Received: 23 May 2017 | Revised: 23 August 2017 | Accepted: 29 August 2017

DOI: 10.1002/ajpa.23311

RESEARCH ARTICLE

WILEY American Journal of PHYSICAL ANTHROPOLOGY

Femoral neck-shaft angle and climate-induced body proportions

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Funding information
Leakey Foundation, Wenner-Gren Foundation, National Science Foundation, Grant/Award Number: BCS-0549925

Abstract

Objectives: Declination in femoral neck-shaft angle (NSA) is commonly linked to an increased level of physical activity during life. More recently, however, research suggests that lower NSA might also be explained, in part, as the mechanical consequence of differences in ecogeographic body proportions. This study tests the proposed link between NSA and climatic-induced body proportions, using relative body mass (RBM), throughout the course of development.

Materials and Methods: NSA and RBM were collected for 445 immature remains from five geographic locations. NSA and RBM were standardized for age-effects. ANOVA was used to examine when population differences emerged in both NSA and RBM. Regression analyses were used to examine the pattern of relationship between NSA and RBM.

Results: Populations differ significantly in NSA and RBM before skeletal maturity, and these differences occur early in life. While both NSA and RBM change over the course of development, no significant relationship was found between NSA and RBM for any sample, or any age category ($p = .244$).

Discussion: Individuals who have relatively greater relative body mass do not necessarily have lower NSA. Population differences in NSA were found to be variable, while differences in RBM remained consistent across the developmental span. Taken together, these results suggest that regardless of body proportions, the degree of declination of NSA is presumed to be similar among individuals with similar gait and ambulatory behaviors. Conversely, populations differ in RBM from birth, and these differences are consistent throughout development. These two measures likely are responsive to diffing stimuli, and any potential relationship is likely complex and multifactorial.

KEYWORDS
collo-diaphyseal angle, ecogeography, femur, ontogeny

1 | INTRODUCTION

Femoral neck-shaft angle (NSA) is a measure of the medial inclination of the proximal femur [Martin No. 29 (Bräuer, 1988)]. It varies widely during growth, across geographic space, and across temporal periods. In general, there is a trend of increasing femoral inclination throughout the Holocene with the transition from hunting and gathering to urban, or industrial, societies (Anderson & Trinkaus, 1998; Backman, 1957; Larsen, 1995, 1997; Pearson & Buikstra, 2006; Ruff, Larsen, & Hayes, 1984). While a large body of research has been directed toward documenting this variation (Frankel, 1960; Garden, 1961; Henriksson, 1980; Hoaglund & Low, 1980; Inman, 1947; Isaac, Vettivel, Prasad, Jeyaseelan, & Chandi, 1997; Pick, Stack, & Anson, 1941; Reikeras & Hoiseth, 1982; Reikeras, Hoiseth, Reigstad, & Fönstelien, 1982, 1983; Sears, 1898), debates as to the functional and mechanical significance of this variation are ongoing. Specifically, it is unclear if population differences in adult NSA are stimulated by differences in activity levels between groups (Anderson & Trinkaus, 1998; Houston & Zaleski, 1967; Humphry, 1889; Trinkaus, 1993; Walmsley, 1915); or, if they are a secondary consequence of climate-induced body proportions (Gilligan, 2010; Gilligan, Chandraphak, & Mahakkanukrauh, 2013; Weaver, 2003). This study examines the proposed relationship between NSA and relative body mass over the course of development in a sample of geographically diverse immature remains which differ in body form.

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2 | BACKGROUND

2.1 | Postnatal declination of NSA

NSA changes across much of the growth period, with characteristically high values in neonates, ranging between 140° and 160° at birth. NSA declines over the course of development in response to changing hip joint reaction forces associated with shifting weight distribution during gait development (Ribble, Santare, & Miller, 2001; Shefelbine & Carter, 2004; Villemure & Stokes, 2009). With normal weight-bearing activity, adult values are reached during early adolescence and generally range between 122° and 136° in most populations (Hay, 1996; Miller et al., 1993). After the proximal epiphysis fuses with the diaphysis, the angle becomes "fixed," with no further changes observed with advancing age (Bonneau, Simonis, Seringe, & Tardieu, 2012; Humphry, 1889; Toogood, Skalak, & Cooperman, 2009; Unnanuntana, Toogood, Hart, Cooperman, & Grant, 2010; although see Isaac et al., 1997; Kingsley & Olmstead, 1948; Nobel et al., 1995; Reikeras & Hoiseth, 1982 for an alternative view).

