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ABSTRACT

Behavioral studies indicate that adult mountain gorillas (*Gorilla beringei*) are the most terrestrial of all nonhuman hominoids, but that infant mountain gorillas are much more arboreal. Here we examine ontogenetic changes in diaphyseal strength and length of the femur, tibia, humerus, radius, and ulna in 30 Virunga mountain gorillas, including 18 immature specimens and 12 adults. Comparisons are also made with 14 adult western lowland gorillas (*Gorilla gorilla gorilla*), which are known to be more arboreal than adult mountain gorillas. Infant mountain gorillas have significantly stronger forelimbs relative to hind limbs than older juveniles and adults, but are nonsignificantly different from western lowland gorilla adults. The change in inter-limb strength proportions is abrupt at about two years of age, corresponding to the documented transition to committed terrestrial quadrupedalism in mountain gorillas. The one exception is the ulna, which shows a gradual increase in strength relative to the radius and other long bones during development, possibly corresponding to the gradual adoption of stereotypical fully pronated knuckle-walking in older juvenile gorillas. Inter-limb bone length proportions show a contrasting developmental pattern, with hind limb/forelimb length declining rapidly from birth to five months of age, and then showing no consistent change through adulthood. The very early change in length proportions, prior to significant independent locomotion, may be related to the need for relatively long forelimbs for climbing in a large-bodied hominoid. Virunga mountain gorilla older juveniles and adults have equal or longer forelimb relative to hind limb bones than western lowland adults. These findings indicate that both ontogenetically and among closely related species of *Gorilla*, long bone strength proportions better reflect actual locomotor behavior than bone length proportions.

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Introduction

Growth trajectories of postcranial skeletal dimensions have been widely studied among nonhuman hominoids (Lumer, 1939; Shea, 1981, 1986; Jungers and Susman, 1984; Jungers, 1984a, b; Jungers and Hartmann, 1988; Inouye, 1992, 2003; Taylor, 1995, 1997; Dainton and Macho, 1999). A primary aim of such studies has been to identify deviations from common ontogenetic scaling,

as indicators of both phylogenetic and functional distinctions among taxa. Ontogenetic analyses can also serve as a kind of 'natural experiment' in taxa that undergo behavioral transitions during growth, with implications for interpreting evolutionary changes in morphology (Turnquist and Wells, 1994). For example, femoral to humeral strength proportions in pre-bipedal human infants are similar to those in quadrupedal baboons (Ruff, 2003b), but change dramatically after the onset of walking at about one year of age (Sumner and Andriacchi, 1996; Ruff, 2003b; Cowgill, 2008). In contrast, limb bone length proportions are already distinctive in human neonates, prior to walking (the femur is much longer than the humerus), and clearly different from those of infant baboons, who undergo only modest changes in inter-limb proportions during growth (Ruff, 2003b). Furthermore, no sudden change in length
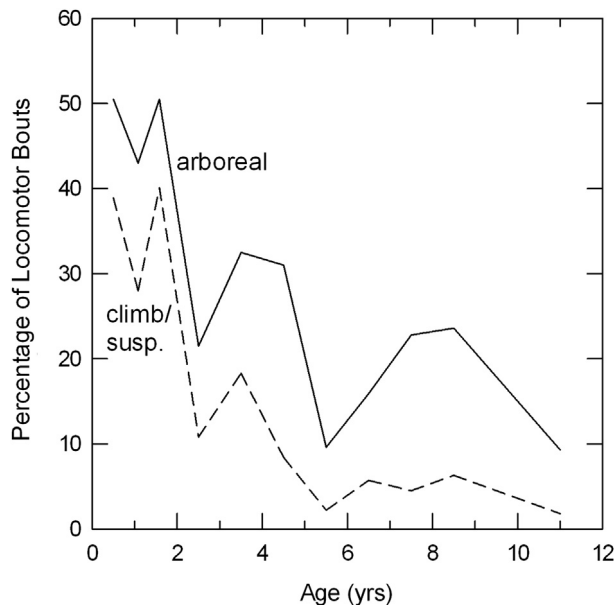
Figure 1. Ontogenetic changes in mountain gorilla locomotion (data from Doran, 1997). 'Arboreal' excludes locomotion on mother (Doran, 1997: Table 2). 'Climbing/susp.': sum of 'Climb/scramble' and 'Suspensory'; includes locomotion on mother (Doran, 1997: Table 1). Oldest data points (plotted arbitrarily at 11 years) are averages of male and female adult values. Percentage of locomotor bouts incorporates distance (Doran, 1992).

Table 1
Study sample.

Taxon	n	Age (yrs)	Sex	Source[a]
G. beringei beringei	1	0.001	F	MGSP
	1	0.04	M	MGSP
	1	0.10[b]	?	Smithsonian
	1	0.45	F	MGSP
	1	0.45	M	MGSP
	1	0.90[b]	M	Smithsonian
	1	1.50	F	MGSP
	1	1.67	F	MGSP
	1	2.45[c]	F	MGSP
	1	2.50[b]	F	MGSP
	1	2.50[b]	M	Smithsonian
	1	2.76[c]	M	MGSP
	1	3.72	M	MGSP
	1	3.83[c]	F	MGSP
	1	5.48[c]	M	MGSP
	1	6.08	F	MGSP
	1	9.00[b]	?	MGSP
	1	10.69	F	MGSP
	3	Adult	M	MGSP
	3	Adult	F	MGSP
	3	Adult	M	Smithsonian
	5	Adult	F	Smithsonian
G. gorilla gorilla	6	Adult	M	Smithsonian
	2	Adult	F	Smithsonian
	1	Adult	M	Harvard MCZ
	3	Adult	F	Harvard MCZ

[a] MGSP: Mountain Gorilla Skeletal Project.
[b] Estimated age (see text).
[c] Based on probable identify (see text).

proportions occurs at the onset of bipedal walking in humans. This strongly implies that limb lengths are more genetically canalized and less developmentally sensitive to direct effects of mechanical loading than are diaphyseal cross-sectional dimensions, an interpretation supported by much other evidence (e.g., see Lanyon, 1980; Carrier and Leon, 1990; Trinkaus et al., 1994; Auerbach and Ruff, 2006). This in turn has implications for interpreting patterns of variation in limb bone proportions in the fossil record (Ruff, 2009; Haile-Selassie et al., 2010).

Investigations of long bone growth trajectories in nonhuman hominoids have primarily focused on lengths, although breadths or circumferences have also been included in a few studies (Taylor, 1997; Inouye, 2003). No study to date of a nonhuman hominoid species has examined ontogenetic changes in long bone diaphyseal structural properties, which as shown above, may be more sensitive indicators of age changes in mechanical loadings and thus behavior. Furthermore, previous studies have focused almost exclusively on proportional changes as a function of size, not age. While this approach can yield important information on general ontogenetic scaling, as noted by Klingenberg (1998: 115), "several lines of evidence, both theoretical and empirical, demonstrate that size cannot be a substitute for age data; the dimension of time is indispensable for inferring heterochronic processes". Chronological age is also important for relating skeletal morphology to behavioral studies that have used age as a baseline for observations (Carrier and Leon, 1990; Ruff, 2003b; also see below). For obvious reasons, ontogenetic studies of long bone growth in nonhuman primates that have included age as a variable have mainly been of captive animals (Gavan, 1971; Jungers and Fleagle, 1980; Schaefer and Nash, 2007; Young et al., 2010), which may vary in a number of ways from wild populations in terms of mechanical loadings and other environmental variables (Fleagle and Meldrum, 1988; O'Regan and Kitchener, 2005). As far as we are aware, the present study is the first to include chronological ages of wild individuals to study ontogenetic trajectories of long bone strengths in a nonhuman

primate. Finally, many previous studies have used linear regression analysis (usually on log-transformed data) to analyze ontogenetic trajectories, which may obscure more subtle non-linear trends, particularly during early stages of growth (Ruff, 2003b; Schaefer and Nash, 2007).

