	Femur		Humerus		Fem./Hum.		Femur		Humerus		Fem./Hum.		Thigh		Forearm		Thigh/Forearm	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
0.5	4.85	0.18	4.57	0.16	0.28	0.16	4.81	0.02	4.52	0.07	0.29	0.07	7.04	0.18	6.63	0.14	0.41	0.37
1.0	5.42	0.22	5.13	0.19	0.29	0.17	4.99	0.04	4.70	0.04	0.29	0.03	7.23	0.24	6.84	0.14	0.39	0.36
1.5	5.75	0.20	5.27	0.19	0.49	0.18	5.12	0.05	4.82	0.05	0.30	0.03	7.32	0.33	6.93	0.15	0.39	0.40
2.0	5.91	0.19	5.35	0.14	0.56	0.14	5.22	0.05	4.91	0.05	0.32	0.04	7.52	0.27	7.01	0.13	0.51	0.50
2.5	6.03	0.14	5.43	0.16	0.60	0.15	5.30	0.05	4.97	0.05	0.33	0.03	7.59	0.22	7.05	0.15	0.54	0.52
3.0	6.16	0.16	5.48	0.16	0.68	0.18	5.37	0.05	5.04	0.05	0.33	0.04	7.78	0.22	7.08	0.16	0.71	0.51
3.5	6.24	0.15	5.52	0.18	0.72	0.18	5.42	0.05	5.09	0.05	0.34	0.03	7.84	0.22	7.15	0.16	0.69	0.62
4.0	6.33	0.17	5.60	0.18	0.73	0.19	5.48	0.05	5.14	0.06	0.35	0.03	7.98	0.13	7.20	0.12	0.78	0.60
4.5	6.42	0.15	5.67	0.18	0.75	0.18	5.53	0.05	5.17	0.07	0.36	0.03	8.01	0.12	7.27	0.09	0.74	0.66
5.0	6.49	0.16	5.76	0.19	0.72	0.16	5.57	0.05	5.22	0.05	0.35	0.02	8.08	0.14	7.34	0.15	0.75	0.70
5.5	6.57	0.18	5.84	0.18	0.73	0.17	5.62	0.06	5.27	0.06	0.35	0.03	8.13	0.20	7.40	0.10	0.73	0.67
6.0	6.64	0.17	5.90	0.21	0.74	0.14	5.65	0.06	5.30	0.06	0.35	0.03	8.11	0.17	7.42	0.15	0.69	0.69
6.5	6.72	0.16	5.92	0.20	0.81	0.16	5.69	0.06	5.34	0.06	0.35	0.03	8.25	0.20	7.42	0.11	0.83	0.74
7.0	6.80	0.16	6.01	0.21	0.79	0.15	5.73	0.06	5.37	0.06	0.36	0.03	8.26	0.19	7.50	0.14	0.76	0.69
7.5	6.87	0.17	6.07	0.22	0.80	0.17	5.76	0.06	5.40	0.06	0.36	0.03	8.27	0.20	7.53	0.17	0.74	0.73
8.0	6.94	0.19	6.12	0.23	0.82	0.16	5.79	0.06	5.43	0.05	0.36	0.03	8.40	0.19	7.59	0.15	0.82	0.69
8.5	7.01	0.19	6.19	0.24	0.82	0.17	5.82	0.06	5.45	0.06	0.38	0.03	8.40	0.19	7.62	0.16	0.79	0.79
9.0	7.09	0.19	6.24	0.24	0.85	0.16	5.85	0.06	5.48	0.05	0.38	0.03	8.52	0.15	7.66	0.13	0.86	0.67
9.5	7.14	0.19	6.27	0.23	0.87	0.16	5.88	0.07	5.50	0.06	0.38	0.03	8.55	0.18	7.71	0.13	0.84	0.76
10.0	7.23	0.19	6.28	0.25	0.95	0.17	5.91	0.07	5.52	0.07	0.38	0.03	8.56	0.25	7.75	0.14	0.81	0.76
10.5	7.26	0.21	6.34	0.25	0.92	0.17	5.93	0.07	5.55	0.07	0.38	0.02	8.66	0.21	7.79	0.15	0.87	0.76
11.0	7.36	0.21	6.41	0.20	0.95	0.15	5.96	0.07	5.58	0.06	0.38	0.02	8.74	0.25	7.79	0.14	0.96	0.79
11.5	7.42	0.20	6.44	0.23	0.98	0.20	5.98	0.07	5.60	0.07	0.38	0.03	8.78	0.23	7.82	0.15	0.96	0.84
12.0	7.51	0.21	6.51	0.22	1.00	0.19	6.01	0.07	5.63	0.06	0.38	0.03	8.84	0.23	7.88	0.13	0.97	0.88
12.5	7.58	0.22	6.57	0.23	1.02	0.19	6.03	0.06	5.64	0.06	0.39	0.03	8.85	0.19	7.92	0.12	0.93	0.93
13.0	7.66	0.21	6.63	0.25	1.03	0.20	6.05	0.05	5.67	0.05	0.39	0.03	8.92	0.18	7.95	0.12	0.97	0.85
13.5	7.73	0.20	6.70	0.23	1.03	0.19	6.06	0.04	5.68	0.05	0.38	0.03	8.90	0.22	8.04	0.13	0.87	0.88
14.0	7.79	0.19	6.71	0.19	1.08	0.23	6.08	0.04	5.70	0.05	0.38	0.03	8.97	0.18	8.02	0.14	0.95	0.84
15.0	7.85	0.16	6.79	0.17	1.06	0.20	6.10	0.04	5.72	0.04	0.38	0.03	9.07	0.19	8.04	0.15	1.03	0.76
16.0	7.87	0.15	6.84	0.16	1.03	0.19	6.10	0.04	5.73	0.05	0.38	0.03	9.03	0.20	8.10	0.12	0.93	0.76
17.0	7.90	0.16	6.86	0.11	1.04	0.17	6.10	0.04	5.73	0.05	0.38	0.03	8.98	0.29	8.08	0.13	0.90	0.70
19.0	7.93	<sup>a</sup>	6.85	<sup>a</sup>	1.06	<sup>a</sup>	6.10	<sup>a</sup>	5.73	<sup>a</sup>	0.37	<sup>a</sup>	8.87	<sup>a</sup>	8.12	<sup>a</sup>	0.75	<sup>a</sup>

