Ontogeny of long bone geometry in capuchin monkeys (*Cebus albifrons* and *Cebus apella*): implications for locomotor development and life history

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Studies of a diverse array of animals have found that young individuals often have robust bones for their body size (i.e. augmented cross-sectional dimensions), limiting fracture risk despite general musculoskeletal immaturity. However, previous research has focused primarily on precocial taxa (e.g. rodents, lagomorphs, bovids, goats and emu). In this study, we examined the ontogenetic scaling of humeral and femoral cross-sectional robusticity in a mixed-longitudinal sample of two slow-growing, behaviourally altricial capuchin monkeys. Results showed that, when regressed against biomechanically appropriate size variables (i.e. the product of body mass and bone length), humeral and femoral bending strengths generally scale with negative allometry, matching the scaling patterns observed in previous studies of more precocial mammals. Additionally, bone strength relative to predicted loads (e.g. ‘safety factors’) peaks at birth and rapidly decreases during post-natal growth, falling to less than 5 per cent of peak values by weaning age. We suggest that increased safety factors during early ontogeny may be an adaptation to mitigate injury from falling during initial locomotor efforts. Overall, the results presented here suggest that ontogenetic declines in relative long bone strength may represent a common pattern among mammals that is perhaps preadaptive for different purposes among different lineages.

Keywords: cross-sectional geometry; allometry; ontogeny; biomechanics; locomotion

1. INTRODUCTION

Previous studies of a diverse array of mammals and birds have found that limb bone cross-sectional

dimensions generally scale with negative allometry during growth (e.g. rodents, lagomorphs, bovids, gulls and emu: Carrier 1983; Carrier & Leon 1990; Heinrich *et al.* 1999; Lammers & German 2002; Main & Biewener 2007). Negative ontogenetic allometry of cross-sectional dimensions indicates that young individuals have relatively robust bones for their body size. Increased geometric robusticity, in combination with reduced stiffness owing to incomplete mineralization (Carrier 1983; Carrier & Leon 1990; Heinrich *et al.* 1999) increases the work required to fracture young bone, thereby increasing the safety factor despite general musculoskeletal immaturity (Main & Biewener 2006). Proportionally stouter long bones have thus been argued to permit young animals to achieve strenuous, even adult-like levels of locomotor performance, such as during rapid group travel or predator evasion, with reduced risk of injury (Carrier 1996; Main & Biewener 2006).

However, previous research has focused on precocial taxa, in which neonates are morphologically well-developed and able to locomote soon after birth (Starck & Ricklefs 1998). Altricial species, in which neonates are poorly developed and relatively immobile, have received little attention. We examined longitudinal changes in humeral and femoral cross-sectional robusticity in two primates—white-fronted and brown capuchin monkeys (*Cebus albifrons* and *C. apella*). Primates, including capuchin monkeys, possess well-developed sensory systems at birth but are nevertheless strongly dependent on their parents for subsistence and transport, prompting Portmann (1958) to classify them as ‘secondarily altricial’. Moreover, capuchins are markedly slow-growing and behaviourally altricial, even relative to other closely related platyrrhine primates, and receive protracted parental investment throughout the first year of life (Garber & Leigh 1997). As such, we hypothesized that owing to their unique life history and behavioural ecology, growing capuchins should be sheltered from the selective pressures thought to influence bone growth in more precocial mammals. We tested two predictions suggested by this hypothesis. First, if negative allometry of bone robusticity is a developmental adaptation specific to precocial animals, measures of bone strength should scale isometrically or with positive allometry in growing capuchin monkeys. Second, if long bone growth trajectories are determined by the intensity of early locomotor demands, age-related changes in bone strength should be correlated with markers of juvenile ecological independence (Carrier & Leon 1990; Ruff 2003). Specifically, we hypothesized that the age at which peak relative bone strength is obtained should closely coincide with infant ecological independence, as gauged by the attainment of locomotor independence and weaning.