Mountain gorillas (*Gorilla beringei beringei*) make a particularly interesting model for studying the relationship between locomotor behavior and skeletal morphology during growth. Here we follow the lead of most recent investigators in assigning specific status to *G. beringei* and subspecific status to *G. beringei beringei*, which excludes *G. beringei graueri* (Groves, 2001; Tocheri et al., 2011; Scally et al., 2012). Virunga mountain gorillas were the subject of a previous detailed study of locomotor ontogeny (Doran, 1997), carried out on a sample of habituated individuals monitored by the Karisoke Research Center in Volcanoes National Park, Rwanda. Locomotor behavior was shown to change dramatically during development in Virunga mountain gorillas, with infants prior to the third year of life engaging in much more frequent arboreal behavior, including climbing and forelimb suspension, than older juveniles and adults (Fig. 1). Individuals observed by Doran (1997) were members of the same general population from which the current study specimens were derived (see below). If morphology parallels behavior, then we would predict similarly marked changes in skeletal structure during ontogeny. Specifically, based on previous observations (Carrier and Leon, 1990; Ruff, 2003b), there should be greater changes at or near the age of the locomotor transition in inter-limb diaphyseal strength proportions than in length proportions, with relatively greater forelimb bone strength in young infants than in older juveniles or adults.

Mountain gorillas are also interesting in that adults exhibit the lowest ratio of humeral/femoral diaphyseal strength of any nonhuman hominoid (Ruff, 2002). They are also the most terrestrial of all nonhuman hominoids (as adults) (Schaller, 1963; Tuttle and Watts, 1985; Doran, 1996, 1997; Remis, 1998). However, like all gorillas, they have long forelimbs relative to hind limbs — longer

than in chimpanzees (Schultz, 1937; Jungers and Susman, 1984; Ruff, 2002; also see below). Western lowland gorilla (*Gorilla gorilla gorilla*) adults are much more arboreal than mountain gorillas (Remis, 1995, 1997, 1998, 1999; Doran, 1996; Masi, 2004; Doran-Sheehy et al., 2009; Doran-Sheehy, Personal communication). While mountain and western lowland gorilla adults have similar inter-limb length proportions,[1] they have different strength proportions, with greater forelimb/hind limb strength in western lowland gorillas (Ruff, 2002). Thus, differences between the species in strength proportions correspond more closely to behavioral differences. If this is also true during development, we would expect infant mountain gorillas to show inter-limb strength proportions more similar to those of adult western lowland gorillas than to adult mountain gorillas.

In this study we test these predictions through an ontogenetic analysis of limb bone structural properties in a sample of *G. beringei beringei*, with comparisons with both adult mountain gorillas from the same population as well as western lowland adult gorillas.

Materials and methods

Samples

A total of 18 immature *G. beringei beringei*, 14 adult *G. b. beringei*, and 12 adult *G. gorilla gorilla* were included in the study (Table 1). Fifteen of the immature and six of the adult *G. beringei beringei* specimens were collected as part of the Mountain Gorilla Skeletal Project (MGSP), a collaborative effort to assist the Rwanda Development Board's Department of Tourism and Conservation (RDB, the national parks authority) in the recovery and curation of skeletal remains of recently-deceased mountain gorillas from the Volcanoes National Park in Rwanda (McFarlin et al., 2009, 2013). Nine individuals from this subset of our sample are of known age, having been the focus of observational studies and health monitoring by the Dian Fossey Gorilla Fund International's Karisoke Research Center and the Gorilla Doctors in partnership with RDB (Table 1). In two cases, the identity and/or chronological age of individuals is unknown; in these cases ages were estimated by the mountain gorilla veterinarians based on comparisons of dental and somatic development with those of other known-aged individuals, or based on dental histology (McFarlin et al., 2013). In four other cases (2.45, 2.76, 3.83, 5.48 years old), an individual is considered of 'probable ID', as of yet unconfirmed. These individuals died before the Mountain Gorilla Skeletal Project began, and were necropsied from 2001 to 2006. However, other contextual information (burial label) was lost prior to initiation of the project. In these four cases, identity was determined by the Mountain Gorilla Veterinary Project based on matching of dental emergence status, linear measurements, and other skeleto-dental observations against data recorded in necropsy reports dating from that time interval. Dental emergence status and skeletal dimensions are also consistent with other similarly-aged individuals of established identification. Genetic and histological analyses are currently underway to provide positive identifications for these individuals.

Three of the immature *G. b. beringei* specimens are from the collections of the Smithsonian Institution (Washington, DC). Ages for these individuals were estimated based on dental development and comparisons with the MGSP known-age sample, as well as published data on deciduous and adult tooth emergence for gorillas (Smith et al., 1994). Eight *G. b. beringei* adults were also obtained from the Smithsonian Institution. Although exact ages are known for the MGSP adults, all adults are grouped together for the purposes of this study. All Smithsonian *G. b. beringei* specimens included in the current study were originally collected in the Virunga mountains region of neighboring Rwanda and Democratic Republic of Congo.

The 12 *G. gorilla gorilla* adults included in the study were obtained from the collections of the Smithsonian Institution and the Harvard Museum of Comparative Zoology (MCZ) (Table 1). All identified specimens were collected in Gabon or Cameroon (in one case the locality was unlisted). All specimens in the study were wild-shot or collected. Most of the adult specimens from the Smithsonian Institution and Harvard MCZ were included in a previous study (Ruff, 2002).[2] Males and females are combined in the present analyses. Although adult mountain gorilla females are somewhat more arboreal than males, the frequency of arboreal behavior as a percentage of total locomotor behavior in adults is very low in both sexes (Schaller, 1963; Tuttle and Watts, 1985; Doran, 1997). Sex differences in arboreality may be more marked in adult western lowland gorillas, although both sexes are much more arboreal than either sex of adult mountain gorilla (Remis, 1995, 1997, 1998, 1999; Doran, 1996; Masi, 2004; Doran-Sheehy et al., 2009; Doran-Sheehy, Personal communication). Among immature mountain gorillas, there are no apparent differences between the sexes at similar ages in any of the inter-limb proportions examined here, and differences between adult males and females within mountain or western lowland gorillas are all nonsignificant.