Section moduli in mm<sup>3</sup>, lengths in mm, areas in mm<sup>2</sup>.

<sup>a</sup>19 year-old mean calculated from 17-year mean as described in text (n=7). All data natural log-transformed prior to calculation of means.

Appendix Table 3

Means and SD's of log-transformed data by age group, males (n=10)<sup>a</sup>

Age (yrs)	Ln (Section Modulus)						Ln (Maximum Length)						Ln (Muscle Area)					
	Femur		Humerus		Fem./Hum.		Femur		Humerus		Fem./Hum.		Thigh		Forearm		Thigh/Forearm	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
0.5	4.98	0.13	4.60	0.09	0.38	0.13	4.77	0.05	4.47	0.05	0.29	0.06	7.00	0.22	6.63	0.18	0.37	0.24
1.0	5.27	0.20	5.10	0.16	0.18	0.16	4.97	0.03	4.67	0.06	0.30	0.04	7.21	0.24	6.85	0.12	0.36	0.18
1.5	5.63	0.15	5.34	0.09	0.29	0.18	5.10	0.04	4.80	0.05	0.31	0.05	7.34	0.21	6.94	0.10	0.40	0.21
2.0	5.87	0.10	5.45	0.09	0.42	0.13	5.20	0.04	4.91	0.04	0.30	0.02	7.50	0.09	7.00	0.14	0.50	0.15
2.5	5.98	0.11	5.52	0.10	0.46	0.13	5.28	0.04	4.98	0.05	0.31	0.03	7.58	0.11	7.06	0.13	0.52	0.12
3.0	6.07	0.11	5.56	0.12	0.51	0.12	5.35	0.04	5.03	0.05	0.32	0.02	7.67	0.08	7.16	0.14	0.51	0.14
3.5	6.17	0.10	5.65	0.13	0.53	0.14	5.41	0.05	5.08	0.05	0.33	0.02	7.76	0.10	7.14	0.11	0.62	0.14
4.0	6.25	0.12	5.70	0.14	0.54	0.11	5.47	0.05	5.13	0.05	0.34	0.03	7.81	0.20	7.21	0.06	0.60	0.19
4.5	6.30	0.13	5.74	0.18	0.56	0.13	5.51	0.05	5.17	0.05	0.34	0.03	7.93	0.15	7.27	0.11	0.66	0.13
5.0	6.38	0.13	5.80	0.20	0.58	0.14	5.55	0.05	5.21	0.05	0.35	0.02	8.01	0.13	7.31	0.13	0.70	0.16
5.5	6.46	0.14	5.86	0.20	0.61	0.16	5.60	0.05	5.25	0.04	0.36	0.02	8.04	0.16	7.37	0.12	0.67	0.19
6.0	6.54	0.14	5.94	0.20	0.61	0.16	5.64	0.06	5.29	0.05	0.36	0.03	8.13	0.20	7.44	0.07	0.69	0.22
6.5	6.65	0.15	6.02	0.19	0.64	0.17	5.68	0.06	5.32	0.05	0.36	0.03	8.21	0.16	7.47	0.08	0.74	0.13
7.0	6.74	0.13	6.07	0.18	0.67	0.13	5.72	0.06	5.35	0.05	0.36	0.03	8.22	0.13	7.53	0.10	0.69	0.10
7.5	6.81	0.14	6.11	0.16	0.71	0.12	5.75	0.06	5.39	0.05	0.36	0.03	8.32	0.12	7.59	0.10	0.73	0.10