Postnatal declination of the proximal femur is dependent on the magnitude and orientation of shear stresses experienced at the hip during endochondral growth. This mechanical modulation of growth has been discussed and modeled via finite element analysis (Carter & Beaupré, 2001; Carter & Orr, 1992; Carter & Wong, 1988; Carter, Orr, Fyrie, & Schurman, 1987, 1991, 1998; Heegaard, Beaupré, & Carter, 1999), as well as demonstrated experimentally (Appleton, 1934; Arkin & Katz, 1956; Ryöppy & Karaharju, 1974). In accordance with these studies, growth of the proximal physis, or growth plate, is promoted in regions under intermittent octahedral shear stress, and inhibited in areas under intermittent hydrostatic compressive stresses. The physis will deform in response to changing orientations of the resultant hip joint forces it experiences during development to attain a state of low shear stress (Carter et al., 1987; see Carter & Beaupré, 2001 for a detailed review).

The changing orientation of shear stresses experienced across the developing physis is generated by altering musculature of the hip, postural behaviors, and weight-bearing forces associated with the acquisition of a mature gait pattern. Before a child begins to walk, the proximal physeal surface is flat and growth proceeds in the middle of the physis due to the relatively equal stress gradient along the mediolateral axis (Bobroff, Chambers, Sartoris, Wyatt, & Sutherland, 1999; Fabry, Cheng, & Molenaers, 1994; Salter, 1966). At about one year of age, the child begins to walk with an abducted thigh and flexed hip and leg (Cowgill, Warrener, Pontzer, & Ocobock, 2010; Inman, Ralston, & Todd, 1981; McGraw, 1940; Okamoto & Okamoto, 2007). This places relatively greater shear stresses along the medial physeal surface compared to the lateral surface, thereby promoting growth within the medial physis. Consequently, individuals within this age range exhibit relatively high NSA. Between the years of approximately two and six, the orientation of shear stresses within the developing physis shifts to a more lateral position due to the combined activity of the abductors and the acquisition of a mature gait pattern, thereby stimulating a decline in the NSA (Shefelbine & Carter, 2004). By around eight years of age, the angulation of the proximal femur has declinated to approximately 125°, and little to no further declination occurs with advancing years, since relatively low shear stresses are experienced in both medial and lateral surfaces in this orientation. The declination of the proximal femur has an important biomechanical role. The NSA works to optimize lever arm lengths, decrease bending moments of the neck, and inhibits dislocation, thereby producing a more stable joint (Brien, Lane, & Healey, 1995; Duda, Schneider, & Chao, 1997, 1998; Hay, 1996; Murray & Robb, 2006; Nordin & Frankel, 1980; Trinkaus, 1993).

2.2 | Temporal and geographic variation in NSA

Given its developmental plasticity and principle role in the transmission of the body's weight through the hip, NSA is frequently used to investigate locomotor and postural differences among and within modern humans and earlier hominin taxa. Within the Holocene, there is a general temporal trend of increasing femoral neck inclination associated with the transition from hunter gathering to industrial societies (Larsen, 1995, 1997). However, there is considerable variation in NSA among modern human populations (Backman, 1957; Frankel, 1960; Garden, 1961; Henriksson, 1980; Hoaglund & Low, 1980; Inman, 1947; Isaac et al., 1997; Pick et al., 1941; Reikeras & Hoiseth, 1982; Reikeras et al., 1982, 1983; Sears, 1898; Walensky & O'Brien, 1968). A lower NSA is still more frequently reported among more mobile populations compared to more sedentary populations, suggesting a dependency of NSA on weight-bearing activities during development (Anderson & Trinkaus, 1998; Ruff, Trinkaus, Walker, & Larsen, 1993; Trinkaus, 1993, 1994). The mechanical sensitivity of metaphyseal modeling to changes in the magnitude and orientation of forces in the hip during development is well documented (Arkin & Katz, 1956; Appleton, 1934; Brien et al., 1995; Delp, Komattu, & Wixson, 1994; Duda et al., 1997, 1998; Heller et al., 2001; Murray & Robb, 2006; Salter, 1966; Shefelbine & Carter 2004; van der Meulen, Ashford, Kiratli, Bachrach, & Carter, 1996; Villemure & Stokes, 2009) and supported by the absence of declination observed in nonambulatory or reduced mobility individuals (Bobroff et al., 1999; Brien et al., 1995; Delp et al., 1994; Houston & Zaleski, 1967; Laplaza, Root, Tassanawipas, & Glasser, 1993; Maquet, 1999; Ribble et al., 2001; Yamaguchi, 1993).