'Adult' was defined as complete fusion of all long bone epiphyses. Two of the *G. gorilla gorilla* specimens had partially unfused epiphyses but fully erupted M3s, and were grouped with adult specimens for comparative purposes. For statistical comparisons, immature *G. b. beringei* specimens are grouped into two age groups: under two years and two-11 years. This follows from the behavioral study of this population (Doran, 1997), where, as discussed above, major changes in locomotor behavior occurred after two years of age. Data scatters for all individual specimens against age are also shown here for visual assessment of age (and species) effects.

Dimensions

Diaphyseal lengths of the femur, tibia, humerus, radius and ulna were taken on all immature specimens, and maximum lengths on mature specimens, in all cases parallel to the long axis of the diaphysis (in two cases where epiphyses were partially fused – 9.00 and 10.69 years (Table 1) – both lengths were taken). Another length measurement, length', defined as in Ruff (2002), was taken on mature specimens and used to identify diaphyseal cross section locations. Length' is equivalent to inter-articular length, except that in the femur it is measured to the proximal surface of the femoral neck rather than the head. Sections at 50% of length' in the femur, tibia, radius and ulna, and at 40% of length' from the distal end of the humerus, were analyzed, as in previous studies (Ruff, 2002, 2003b, 2009). In immature specimens, equivalent locations were identified by comparing percentages of length' with percentages of diaphyseal length in specimens with partially fused epiphyses. The equivalent locations, measured from the distal end of the diaphysis, were 45% for the femur, 41% for the humerus, 53% for the tibia, and 50% for the radius and ulna. Values for the femur and humerus are almost identical to those determined for a juvenile human sample

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[1] Earlier claims for lower intermembral indices in mountain gorillas (Schultz, 1934; Groves, 1970) have been disproven by more recent evidence (Groves and Stott, 1979; Jungers and Susman, 1984; Taylor, 1997; and see below).

[2] Two specimens of *G. beringei* (from the Harvard MCZ) included in this previous study were not included here, because it is apparent from their collection locality that they are *G. beringei graueri*.

Table 2
Age group and adult species comparisons for diaphyseal strengths.[1]

| Property[4] | G. beringei beringei | | | | | | G. gorilla gorilla | |
| | <2 yr (n = 8)[2] | | 2–11 yr (n = 10) | | Adult (n = 14)[3] | | Adult (n = 12) | |
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
ln(FZp/HZp)	0.167[a]	0.042	0.493[b]	0.020	0.502[b]	0.033	0.257[a]	0.030
ln(FZp/RZp)	1.573[a]	0.050	2.055[b]	0.042	2.132[b]	0.037	1.694[a]	0.043
ln(FZp/UZp)	1.560[ab]	0.063	1.680[a]	0.078	1.556[ab]	0.028	1.484[b]	0.037
ln(TZp/HZp)	−0.785[a]	0.076	−0.512[b]	0.026	−0.467[b]	0.031	−0.585[b]	0.053
ln(TZp/RZp)	0.655[a]	0.076	1.049[b]	0.038	1.163[b]	0.033	0.852[a]	0.058
ln(TZp/UZp)	0.631[a]	0.097	0.675[a]	0.075	0.591[a]	0.035	0.643[a]	0.059
ln(UZp/RZp)	0.013[ad]	0.053	0.375[bd]	0.078	0.587[c]	0.049	0.210[d]	0.030

[1] Different superscripts indicate significant ($p < 0.05$) differences between the four groups, Tukey tests. For example, groups with superscript 'a' are nonsignificantly different from each other, but are different from groups with superscript 'b', etc.
[2] $N = 7$ for ratios involving the tibia.
[3] $N = 13$ for ratios involving the ulna.
[4] F: femur; H: humerus; T: tibia: R: radius: U: ulna; Zp: polar section modulus.

(the radius and ulna were not included in that study) (Ruff, 2003b). One immature *G. beringei beringei* (0.45 year-old female) was missing a tibia, and one adult *G. b. beringei* was missing an ulna.

Cross-sectional geometric properties were determined using CT scanning. All immature specimens, the six adult MGSP specimens, and two of the adult *G. gorilla gorilla* specimens from the Smithsonian Institution were scanned using a pQCT (peripheral quantitative CT) (Ferretti et al., 1996) scanner in our laboratory (Habib and Ruff, 2008). The maximum resolution of the system is 0.09 mm, allowing clear resolution of long bone periosteal and endosteal surfaces in even neonatal specimens. Larger specimens were scanned with appropriately larger resolutions, varying from 0.15 to 0.30 mm in adults. Tests carried out with cylindrical phantoms constructed of bone-equivalent material (White et al., 1977) produced errors of less than 1% in calculation of section properties in specimens as small as 3.0 mm in external breadth and 0.5 mm in cortical thickness, below the size range of the smallest specimens in this study. The other 18 adult specimens were CT scanned using medical CT scanners as described previously (Ruff, 2002). Spatial resolution of these scanners is about 0.3 mm, which is more than adequate for resolving cortical boundaries of adult gorilla long bones (Ruff and Leo, 1986), which in the present study ranged from about 3.0 to 9.0 mm in cortical thickness.

The pQCT system includes software for calculating standard section properties (areas, second moments of area, section moduli) directly from images. Section properties of specimens scanned using the medical CT scanners were derived from section images as described previously (Ruff, 2002). Only the polar section modulus, Z_p, was analyzed here. The polar section modulus is a good overall indicator of torsional and (twice) average bending strength and as such has been used in previous ontogenetic studies of long bone structure in primates (Ruff, 2003b; Young et al., 2010). When sections depart too far from circularity, the polar second moment of area, J (and by extension, Z_p, which is derived from J) becomes less accurate as a measure of torsional rigidity (Piziali et al., 1976; Daegling, 2002). However, even in these cases Z_p is still a good indicator of average bending strength: regressions of Z_p on the average of bending strengths (section moduli) measured in the anteroposterior (A-P) and mediolateral (M-L) planes for the five long bones in the present study sample all have r^2 values of 0.999 or higher, and percent standard errors of estimate of 5% or less. In a previous analysis of a wider range of anthropoid primates, the A-P section modulus, Z_x, rather than Z_p, was used to assess bending strength of the hind limb bones (Ruff, 2002). However, a major goal of that study was to distinguish species engaging in frequent leaping and running behaviors, which is not a primary focus of the

present study. Use of Z_x rather than Z_p for the femur and tibia has no effect on any of the statistical results of the present study.

The pQCT software calculates Z_p directly as J/(maximum distance from section centroid to outer surface). Software used previously to analyze adult nonhuman hominoid long bone sections did not include calculation of Z_p, which instead was approximated by dividing J by the average of half the A-P and M-L external breadths (Ruff, 2002). However, while internally consistent, this method also systematically overestimates true Z_p (because the maximum distance from the centroid to the outer surface will always be larger than the average distance). To combine the old and new adult data, we calculated correction factors for the previous Z_p values based on 12 individuals aged six years or over (including one 7.40 year-old *G. gorilla gorilla* specimen not included in the present study) for which we had pQCT Z_p values, as well as values estimated using the old method. These average correction factors (and their standard deviations [SD]) were as follows: femur: 0.989 (0.022); tibia: 0.822 (0.028); humerus: 0.956 (0.027); radius: 0.905 (0.044); ulna: 0.863 (0.062). The difference between correction factors reflects the relative circularity of the sections (less correction in the rounder femur and humerus) and the consistency of shape (larger SD in the more irregularly shaped radius and ulna).