2. MATERIAL AND METHODS

The data for this study were taken from a longitudinal series of radiographs and associated morphometrics originating from a long-term study of the nutritional determinants of capuchin monkey growth (Fleagle & Samonds 1975). A subset of 15 male *C. albifrons* and three male *C. apella* were selected for the current study (i.e. all available control group males from the original study). Linear measurements on a total of 640 radiographs (*C. albifrons*: $n = 493$; *C. apella*: $n = 147$) were used to calculate two estimates of bone strength, assuming a circular cross-section (figure S1 in the

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Table 1. Ontogenetic scaling of humeral and femoral dimensions in *C. albifrons* and *C. apella*. Parameters are presented as value $\pm$ 95% confidence interval. Symbols in parentheses next to slopes indicate observed scaling trends: isometry (=), negative allometry (–), positive allometry (+). Intercepts have been back-transformed to the original units.

	expected slope	<i>C. albifrons</i>			<i>C. apella</i>		
		R^2	slope	intercept	R^2	slope	intercept
humerus Z_p (mm ³) on mass (kg)	1	0.90	0.96 ± 0.111 (=)	3.5 ± 0.40	0.78	0.60 ± 0.077 (–)	4.4 ± 0.66
femur Z_p (mm ³) on mass (kg)		0.90	1.14 ± 0.150 (=)	4 ± 0.47	0.94	1.01 ± 0.045 (=)	4.2 ± 0.36
humerus length (mm) on mass (kg)	0.33	0.94	0.53 ± 0.046 (+)	35.5 ± 1.51	0.97	0.42 ± 0.035 (+)	34.7 ± 1.11
femur length (mm) on mass (kg)		0.93	0.61 ± 0.049 (+)	42.4 ± 1.95	0.96	0.65 ± 0.035 (+)	37.8 ± 1.53
humerus Z_p (mm ³) on mass $\times$ length (kg mm)	0.75	0.92	0.62 ± 0.065 (–)	0.39 ± 0.110	0.78	0.42 ± 0.050 (–)	0.99 ± 0.263
femur Z_p (mm ³) on mass $\times$ length (kg mm)		0.93	0.77 ± 0.107 (=)	0.22 ± 0.115	0.93	0.63 ± 0.075 (–)	0.42 ± 0.128

electronic supplementary material). The assumption of circularity is justified for capuchin monkeys, as humeral and femoral anterior–posterior/mediolateral ‘shape ratios’ at midshaft (i.e. I_{XX}/I_{YY}) do not significantly differ from 1 (Runestad 1994). Polar section modulus (Z_p), proportional to average bending strength, was calculated as:

$$\frac{2\pi(T^4 - M^4)}{32T},$$

where T and M represent the total and medullary diameters of the bone, respectively (Ruff 2003). Geometric safety factor (GSF), an estimate of bone strength relative to predicted loads, was calculated as $Z_p(LM_b)^{-1}$, where L is maximum bone length, including epiphyses, and M_b is body mass. Assuming that substrate reaction forces (SRF) are proportional to body weight during ontogeny (cf. Main & Biewener 2004, 2007; Halleman *et al.* 2006), and SRF load arm lengths are proportional to bone lengths (Biewener 1983), the product of bone length and body mass represents a reasonable morphometric proxy for bending loads (Alexander 1983). All raw and calculated measurements are provided in the electronic supplementary material.

Bivariate log–log regressions were used to investigate the ontogenetic scaling of cross-sectional dimensions. Allometry was recognized if the 95 per cent confidence intervals on calculated slopes did not encompass the isometric expectation (as defined in table 1). Age-related changes in GSF were fit to a nonlinear Gompertz model (German & Meyers 1989):

$$Y = Ae^{-be^{kt}},$$

where Y represents the parameter of interest, t the postnatal age in days and e the base of the natural logarithm. A , b and k are constants, calculated iteratively, that are, respectively, proportional to the lower asymptote of the curve, the exponential rate of decay and the tangential slope at birth. Further details on our animal sample, measurement protocols, statistical methodology and model-fitting procedures are provided in the electronic supplementary material.

3. RESULTS

Humeral Z_p scales to body mass with isometry in *C. albifrons* and negative allometry in *C. apella*, whereas femoral Z_p scales with isometry in both species (table 1). Therefore, as predicted, long bone robusticity generally scales to body mass with isometry in capuchin monkeys. However, bone lengths scale to body mass with strong positive allometry (table 1) across limbs and species, indicating that young capuchin monkeys are relatively short-limbed for their body size (cf. Jungers & Fleagle 1980). Because bending loads are proportional to both force magnitude and

bone length, developmental changes in relative limb length should be incorporated into assessments of bone strength (Alexander 1983). Indeed, when humeral and femoral Z_p are scaled to the product of body mass and bone length, a biomechanically more appropriate size variable, negative allometry generally pertains (table 1). Only the *C. albifrons* femur, which scales isometrically, differs from the predominant pattern of negative allometry.