Since the proximal femur is influenced by pelvic configurations (Ruff, 1995), it has been suggested that differences in pelvic breadths observed in different climatic regions, or sexes, might place different bending stresses along the femoral neck, thereby resulting in differing adult NSA (Hay, 1996; Weaver, 2003). Within populations, females tend to exhibit relatively lower NSA compared to males (Unnanuntana et al., 2010), however, other studies have reported lower angles for males compared to females (Hay, 1996), or no relationship between NSA and sex at all (Bonneau et al., 2012; Gilligan et al., 2013; Lee et al., 2011; Reikeras & Hoiseth, 1982; Toogood et al., 2009). Taken together, this suggests that the magnitude of sexual dimorphism expressed in NSA is relatively small and inconsistent (Anderson & Trinkaus, 1998; Hay, 1996).

Recent research has addressed the potential influence of climate on variation in NSA. Many studies have investigated the applicability of

Bergmann's rule (1847) and Allen's rule (1877) to ecogeographic variation in human body proportions (Auerbach, 2007, 2010, 2011, 2012; Gilligan & Bulbeck, 2007; Hiernaux & Froment, 1976; Holliday, 1997a 1999, 2002; Holliday & Ruff, 2001; Holliday & Trinkaus, 1991; Leonard & Katzmarzyk, 2010; Meiri & Dayon, 2003; Pearson, 2000; Ruff, 1991, 1993, 1994, 2002; Trinkaus, 1981; Temple, Auerbach, Nakatsukasa, Sciulli, & Larsen, 2008; Weinstein, 2005). Human populations from high latitudes frequently display relatively wide bodies, high body masses for stature, short limbs relative to trunk length and foreshortened distal extremities, whereas populations from low latitudes have relatively narrow bodies, low body masses for stature, long limbs, and long distal limb extremities. These patterns are likely produced by selection for minimized surface area relative to volume for heat retention in cold climates and maximized surface area relative to volume for heat dispersal in warm climates, and are the consequence of the combined effects of neutral microevolutionary processes (shared genetic and evolutionary history) and selection acting on thermoregulatory efficacy (Betti, 2014; Betti, von Cramon-Taubadel, & Lycett, 2012, 2013; Roseman & Auerbach, 2015; Savell, Auerbach, & Roseman, 2016).

Gilligan (2010, 2012) and Gilligan and coworkers (2013) examined the relationship between annual and seasonal (summer and winter) temperatures and NSA in a large sample ($n > 8000$) of modern human femora from over 80 different countries. While they only detected a modest correlation between NSA and the economic transition between agriculture and urbanism, they did find higher NSA in warmer clines and lower NSA in colder ones, and this climate trend was found within continental regions as well as at the global level (but see Anderson & Trinkaus, 1998 for an alternative view).

Furthermore, Weaver (2003) questioned whether the lower NSA observed in Neandertals, when compared to early modern humans, might be a direct result of higher activity levels, or the secondary consequence of differences in eco-geographic body proportions between these groups. Although the link between NSA and activity patterns is understood, it remains unclear whether relatively wider pelvis breadth and/or relatively higher body mass influences femoral neck angulation at the hip. Weaver (2003) suggested that changes in "hip geometry during development in children with different body proportions needs to be investigated in detail to test this hypothesis rigorously" (p. 6928), and is the impetus for this study.

3 | RESEARCH OBJECTIVES

Following Weaver (2003), it remains possible that differences in body proportions might influence the angulation of the femoral neck via changes to hip geometry or the distribution of body mass during development. This study tests this hypothesis by examining the potential influence of body proportion (distribution of body mass) on the inclination of the proximal femur in a large, geographically diverse sample of immature Holocene remains. If variation in the angulation of the proximal femur results, in part, as a secondary consequence of differences in ecogeographic body proportions, then a reassessment of behavioral reconstructions from this skeletal feature (NSA) is required among populations and/or species that vary in body form.

This study examines three questions. First, do populations differ in body proportions and NSA before skeletal maturity? Second, if so, *when* do population differences emerge? Given the large body of research that report geographic and temporal variation in both NSA and ecogeographic body proportions before skeletal maturity, we expect to find among-group differences in these two features at an early age. Here, we are interested in whether geographic samples exhibit a similar and expected pattern of decreasing NSA and increasing body mass and stature across the developmental span, and also exhibit consistency in their ordinal rankings in NSA and body proportions across the developmental span. Third, what is the pattern of relationship between body proportions and NSA over the course of development? If the declination of NSA is influenced, in part, by ecogeographic body proportions, then we should observe opposite ordinal rankings of the two features within geographic samples, whereby geographic samples with relatively larger bodies have relatively lower NSA, and vice versa. Similarly, if there is a functional or mechanical link between NSA and body proportions, we should expect to find close concomitance between the two features among age cohorts, as they similarly shift in response to changing mechanical environments.