Analyses

Because numerous previous studies have demonstrated a strong correlation between inter-limb proportions and locomotor behavior among primates (e.g., Schultz, 1937; Jungers, 1985; Schaffler et al., 1985; Ruff, 2002, 2003b), the present study is concentrated on direct comparisons between hind limb and forelimb properties. We also do not have body mass data for any of these specimens, so an allometric study of limb length or strength relative to body size is not feasible. Following previous investigations (Ruff, 2002, 2003b), proportional differences are evaluated through analysis of log ratios of properties (see above references for discussion and rationale). For consistency with the previous study of human and baboon ontogeny (Ruff, 2003b), these are expressed as hind limb to forelimb ratios. For bone length analyses, diaphyseal lengths are used for immature specimens, and maximum lengths for adults (for the two *G. beringei beringei* adolescents with partially fused epiphyses, diaphyseal lengths are used).

Tukey multiple comparison tests are used to test differences in strength proportions between the three *G. beringei beringei* age groups and the *G. gorilla gorilla* adults, with $p < 0.05$ considered significant. In almost all cases, distributions within groups are
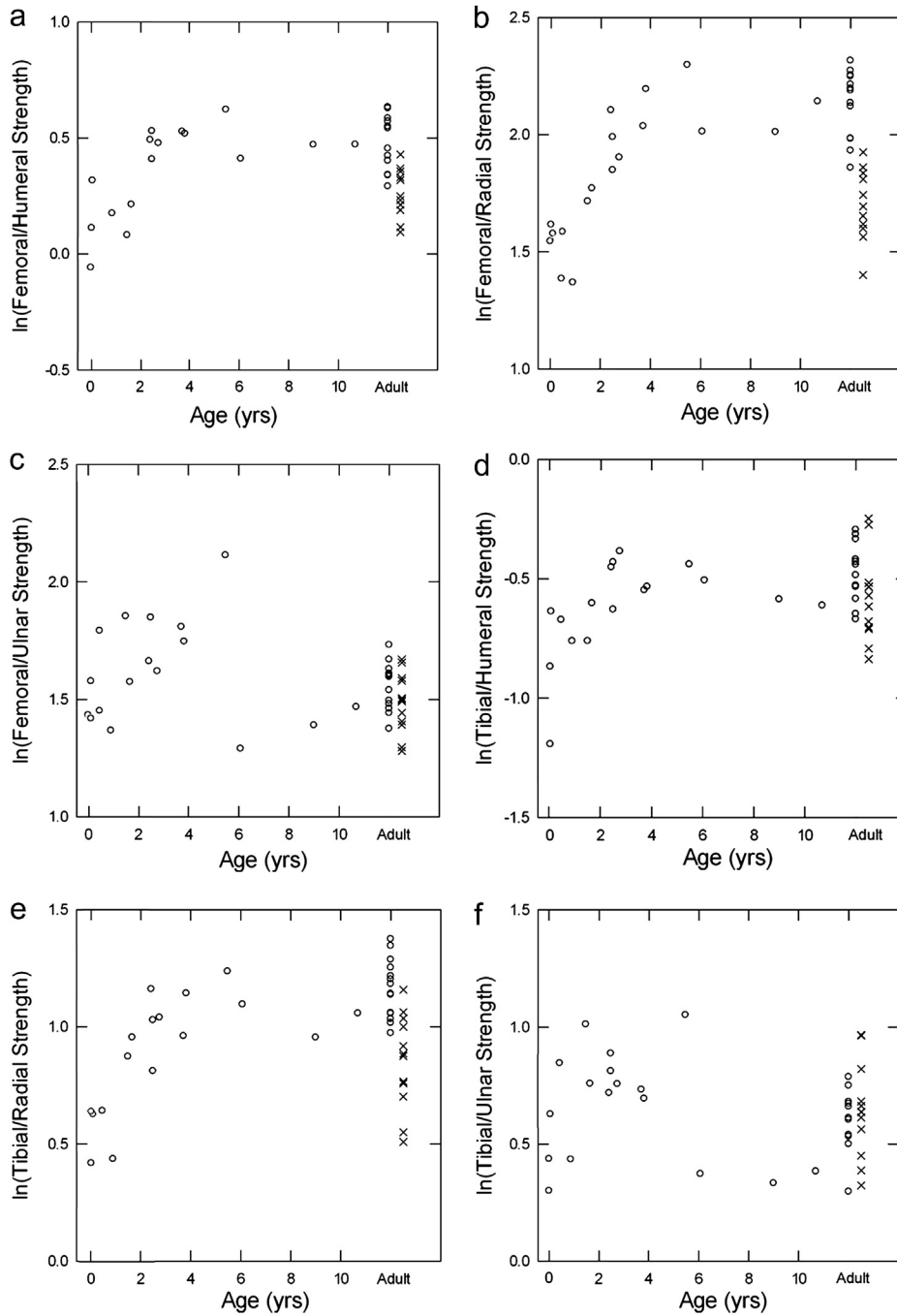
Figure 2. Hind limb/forelimb diaphyseal strength (polar section modulus, Z_p) proportions in immature and adult *G. beringei beringei* (circles) and adult *G. gorilla gorilla* (crosses): a) femur/humerus; b) femur/radius; c) femur/ulna; d) tibia/humerus; e) tibia/radius; f) tibia/ulna.

normal (nonsignificant skewness or kurtosis, nonsignificant Shapiro–Wilks statistic). The only exception is tibia to ulna Z_p in adult *G. beringei beringei*, with a marginally significant Shapiro–Wilks value ($p = 0.04$). As shown below, no significant inter-group differences were found for this property. Two sample *t* tests are used to assess differences in diaphyseal length proportions between the two immature *G. beringei beringei* groups, and in maximum length proportions between the two adult groups. Femur/humerus, tibia/radius, and total hind limb (femur + tibia) to total forelimb (humerus + radius) length proportions are compared. Because the relative size of epiphyses in the five different bones is different, the two types of length proportions are not directly equivalent, so

comparisons are not carried out between juveniles and adults. However, adults are included in scatterplots for visually assessing the degree of overlap between species compared with that between the two immature *G. beringei beringei* age groups.