Across limbs and species, GSF peaks at birth and rapidly declines during the first year, refuting our prediction that maximal relative bone strength should coincide with infant ecological independence (figure 1). Humeral and femoral GSF declines to 22–49% of peak by the onset of independent locomotion, 1–11% of peak by locomotor independence and 0.5–4% of peak by weaning.

4. DISCUSSION

This study demonstrated that when biomechanically appropriate size variables are used, long bone cross-sectional dimensions generally grow with negative allometry in altricial capuchin monkeys, matching the scaling patterns observed in previous ontogenetic studies of more precocial animals (e.g. Carrier 1983; Heinrich *et al.* 1999; Lammers & German 2002; Main & Biewener 2004, 2007). Predominant negative allometry of cross-sectional dimensions during growth would stand in marked contrast to observed interspecific scaling patterns, where long bone cross-sectional dimensions have been shown to scale with isometry or weak positive allometry as body size increases (Alexander *et al.* 1979), requiring postural adjustments to maintain adequate safety factors (Biewener 1983). The degree to which ontogenetic changes in limb posture might influence bone loading has received little attention (cf. Young 2009), and is certainly a fruitful topic for future research.

Additionally, the current study showed that relative bone strength (i.e. GSF) peaks at birth in capuchins

Figure 1. Age-related changes in humeral (a,b) and femoral (c,d) GSF in *C. albifrons* and *C. apella*. Vertical dashed lines indicate approximate ages at the onset of independent locomotion (2 months), locomotor independence (7 months) and weaning (*C. albifrons*: 9 months; *C. apella*: 12 months) (Kappeler *et al.* 2003; Fragaszy *et al.* 2004). Grey symbols and dashed trend lines represent *C. albifrons*, black symbols and solid trend lines represent *C. apella*.

and declines to less than 5 per cent of peak values by weaning. These results complement previous experimental studies of long bone ontogeny (Main & Biewener 2004, 2006, 2007), where bone strains and associated cross-sectional properties measured in growing goats (*Capra hircus*) and emu (*Dromaius novahollandiae*) also suggested that safety factors decline with age. Among capuchin monkeys, the rapid decline in humeral and femoral GSF prior to ecological independence indicates that bone strength was maximal during early infancy and initial locomotor efforts, when the risk of falling from trees would be greatest. Field studies of several arboreal primate species, ranging from prosimians to apes, have shown that infants typically fall more than mature group mates, at times resulting in fatal injury (Carpenter 1934; van Lawick-Goodall 1967; Morland 1990; Dunbar & Badam 1998). As such, relatively greater bone strength early in life could adaptively mitigate the risk of skeletal injury from falling. If this were the case, more terrestrial primates, with reduced falling

risk, should show less dramatic declines in relative bone strength during early ontogeny. Indeed, data from Ruff (2003) on long bone growth in baboons (*Papio cynocephalus*), among the most terrestrial primates (Fleagle 1999), are consistent with this hypothesis. Although baboons also exhibit age-related declines in humeral and femoral GSF, rates of decline are much lower than observed among capuchin monkeys (figure S2 in the electronic supplementary material). Additional study of variation in primate long bone growth trajectories as a function of preferred habitat would be required to test our hypothesis.

Because capuchin monkeys are markedly slow growing and behaviourally altricial, the results presented here beg the question of whether ontogenetic declines in long bone robusticity may be a common pattern across vertebrates. Such a pattern could represent an epiphenomenon of the natural growth process, merely reflecting differences in the tempo of linear growth at the growth plates relative to circumferential growth at the periosteum. To evaluate the degree to

which ontogenetic declines in relative long bone robusticity might alternatively be adaptive, future research should move beyond simple binary altricial/precocial distinctions and explicitly consider how changing selective pressures might influence bone growth at specific ages (cf. Carrier 1996; Herrel & Gibb 2006). Possible age-specific selective pressures could include size or experience dependent risks (e.g. predation risk or propensity for accidental trauma), dispersal or migration events, or levels of intragroup conflict for resources, among others. Ecological, morphometric and performance data on animals exhibiting a range of life history variation would be needed to further explore the degree to which bone growth trajectories might be adaptive.

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