4 | MATERALS

Data were collected from a sample of 445 immature right or left femora from seven geographic Holocene populations. Individuals in the sample range from birth to eighteen years of age. As in many growth studies, sample sizes for certain age categories are small, in spite of the large and robust sample size overall. The samples were selected to represent a diverse range of geographic regions and subsistence strategies. Table 1 provides sample locations, time periods, general subsistence strategy, and sample size for each sample used in this study (see Cowgill 2008, 2010 for a detailed review). No attempt was made toward creating sex-specific sub-groups in this study, given that sex estimation of immature skeletal remains is unreliable, at best, and the effects of sexual dimorphism on NSA are equivocal in adults.

5 | METHODS

5.1 | Age estimation

Age was unknown for all samples except the Luis Lopes sample. For these remaining samples, age was estimated by dental development whenever dental and long bone remains were reliably associated. For these individuals, crown and root formation were evaluated from lateral mandibular radiographs, following the dental development standards for deciduous dentition (Liversidge & Molenson, 2004) or permanent dentition (Smith, 1991).

For individuals with no associated dental and postcranial remains, previously developed sample-specific regression formulae were used to predict chronological age based on femoral lengths (see Cowgill, 2008 for a detailed review). The use of sample-specific formulae minimizes

TABLE 1 Sample description, subsistence, and size

Sample	Location	Approx. Time Period	Subsistence	Sample Size
Kulubnarti	Upper Nubia	Medieval	Agriculturalists	90
Luis Lopes	Lisbon, Portugal	20th century	Urban	44
Dart	Johannesburg, South Africa	20th century	Mixed urban and rural	65
Indian Knoll	Green River, Kentucky	4143–6415 BP	Semi-sedentary foragers	88
California Amerindian	Northern California	500–4600 BP	Semi-sedentary foragers	68
Mistihalj	Bosnia-Herzegovina	Medieval (15th century)	Nomadic pastoralists	43
Point Hope	Point Hope, Alaska	300–2100 BP	Arctic foragers	47
				Total = 445

the potential confounding effects of variation in body size and proportion among samples before skeletal maturity. While age estimates based on either dental or skeletal features may produce minor disparities in the estimation of chronological age, these disparities are unlikely to bias the results of this study since individuals were subsequently grouped into broader age categories for analyses (see below).

5.2 | Age categories

To examine *when* ontogenetic changes in NSA and relative body proportions emerge, the study sample was divided into five age categories that reflect important developmental changes in the angular development of the femur. The youngest age category (birth to 0.9 years) is restricted to the first year of life to facilitate exploration of very early differences in NSA between populations prior to walking. The second age category (1.0–2.9 years) is slightly broader, and permits detection of changes in NSA associated with the acquisition of independent gait. The third age category (3.0–5.9 years) allows examination of changes in NSA associated with the acquisition of a mature gait (McGraw, 1940; Norlin, Odenrick, & Sandlund, 1981; Okamoto & Okamoto, 2007; Statham & Murray, 1971; Sutherland, Olsen, Cooper, & Woo, 1980, 1988). The fourth age category (6.0–11.9 years) allows detection of changes in NSA experienced until near the time of puberty, when growth velocity is relatively slow. The fifth age category (12.0–17.9 years) is bounded to reveal changes in NSA associated with puberty and thereafter, reflecting a relatively rapid increase in growth velocity at this age.

5.3 | Lower limb measurements

Given the relatively low levels of asymmetry reported in the lower limb (Anderson & Trinkaus, 1998; Auerbach & Ruff, 2006; Isaac et al., 1997; Reikeras et al., 1982; Unnanuntana et al., 2010), data were collected from either the right or left femur and tibia for each individual. Dimensions measured were femoral neck-shaft angle (NSA), distal femoral metaphyseal breadth (FMB), femoral head diameter (FHD), maximum femoral length (MFL), and maximum tibial length (MTL). NSA was measured using a protractor and recorded to the nearest degree. FMB and FHD were measured using calipers and recorded to the nearest millimeter. MFL and MTL were recorded using an osteometric board and recorded to the nearest millimeter. Table 2 presents each dimension and its mechanical relevance to the study.