Results

Results of Tukey multiple comparison tests of bone strength proportions between *G. beringei beringei* age groups and *G. gorilla gorilla* adults are given in Table 2. Scatterplots of hind limb/forelimb strength proportions against age are shown in Fig. 2a–f. All adults are grouped together at age 12 for graphing purposes. In the
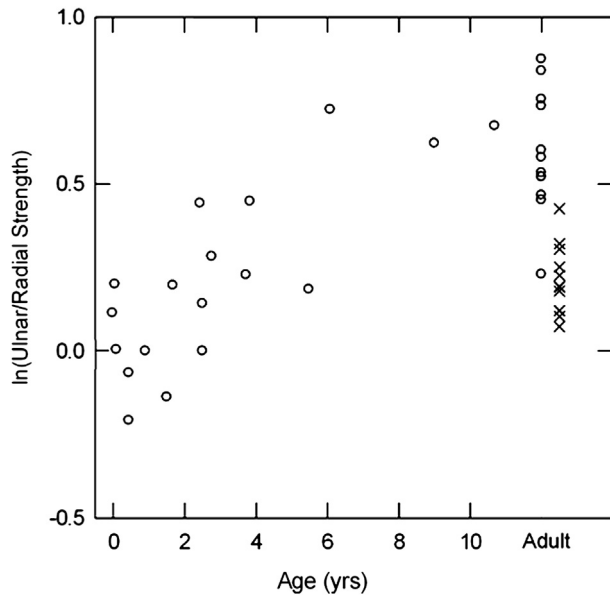
Figure 3. Ulnar/radial diaphyseal strength proportions (polar section modulus, Z_p) in immature and adult *G. beringei beringei* (circles) and adult *G. gorilla gorilla* (crosses).

following description of results, for convenience, 'infant' refers to individuals under two years of age, and 'juvenile' to two-11 year-olds. We note that individuals up to 3.5 years of age are traditionally recognized as infants, according to other behavioral criteria (Watts and Pusey, 1993; Williamson and Gerald-Steklis, 2001).

Except for comparisons involving the ulna, all hind limb/fore-limb strength proportions show a common developmental pattern among *G. b. beringei* of low values in infants, increases in juveniles, and no further change in adults (Fig. 2, Table 2). The change in proportions after two years of age is particularly abrupt in femoral/humeral strength (Fig. 2a), with slightly more gradual changes between 1.5 and 2.5 years in other strength proportions (Fig. 2b, d, e). However, there is no indication of a continuing positive trend among two to 11 year-old juveniles (no significant linear regression slopes, $p > 0.10$) or into adulthood. *G. g. gorilla* adults have signif-icantly lower femoral/humeral, femoral/radial, and tibial/radial strength proportions than *G. b. beringei* adults or juveniles, but are nonsignificantly different from *G. b. beringei* infants in these proportions.

Strength proportions involving the ulna show a more complex pattern of age and species differences. There are no significant age group differences within *G. b. beringei* in femoral/ulnar or tibial/ulnar proportions (Table 2). However, there is an apparent decline in these proportions among the oldest juveniles (six to 11 years) (reaching statistical significance in linear regressions among juve-niles for tibial/ulnar strength, $p < 0.05$) (Fig. 2c, f). The increased variation among juvenile *G. b. beringei* is also indicated by the much larger standard errors for these proportions compared with those for other hind limb/forelimb strength proportions in this group (Table 2). *G. gorilla gorilla* and *G. b. beringei* adults are not signifi-cantly different in femoral/ulnar and tibial/ulnar strength, although juvenile *G. b. beringei* as a group have greater femoral/ulnar strength than adult *G. gorilla gorilla*.

The contrast in age and species differences between hind limb/forelimb strength indices involving the humerus and radius and those involving the ulna implies that the ulna is strengthened relative to other forelimb long bones in *G. b. beringei*. This is confirmed by direct comparisons between the ulna and radius (Table 2 and Fig. 3). Ulnar/radial strength is significantly greater in adult *G. b. beringei* than in adult *G. g. gorilla*. Furthermore, this dif-ference develops gradually in *G. b. beringei*, with low values in in-fants, higher values in juveniles (as a whole), and a further increase in adults. This is the only strength proportion (intra- or inter-limb) to show a significant difference between juvenile and adult *G. b. beringei*, i.e., a continuing age trend (Table 2). The change among juveniles appears to occur prior to six years of age, with older ju-veniles being similar to adults (Fig. 3) (linear regression on age among juveniles, $p < 0.05$). Infant and juvenile *G. b. beringei* are nonsignificantly different in ulnar/radial strength from adult *G. g. gorilla*. Other comparisons between the humerus and ulna and radius (not shown) also support an increase in ulnar relative to radial strength during development in *G. b. beringei*, with a signif-icant increase in ulnar/humeral strength and a significant decline in radial/humeral strength between infant and older *G. b. beringei*. Adult *G. g. gorilla* are significantly different than *G. b. beringei* in both proportions, but not significantly different from infant *G. b. beringei*.

Comparisons of inter-limb bone length proportions are shown in Table 3 and Fig. 4a–c. Femoral/humeral, tibial/radial, and total hind limb/total forelimb length proportions are higher in infant than in juvenile *G. b. beringei*. However, this is due to some very high indices in four out of the five youngest individuals (three out of four for comparisons involving the tibia) – those under 0.5 years of age (also see Table 1). The three older infants are indistinguishable from juveniles or adults (Fig. 4a–c). Thus, there is no evidence for any change in length proportions at about two years of age. Adult *G. b. beringei* and *G. g. gorilla* show no significant difference in femoral/humeral length proportions, but adult *G. b. beringei* have relatively shorter distal hind limbs (tibia/radius length) and total hind limbs.

Table 3
Age group and adult species comparisons for bone lengths.

Property[c]	G. beringei beringei						G. gorilla gorilla	
	<2 yr (n = 8)[a]		2–11 yr (n = 10)		Adult (n = 14)[b]		Adult (n = 12)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
ln(F/H diaph.)	−0.135*	0.012	−0.164*	0.005				
ln(T/R diaph.)	−0.151*	0.014	−0.194*	0.011				
ln(Hind/Fore diaph.)	−0.144*	0.013	−0.177*	0.007				
ln(F/H max.)					−0.152	0.007	−0.142	0.008
ln(T/R max.)					−0.177*	0.005	−0.147*	0.008
ln(Hind/Fore max.)					−0.164*	0.005	−0.142*	0.007

*$p < 0.05$, t tests, between age groups for immature *G. beringei beringei*, and between species for adults.
[a] $N = 7$ for ratios involving the tibia.
[b] $N = 13$ for ratios involving the ulna.
[c] F: femur; H: humerus; T: tibia: R: radius: U: ulna; Hind: total hind limb (femur + tibia); Fore: total forelimb (humerus + radius); diaph.: diaphyseal length; max.: maximum length.

Discussion

Inter-limb strength proportions

Similar to results found earlier using a somewhat smaller sample (Ruff, 2002), mountain gorilla adults have generally increased hind limb/forelimb strength proportions compared with western lowland gorillas. In fact, adult mountain gorillas have the highest such proportions among extant nonhuman hominoids (Ruff, 2002). However, this is not the case for infant mountain gorillas, who have strength proportions indistinguishable from those of adult western lowland gorillas. Older immature mountain gorillas are not intermediate in this regard. Rather, beginning in the third year of life, they exhibit strength proportions similar to those of adult mountain gorillas and different from those of adult western lowland gorillas.