8.0	6.87	0.11	6.18	0.18	0.69	0.15	5.78	0.06	5.41	0.05	0.37	0.04	8.32	0.12	7.62	0.08	0.69	0.09
8.5	6.96	0.13	6.26	0.20	0.70	0.19	5.81	0.06	5.44	0.04	0.37	0.04	8.44	0.17	7.65	0.08	0.79	0.16
9.0	7.02	0.13	6.29	0.18	0.73	0.16	5.84	0.06	5.47	0.05	0.37	0.03	8.42	0.17	7.75	0.09	0.67	0.14
9.5	7.10	0.11	6.35	0.21	0.75	0.18	5.86	0.06	5.49	0.05	0.38	0.04	8.50	0.19	7.74	0.10	0.76	0.15
10.0	7.15	0.12	6.38	0.21	0.77	0.18	5.89	0.06	5.51	0.05	0.38	0.04	8.56	0.17	7.80	0.09	0.76	0.13
10.5	7.23	0.15	6.42	0.20	0.82	0.17	5.92	0.06	5.53	0.05	0.38	0.04	8.56	0.17	7.80	0.10	0.76	0.13
11.0	7.31	0.12	6.48	0.22	0.82	0.18	5.94	0.06	5.55	0.05	0.39	0.04	8.64	0.16	7.85	0.09	0.79	0.11
11.5	7.36	0.16	6.52	0.23	0.83	0.19	5.97	0.06	5.58	0.05	0.39	0.03	8.71	0.15	7.87	0.09	0.84	0.12
12.0	7.41	0.17	6.58	0.24	0.83	0.21	5.99	0.06	5.59	0.05	0.40	0.03	8.80	0.17	7.92	0.12	0.88	0.10
12.5	7.50	0.17	6.62	0.21	0.88	0.17	6.01	0.07	5.61	0.06	0.40	0.04	8.87	0.16	7.94	0.13	0.93	0.10
13.0	7.56	0.18	6.70	0.24	0.86	0.18	6.04	0.07	5.64	0.07	0.40	0.03	8.88	0.21	8.03	0.18	0.85	0.17
13.5	7.64	0.19	6.75	0.22	0.89	0.14	6.06	0.07	5.67	0.07	0.40	0.03	8.94	0.19	8.06	0.17	0.88	0.14
14.0	7.73	0.17	6.86	0.22	0.88	0.13	6.09	0.06	5.69	0.07	0.40	0.03	9.01	0.16	8.17	0.15	0.84	0.16
15.0	7.95	0.14	7.02	0.17	0.94	0.12	6.14	0.06	5.74	0.06	0.40	0.03	9.08	0.15	8.32	0.16	0.76	0.17
16.0	8.12	0.16	7.16	0.19	0.97	0.19	6.17	0.05	5.78	0.06	0.39	0.03	9.17	0.17	8.41	0.15	0.76	0.18
17.0	8.22	0.15	7.25	0.20	0.97	0.24	6.18	0.04	5.80	0.05	0.38	0.03	9.22	0.16	8.52	0.06	0.70	0.16
19.0	8.28	<sup>a</sup>	7.36	<sup>a</sup>	0.91	<sup>a</sup>	6.19	<sup>a</sup>	5.81	<sup>a</sup>	0.38	<sup>a</sup>	9.17	<sup>a</sup>	8.60	<sup>a</sup>	0.57	<sup>a</sup>

Section moduli in mm<sup>3</sup>, lengths in mm, areas in mm<sup>2</sup>.<sup>a</sup>19 year-old mean calculated from 17-year mean as described in text (n=7). All data natural log-transformed prior to calculation of means.

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