5.3.1 | Neck-shaft angle

NSA is a measure of the medial inclination of the femoral head and neck. In individuals that had partial or complete fusion of the proximal epiphysis, NSA was measured, as it is in adults, as the intersection between the cervical axis of the femoral head and neck and the longitudinal axis of the femoral diaphysis (Figure 1a). In younger remains with unfused epiphyses, the axis of the head and neck was approximated by the center of the proximal metaphyseal surface and neck (Figure 1b), and the angle was measured as the intersection of this axis and the longitudinal axis of the femur on the anterior surface of the femur. The assessment of this dimension on the anterior surface of the femur eliminates any potentially confounding effects due to variation in the antetorsion angle of the proximal femur, and therefore no

TABLE 2 Standard skeletal measurements used in this study

Dimension	Abbreviation	Relevance
Neck-shaft angle	NSA	Medial angulation of proximal femur
Femoral distal metaphyseal breadth	FMB	Body mass estimation for younger than 13.5 years
Femoral head diameter	FDH	Body mass estimation for older than 13.5 years
Maximum femoral length	MFL	With MTL, lower limb length
Maximum tibial length	MTL	With MFL, lower limb length
Relative body mass	RBM	Body mass relative to lower limb length

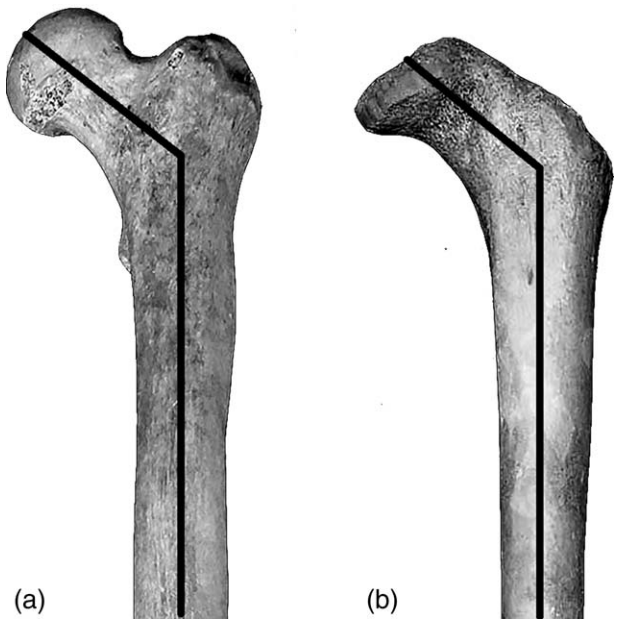

FIGURE 1 Measurement of femoral neck-shaft angle (NSA) in (a) individuals with a fused proximal epiphysis (NSA is 127°); and in (b) individuals with an unfused proximal epiphysis (NSA is 130°)

correction factors for this dimension were necessary (Anderson & Trinkaus, 1998; Gilligan, 2010). Every attempt was made to ensure that angular measurements collected from immature remains were comparable to those collected from individuals with epiphyseal union. While this measurement differs slightly in method from those obtained from more mature individuals, it is unlikely that this difference significantly biased the results of this study since the angulation and orientation of the proximal femur occurs in the region of the developing metaphysis; not the head or the neck (Arnold & Delp, 2001; Bonneau et al., 2012; Dunlap, Shands, Hollister, Stuart, & Streit, 1953; Lundy, Ganey, Ogden, & Guidera, 1998).

NSA intraobserver error was assessed using a subset of 10 immature femora ranging in age from 3 months to 16 years, which were measured by one of us (LWC) twice on two consecutive days. Differences between the first and second measurements ranged between 3 and 8 degrees. The Bland-Altman method for repeated measures (Bland & Altman, 1999, 2010) was used to evaluate agreement between the repeated measurements (Bland & Altman, 2010). The Bland-Altman plot of absolute mean differences between NSA measurements produced a mean difference and standard deviation of $-0.3° \pm 4.572°$ with limits of agreement between $-8.96°$ and $8.66°$ ($\beta = -0.027$; $p = .838$), with a coefficient of repeatability of $\pm 9.143°$. These results indicate that the mean difference between repeated measurements did not significantly differ from zero, that the estimated bias between the repeated measurements is low, and there is no systemic or proportional bias between the repeated measurements (Loughman, 2010; Vaz et al., 2013).

5.3.2 | Body mass estimation and relative body mass

Covariation of NSA with body proportions may be related to differences in pelvic breath or the distribution of body mass, as Weaver (2003) has suggested. Previous studies indicate that a primary determinant of variation in body mass is bi-iliac breadth (Ruff, 2007). However, this measurement is not possible to obtain in immature remains with unfused os coxae, where reconstructing bi-iliac breath is likely to be arbitrary at best. Furthermore, most of the variation in body mass prior to maturity is related to age. Due to these issues, it was therefore necessary to calculate some mechanically relevant measure of body mass relative to body height, or stature, to obtain an approximation of general body shape in children. To this end, a new variable, relative body mass (RBM), was calculated for each individual.