This age trend closely parallels observed behavioral changes during ontogeny in Virunga mountain gorillas (Doran, 1997). Mountain gorillas begin to engage in locomotor activities at 3.5-four months of age, but significant independent locomotion away from the mother does not begin until about six months. Locomotor activity increases until 17–21 months, with much of the activity taking place in arboreal environments, including a high percentage of climbing and forelimb suspensory behavior (Fig. 1). As Doran notes, infants of 17–21 months of age "climb whenever the opportunity presents, are very suspensory in their behavior, are adept climbers, and spend more time above ground … than any other age class" (1997: 331). However, "[t]here is a dramatic shift to more 'adult-like' locomotion in 2-year-old infants … Locomotor activity is now dominated by quadrupedalism, which accounts for 75% of all locomotor activity … The frequency of climbing and scrambling decreases dramatically" (Doran, 1997: 332–333). Older juveniles continue to remain more terrestrial, with quadrupedal knuckle-walking dominating locomotor behavior.

Western lowland gorillas of all ages include a significant arboreal component in their locomotor repertoire, with even large adult males engaging in climbing, scrambling and occasional forelimb suspensory activities, although such behaviors are more common among juveniles and adult females (Remis, 1998; Masi, 2004; Doran-Sheehy et al., 2009; Doran-Sheehy, Personal communication; Remis, Personal communication). Their lower femoral/humeral strength proportions, compared with adult mountain gorillas, are consistent with relatively greater mechanical loading of the forelimb, paralleling associations between relative limb strength and locomotor behavior found among anthropoid primates as a whole (Schaffler et al., 1985; Ruff, 2002). Their similar strength proportions to more arboreal infant mountain gorillas are also consistent with this explanation.

While body size differences − throughout ontogeny and between species − certainly affect both behavior and limb proportions (e.g., Inouye, 1992; Doran, 1997; Taylor, 1997; and see below), allometry alone is unlikely to explain the differences in bone strength proportions observed here. Captive western lowland gorillas continue to increase in body mass until at least 10 years of age (Leigh and Shea, 1995, 1996), and growth in size (limb bone lengths and articular breadths) also continues in our sample beyond six years of age (data not shown), yet almost all inter-limb bone strength proportions stabilize at about two to three years. Adult mountain and western lowland gorillas are very similar in body mass (Jungers and Susman, 1984; Smith and Jungers, 1997),[3]

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[3] As noted earlier, we have no associated body masses for the present study samples. However, femoral head superoinferior breadth, which is a good body mass estimator in nonhuman hominoids (Ruff, 2003c), is not significantly different, within sex, between *G. b. beringei* and *G. g. gorilla* adults in our samples.
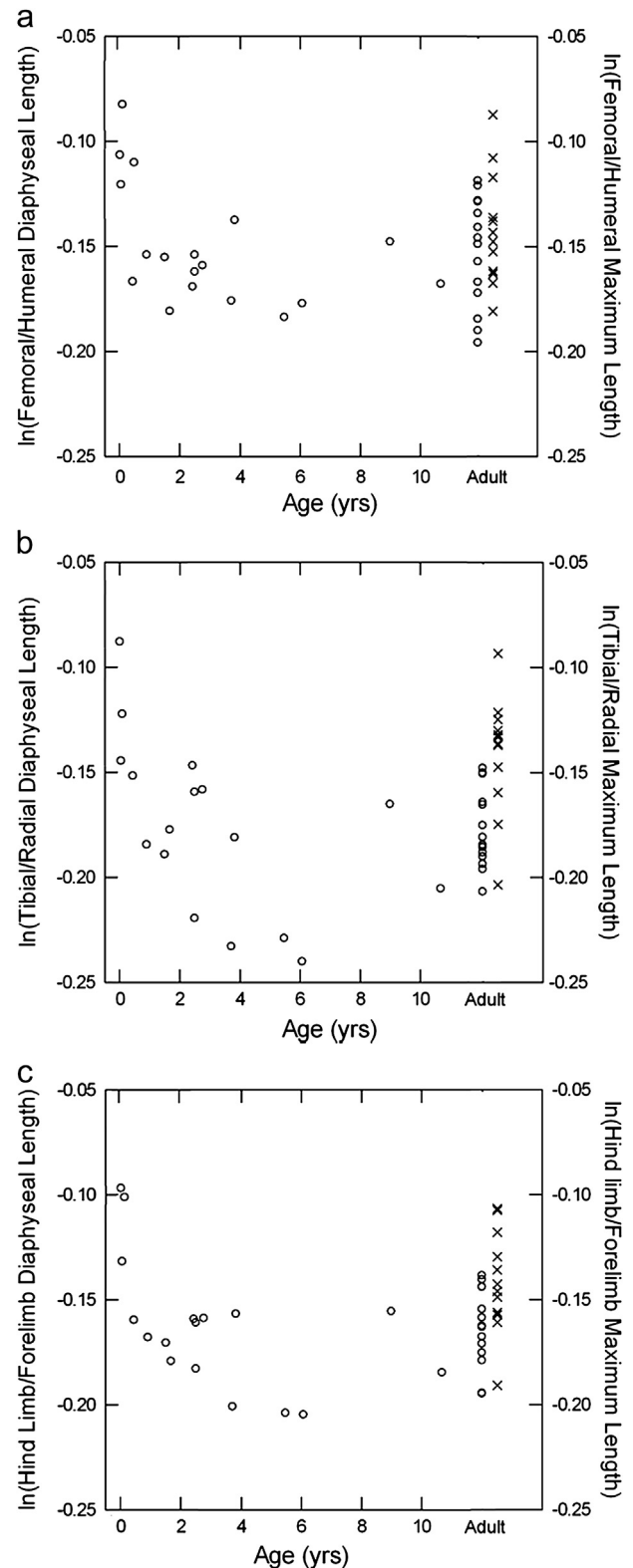

Figure 4. Hind limb/forelimb bone length proportions in immature and adult *G. beringei beringei* (circles) and adult *G. gorilla gorilla* (crosses): a) femur/humerus; b) tibia/radius; c) total hind limb (femur + tibia)/total forelimb (humerus + radius). Note that immature data are based on diaphyseal lengths, and adult data on maximum lengths, so that the two ratios are not directly comparable.

yet they differ significantly in bone strength proportions. This argues for direct behavioral rather than general growth or size-related factors as being the most important influence on bone strength parameters.

Inter-limb length proportions

Inter-limb bone length proportions do not show the same developmental trajectories within mountain gorillas, or the same differences between adult mountain and western lowland gorillas, as do strength proportions. Adult mountain gorillas do not have greater hind limb/forelimb length proportions than adult western lowland gorillas. In fact, their length proportions are lower for the distal limb elements, leading to an overall relatively shorter hind limb/longer forelimb among adults. This supports other observations (Jungers and Susman, 1984; Taylor, 1997; also see Groves and Stott, 1979) that adult mountain gorillas do not have relatively short forelimbs, contra the conclusions of some earlier studies (Schultz, 1934; Groves, 1970). (Schultz (1930) did point out the relatively longer forearms, i.e., higher brachial index, of mountain gorillas.) Forelimb to hind limb length has been shown to exhibit positive allometry across both primates as a whole and within more restricted taxonomic/phylogenetic groupings (Jungers, 1984a, 1985), which has been interpreted as an adaptation to facilitate climbing in a large, clawless animal (Cartmill, 1974; Jungers, 1978, 1985). Thus, relatively long forelimbs can be viewed as a prerequisite for effective climbing in a primate the size of *Gorilla*. Mountain gorillas also have a relatively large humeral head articular surface (Ruff, 2002), again facilitating varied forelimb positioning and thus climbing and arboreal scrambling (Rose, 1989; Larson, 1993). As noted by Schaller (1963), adult Virunga mountain gorillas are quite capable climbers — they just climb very rarely. The arboreal competence of gorillas in general is supported by a relatively low observed frequency of limb bone fractures (Schultz, 1937; Randall, 1944; Brandwood et al., 1986; Lovell, 1990, 1991; although also see Jurmain, 1997).

Mountain gorillas are born with relatively more equal limb lengths, but due to more rapid growth in the forelimb, there is an abrupt decline in hind limb/forelimb length by five to six months of age, followed by no further consistent change among older juveniles. Thus, the inter-limb length proportions of mountain gorillas are established early in life, prior to any significant independent locomotor activity (see above). Even older infant gorillas are not small: captive western lowland gorillas average about 30 kg in body mass at two years of age (Leigh and Shea, 1995, 1996). Developing relatively long forelimbs prior to this age is thus advantageous, given the typical arboreal locomotor repertoire of very young gorillas. In many ways this can be seen as analogous to the relatively long hind limbs that are characteristic of human infants, even before they begin to walk bipedally (Ruff, 2003b). Again, as in humans, there is no abrupt shift in bone length proportions at the onset of a major change in locomotor behavior, while there is a shift in strength proportions. This is consistent with greater genetic developmental canalization of long bone lengths relative to strengths, as noted previously (Ruff, 2003b and references therein). The apparent very rapid change in length proportions in very young infant mountain gorillas is interesting and not paralleled in human infants (Ruff, 2003b). Humans develop relatively longer lower limbs in utero and appear to maintain a fairly similar growth differential between the limbs after birth (Ruff, 2003b). Whether very early postnatal growth trends in mountain gorillas represent a continuation of or deviation from prenatal trends cannot yet be evaluated based on the very sparse data available (Schultz, 1934).

Previous ontogenetic studies of gorillas have reported conflicting results regarding changes in inter-limb length proportions

during growth (Lumer, 1939; Schultz, 1956; Shea, 1981; Jungers and Susman, 1984; Taylor, 1997). However, direct comparisons are hampered by differences in the dimensions evaluated (total limb length versus just the proximal elements) and age range included (although not explicitly stated, based on comparisons with the present study bone lengths, very few previous studies appear to have included infants under two years of age). Also, almost all of these studies were of western lowland rather than mountain gorillas. Taylor (1997) did carry out growth analyses of both *G. gorilla* and *G. beringei* (which actually combined *G. b. beringei* and *G. b. graueri*; Taylor, Personal communication), although her sample included no infant mountain gorillas. The ontogenetic trajectory for femoral/humeral length among *G. beringei* was isometric in her sample, which is consistent with the present study results for immature specimens over six months of age. Interestingly, her growth trajectories for femoral against humeral length in a western lowland gorilla sample, which did include very young (small) infants, were slightly negatively allometric. If a log-linear regression of femoral to humeral length is run through the entire immature present study sample, the slope is also slightly negatively allometric (0.954, 95% CI: 0.911–0.997); the same is true for total (diaphyseal) hind limb/forelimb length (0.947, 95% CI: 0.903–0.991). This suggests that *G. gorilla* and *G. beringei* may have similar ontogenetic trajectories for inter-limb length proportions. However, it is also evident that this approach does not allow assessment of more detailed features of the growth process, i.e., the rapid change in proportions soon after birth, and the stable proportions thereafter (e.g., Fig. 4a). Allowance for non-linear (or log-linear) growth and inclusion of actual ages are necessary to delineate such trends (also see Ruff, 2003b).

Ulnar/radial strength

The only structural proportions to show a consistent age trend among older juvenile mountain gorillas, i.e., after infancy, were those involving ulnar strength. Relative to the hind limb or to other forelimb bones, the ulna gradually increased in strength from late infancy through older juveniles and adults. The ulna was also relatively stronger in adult mountain gorillas than in adult western lowland gorillas, when compared with the radius or the humerus. The change in proportions during growth in mountain gorillas continued well after the shift at about two years from more arboreal to terrestrial locomotion, so this alone seems unlikely to explain it. It is possible that these trends are related to more subtle ontogenetic changes in locomotor behavior in mountain gorillas, specifically, changes in knuckle-walking behavior. Knuckle-walking gradually replaces palmigrade quadrupedalism from six months to the third year of life in mountain gorillas (Doran, 1997). However, a fully adult form of knuckle-walking may not have been practiced until later in development. During knuckle-walking in adult gorillas, the forearm is fully pronated and the hand and wrist are held in the coronal plane (Tuttle and Watts, 1985). Tuttle felt that even younger juvenile gorillas "are likely to fully pronate the hand during knuckle-walking" (1969: 856); however, he presented no quantitative data to support this claim. Based on a preliminary study, Inouye (1994b) repeated this assertion. However, more detailed consideration of her complete set of behavioral observations of captive western lowland gorillas (Inouye, 1994a and Personal communication) indicates that typical hand postures during knuckle-walking do change during development. Specifically, in her 'Size 1' age category, which included individuals under about 40 kg, or about five years of age (Leigh and Shea, 1995, 1996), coronal and sagittal hand postures during knuckle-walking were close to equal in frequency — about 40% each, with 20% 'angled' between these extremes (Inouye, 1994a). Non-coronal positions were less
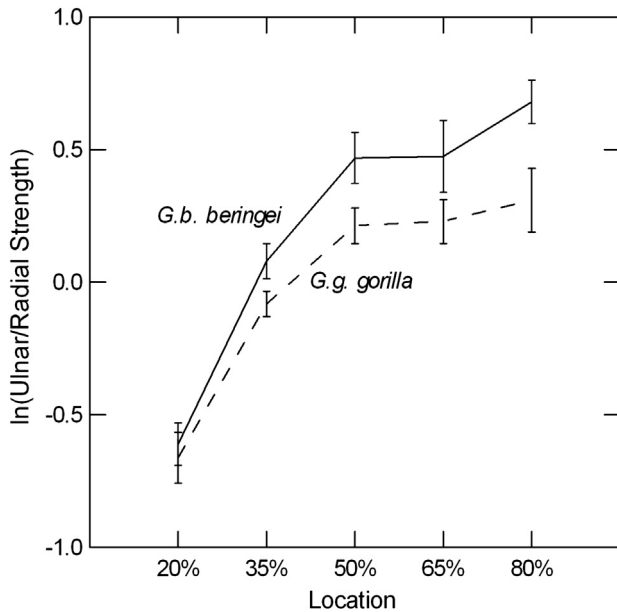
Figure 5. Ulnar/radial strength (polar section modulus, Z_p) proportions at five locations along the forearm, measured as percentages of radial length' from the distal end of the radius (see Ruff, 2002 for sample description). Mean ± 2 SE. Solid line: *G. beringei beringei*, dashed line: *G. gorilla gorilla* (all adults).

common in her 'Size 2' category (about 40–84 kg, or about five to nine years) – in this group about 60% were coronal, 13% sagittal, and 27% 'angled'. Adults (or adolescent males over 85 kg) used almost exclusively coronal hand postures (almost 80% of observations). Thus, juvenile gorillas, at least in this environment, gradually shift as they get older from using more variable hand postures to a more stereotypical coronal position during knuckle-walking, with the fully adult form of behavior not manifested until relatively late in development. This ontogenetic pattern is similar to that observed here for ulnar/radial strength changes (Fig. 3). Interestingly, chimpanzees of all ages also use less stereotypical coronal plane positioning of the hand and wrist during knuckle-walking than gorillas (Tuttle, 1969; Inouye, 1994a), and also have lower ulnar/radial strength proportions at midshaft than adult gorillas (Ruff, 2002), i.e., they are more similar in this respect to juvenile mountain gorillas.