Following Ruff (2007), body mass was first estimated using age-specific regression formulae based on articular breadth dimensions. Age-specific regression formulae were employed since articular breadth proportions relative to body mass change throughout growth. Although any estimate of body mass will have a degree of error associated with the estimate, this is an inherent artifact in all analyses that wish to estimate body mass from skeletal dimensions. In acknowledgement of this fact, the articular dimension with the lowest associated percent standard error was preferentially selected for use in each age-specific prediction formula.

Both distal femoral metaphyseal breadth (FMB) and proximal femoral epiphyseal head diameter (FHD) have been shown to provide reasonable and reliable estimates of body mass in immature remains (Ruff, 2007). Distal metaphyseal breadth was used to predict body mass in all individuals from birth to 13.5 years. Although the proximal femoral epiphysis has slightly smaller associated errors, biases in preservation and recovery of an unfused epiphysis make this feature of little use prior to skeletal maturity (Ruff, 2007). Therefore, distal metaphyseal breadth was used to predict body mass in individuals prior to 13.5 years of age. For individuals older than 13.5 years, and for whom proximal epiphyses were measureable, proximal femoral head diameter was used to predict body mass since estimates based on this feature provides smaller errors than those based on distal metaphyseal breadths. For individuals in whom neither distal nor proximal dimensions were available, body mass was predicted using previously developed formulae based on correlations with proximal tibial metaphyseal dimensions or proximal femoral metaphyseal dimensions, respectively (see Cowgill, 2008 for a detailed review).

Relative body mass (RBM) was then calculated as the estimated body mass divided by the sum of maximum femoral and tibial lengths. The RBM index provides information regarding the distribution of body mass relative to limb length, and serves as a proxy for body proportions in immature remains. Long bone lengths were used here, rather than stature, since this eliminates the additional step of stature estimation, which might introduce an additional source of error. A summation of lower limb long bone lengths was chosen over either singular length, since use of both elements has been shown to provide better approximations of stature than either element alone (Ruff, 2007).

The use of RBM as a proxy for body proportions in immature remains is a novel approach, and the validity of such application has yet to be tested. To this end, the magnitude of agreement between RBM and bi-iliac breadth/limb length in adults was subsequently

TABLE 3 Descriptive statistics for NSA for all samples across all age categories

Sample	Ages Pooled			0–0.9 years			1–2.9 years			3–5.9 years			6–11.9 years			12–17.9 years		
	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
Kulubnarti	99	134.1	6.0	13	142.5	8.4	14	136.6	4.8	25	133.6	3.2	29	131.1	3.5	18	131.6	4.8
Luis Lopes	46	135.5	7.6	5	151.8	3.8	6	133.5	6.8	8	135.0	2.5	16	135.2	4.6	11	130.1	5.6
Dart	66	136.8	8.8	12	145.8	8.2	14	143.3	7.5	4	134.5	8.2	11	134.4	5.9	25	130.4	4.0
Indian Knoll	94	135.8	7.8	15	146.3	5.2	14	138.6	8.8	14	135.9	3.7	31	134.5	4.6	20	128.1	5.5
California Amerindian	86	133.6	7.2	15	145.5	6.0	16	133.9	4.1	11	131.1	3.8	24	130.7	4.5	20	129.5	4.7
Mistihalj	49	134.5	5.7	8	142.9	5.3	10	133.0	2.9	8	132.6	3.8	15	134.3	4.5	8	130.1	5.0
Point Hope	56	133.8	7.0	5	142.6	4.7	7	138.9	10.2	9	131.3	6.8	21	132.9	6.0	14	131.2	4.1
Total NSA	496	134.9	7.3	73	145.1	6.7	81	137.1	7.3	79	133.5	4.4	147	133.0	4.9	116	130.1	4.782

evaluated using the Bland-Altman method for assessment of agreement between two different methods (Bland & Altman, 1999, 2010) using a reference sample of 119 adult skeletal remains from four distinct skeletal samples. According to the Bland-Altman method, two methods are comparable, and thereby interchangeable, when the mean paired difference is near zero (indicating equality), there are few outliers, and the limits of agreement are sufficiently narrow. The resultant $\log_e$-$\log_e$ Bland-Altman plot of absolute mean differences of RBM and bi-iliac/limb length measurements produced a mean difference and standard deviation of 1.4316 ± 0.11481 with limits of agreement between 1.2065 and 1.6566. Linear regression was used to test the null hypothesis that the mean differences between the two methods did not significantly differ from zero. The mean differences between these two methods did not significantly differ from zero ($\beta = 0.007$; $p = .964$), there are very few outliers, and the limits of agreement are sufficiently narrow, providing support for the approximation of body proportions using RBM in immature remains.