In humans, mechanical loading under a compressive load applied to the hand is gradually transferred (in part) from the distal radius to the proximal ulna via the interosseous membrane (Birkbeck et al., 1997). It is highly likely that a similar mechanism characterizes African apes. Fig. 5 is a plot of ulnar to radial strength at five equally spaced locations along the forearm in mountain and western lowland gorilla adults. Data were derived from a previous study (Ruff, 2002; unpublished data except for midshaft [50%] location). As expected, the ulna/radius strength ratio increases from distal to proximal in both taxa. However, it does so at different rates: faster in mountain gorillas and slower in western lowland gorillas. Compressive loads would be transmitted from the hand to the distal radius in both species, and they have correspondingly similar ulnar/radial strength proportions at the most distal location (nonsignificantly different, t tests). However, they progressively deviate more proximally, with mountain gorillas having significantly larger ulna/radius ratios at all of the more proximal locations ($p < 0.05$, t tests). This implies more transfer of load from the radius to the ulna moving proximally along the forearm in mountain gorillas.

Terrestrial knuckle-walking constitutes a relatively greater percentage of total locomotor behavior in adult mountain gorillas than in adult western lowland gorillas (see references above). Assuming that adult mountain gorillas, like western lowland gorillas, knuckle-walk with a stereotypical pronated posture, then the pattern shown in Fig. 5 could be due to a greater percentage of forearm loading in this position in adult mountain gorillas. It would also be consistent with ontogenetic changes in structural proportions in mountain gorillas, again if juvenile mountain gorillas go through the same behavioral transition during knuckle-walking as western lowland juveniles. More data on hand position in mountain gorillas of all ages are needed to more fully evaluate this hypothesis.

In addition, further mechanical modeling of the forearm is needed to explore why knuckle-walking with a more pronated forearm might lead to greater load transfer to the ulna, in mountain gorillas relative to western lowland gorillas, and in gorillas as a whole relative to chimpanzees (Ruff, 2002). It is possible that differences in digit contact, i.e., more frequent use of the fifth digit during knuckle-walking in gorillas than in chimpanzees (Tuttle, 1969; Inouye, 1994a, b), could lead to increased loading on the ulnar side of the hand in gorillas (Dainton and Macho, 1999) and contribute to relatively greater ulnar loading more proximally, although Inouye (1994a, b) reported no age difference in digit use among western lowland gorillas. Elbow morphology is equivocal regarding greater load transfer through or stability of the ulnar articulation in gorillas versus chimpanzees, or mountain gorillas versus western lowland gorillas (Inouye, 2003; Drapeau, 2008). Loading of the forearm during locomotion in primates is complex, and other locomotor behaviors undoubtably also contribute to differential load sharing between the radius and ulna (Swartz et al., 1989; Demes et al., 1998). However, no specific behavioral differences between older juvenile and adult mountain gorillas that could account for the observed age trend in ulnar/radial strength were noted by Doran (1997), unless the slightly greater frequencies of climbing/suspensory behavior in older juveniles relative to adults (Fig. 1) produced relatively less loading of the ulna. If so, though, this behavioral difference between older juveniles and adults was not apparent in comparisons of other bone strength proportions (Fig. 2). More generally, the results of the present study suggest that in addition to joint morphology and other features of the hand bones (e.g., Inouye, 1994b; Dainton and Macho, 1999; Richmond and Strait, 2000; Kivell and Schmitt, 2009), relative strengths of the forearm bones might also preserve signals of subtle differences in knuckle-walking behavior or frequency.

Conclusions

Virunga mountain gorillas (*G. beringei beringei*) show distinct changes in relative limb bone strengths during development that correlate with changes in locomotor behavior. The transition from more arboreal behavior, including frequent climbing and forelimb suspension, to predominantly quadrupedal terrestrial locomotion in the third year of life is paralleled by an abrupt increase in hind limb relative to forelimb bone strength. The change in inter-limb strength proportions is not continuous throughout growth and is thus not simply a product of increasing body size. Furthermore, infant mountain gorillas much more closely resemble adult western lowland gorillas, which are more arboreal than adult mountain gorillas, in every comparison in which adults of the two species differ significantly. Again this indicates that locomotor behavior, rather than body size, is driving these differences in strength proportions.

Another more gradual ontogenetic change characterizes relative strengths of the forearm bones. Relative strength of the ulna

increases from infants through juveniles to adults in mountain gorillas. Again, infant and juvenile mountain gorillas are more similar to adult western lowland gorillas in this regard. This pattern may be a result of gradual acquisition of fully adult, stereotypically pronated knuckle-walking behavior in gorillas, although more detailed observational data and mechanical modeling of the forearm are necessary to evaluate this possibility.

Inter-limb length proportions follow a different developmental trajectory in mountain gorillas, with an initial, rapid decrease in hind limb/forelimb bone lengths between birth and about five months of age, followed by no consistent change. The initial change occurs prior to significant independent locomotion, and there is no discernable change at two years of age, when locomotion does change significantly. Thus, differential growth in limb bone lengths is not tightly correlated with locomotor behavior, i.e., changes in mechanical loadings on the limbs. Rather, the very early change in proportions may be necessary to facilitate efficient climbing, in older infants as well as juveniles and adults (when performed). Among adults, mountain gorillas have relatively longer forelimbs than western lowland gorillas, particularly in the distal long bones. This again implies little if any direct mechanical effect on limb bone length proportions, since mountain gorilla adults rarely engage in climbing or suspensory behaviors.

To what degree different morphological features are subject to developmental plasticity versus genetic constraint is an important issue in many comparative and functional studies of the primate limb skeleton, with implications for reconstructing behavior or phylogenetic relationships among both living and fossil taxa (Dainton and Macho, 1999; Richmond et al., 2001; Ward et al., 2001; Ruff, 2003a, 2009; Inouye and Shea, 2004; Kivell and Schmitt, 2009; Green and Alemseged, 2012). The different patterns of variation − ontogenetic as well as interspecies − in different long bone structural features among gorillas strongly support greater developmental plasticity, and thus potential relevance for reconstructing actual behavior, of long bone diaphyseal strength characteristics. Long bone lengths (and external articular size: Rafferty and Ruff, 1994; Ruff, 2002) appear to be more genetically constrained, and thus may reflect longer-term genetic selection. The results of the present study also demonstrate the power of ontogenetic analyses as 'natural experiments' to illuminate the factors underlying morphological variation within and between species.

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