5.4 | Age standardization of NSA and RBM

Both NSA and RBM are strongly correlated with an individual's age ($p < .001$), as both change over the course of development. It was first necessary to remove the confounding effects of age on both NSA and RBM to examine the relationship between these variables, to avoid the variation related to age confounding any signal related to NSA or RBM. Without first removing the effects of age, differing age distributions among geographic samples might obscure or conflate the potential relationship between the variables of NSA and RBM.

To this end, NSA and RBM were corrected for age by regressing each variable on age before statistical analyses were performed. Bivariate scatterplots of both NSA and RBM on age were assessed to evaluate the most appropriate order of regression analysis. NSA and RBM were regressed on age using cubic and quadratic Ordinary Least Squares (OLS) formulae, respectively, and residual plots were inspected, thereafter, for goodness of fit of the models. Other forms of line fitting techniques have been advocated over OLS when the independent (x) variable is measured with error, which is most certainly the case in this study. However other methods of line fitting assume specific patterns of error variance between the variables (i.e., error variances are either equal or proportional to the ratio of the total sample variances), which is likely not appropriate in this case, either, such that error variances in body mass estimates are most certainly expected to be greater than those associated with a femoral dimension (Pagel & Harvey, 1989). The choice of line fitting was based on the OLS assumption of asymmetry in the variable relationship, where the variables assigned to x and y axes are not interchangeable (Smith, 2009). The resulting age-standardized residuals, which remove the confounding effects of age (see Cowgill, 2008, 2010 for a detailed review) were used in all further analyses.

5.5 | Statistical analyses

Initially, both raw and age-standardized residuals of NSA and RBM were assessed for violations of the assumptions for parametric testing through descriptive (mean, median, kurtosis, skewedness), graphical (scatterplots, histograms, Q-Q plots, P-P plots), and diagnostic (Durbin-Watson, Cook's distance) procedures. The distributions did not depart significantly from normal distributions, and therefore parametric tests were chosen for analyses of the age-standardized variables. Although outliers were noted, all values were checked for errors and determined to be within normal physiological limits. Outlying values with a Cook's distance of greater than one were eliminated from the data set.

To examine whether populations differ in NSA and RBM before skeletal maturity, one-way Analysis of Variance (ANOVA) were used to examine differences in age-standardized residuals of both NSA and RBM for each geographic sample. Tukey's tests were subsequently employed for posthoc comparisons to determine which samples significantly differed from one another. To examine when potential differences emerged, samples were divided into nominal age categories and ANOVA with Tukey's post hoc comparisons were employed to examine geographic sample differences in age-standardized NSA and RBM across each age category. The above comparisons allow us to examine the pattern of variation in NSA and RBM among geographic samples and age cohorts, respectively. To evaluate the potential pattern of relationship between NSA and RBM among geographic samples and among age groups, Pearson's correlation coefficients and OLS

TABLE 4 Descriptive statistics for RBM for all samples across all age categories

	Ages Pooled			0–0.9 years			1–2.9 years			3–5.9 years			6–11.9 years			12–17.9 years		
Sample	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
Kulubnarti	90	0.0433	0.0120	12	0.0315	0.0043	13	0.0356	0.0024	22	0.0379	0.0024	27	0.0440	0.0050	16	0.0645	0.0101
Luis Lopes	44	0.0507	0.0155	4	0.0394	0.0023	5	0.0365	0.0027	7	0.0389	0.0036	16	0.0483	0.0082	12	0.0704	0.0131
Dart	65	0.0483	0.0159	12	0.0326	0.0053	14	0.0362	0.0015	3	0.0368	0.0033	11	0.0454	0.0050	25	0.0653	0.0109
Indian Knoll	88	0.0443	0.0129	15	0.0327	0.0044	12	0.0355	0.0021	13	0.0354	0.0014	30	0.0450	0.0039	18	0.0649	0.0113
California Amerindian	68	0.0496	0.0154	10	0.0360	0.0034	11	0.0370	0.0028	9	0.0395	0.0029	20	0.0473	0.0060	18	0.0725	0.0070
Mistihalj	43	0.0477	0.0158	6	0.0364	0.0048	9	0.0367	0.0031	6	0.0395	0.0022	14	0.0463	0.0053	8	0.0771	0.0104
Point Hope	47	0.0498	0.0153	4	0.0335	0.0039	6	0.0367	0.0029	6	0.0383	0.0044	19	0.0474	0.0070	12	0.0715	0.0095
Total NSA	445	0.0470	0.0146	63	0.0338	0.0047	70	0.0363	0.0020	66	0.0379	0.0030	137	0.0460	0.0058	109	0.0684	0.01091

regression analyses were employed to evaluate the relationship between age-standardized residuals of NSA and RBM for each sample as a whole, and across each age category. All alpha levels were set at 0.05. SPSS version 22.0 was used to perform all statistical analyses in this study.

6 | RESULTS

6.1 | Do populations differ in NSA and RBM before skeletal maturity?

Sample sizes and descriptive statistics for raw (unstandardized) NSA and RBM are listed in Tables 3 and 4, respectively. Raw data were not used in the analyses, and are presented here for descriptive and comparative purposes. Figures 2 and 3 present boxplot distributions of age-standardized residuals of NSA and RBM, respectively, for each sample across the developmental span. Examination of the descriptive statistics reveal a developmental trend of decreasing NSA and increasing RBM among the samples in this study. One-way ANOVA tests reveal significant differences in both age-standardized residuals of NSA ($p = .002$) and RBM ($p < .001$) among geographic samples. The California Amerindian sample had the lowest NSA, and this significantly differed from the relatively higher NSA observed in the Dart and Indian Knoll samples ($p \leq .02$). No other sample differences in age-standardized residuals of NSA were significant. In comparing age-standardized RBM among samples, the Luis Lopes, Point Hope, California Amerindian, and Mistihalj samples had significantly greater RBM ($p \leq .048$) compared to the remaining samples (Table 5).

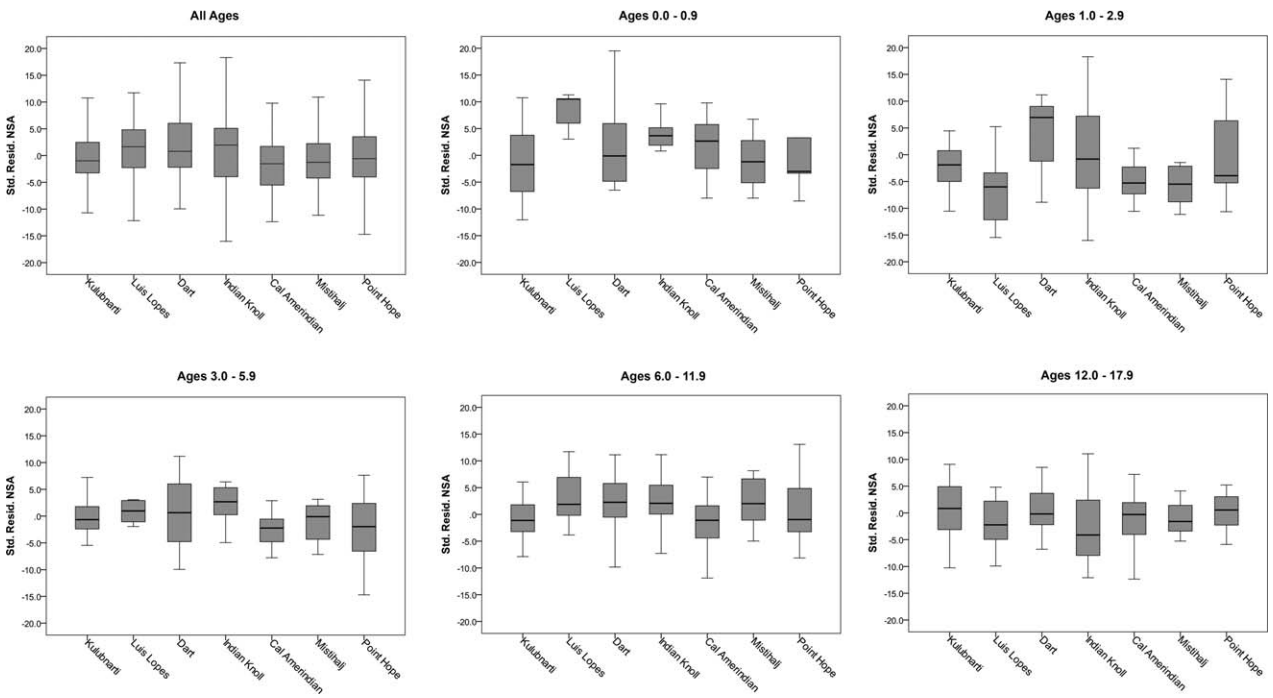

FIGURE 2 Boxplot distributions of age-standardized residuals of neck-shaft angle (Std. Resid. NSA) for each sample in this study, across all age categories

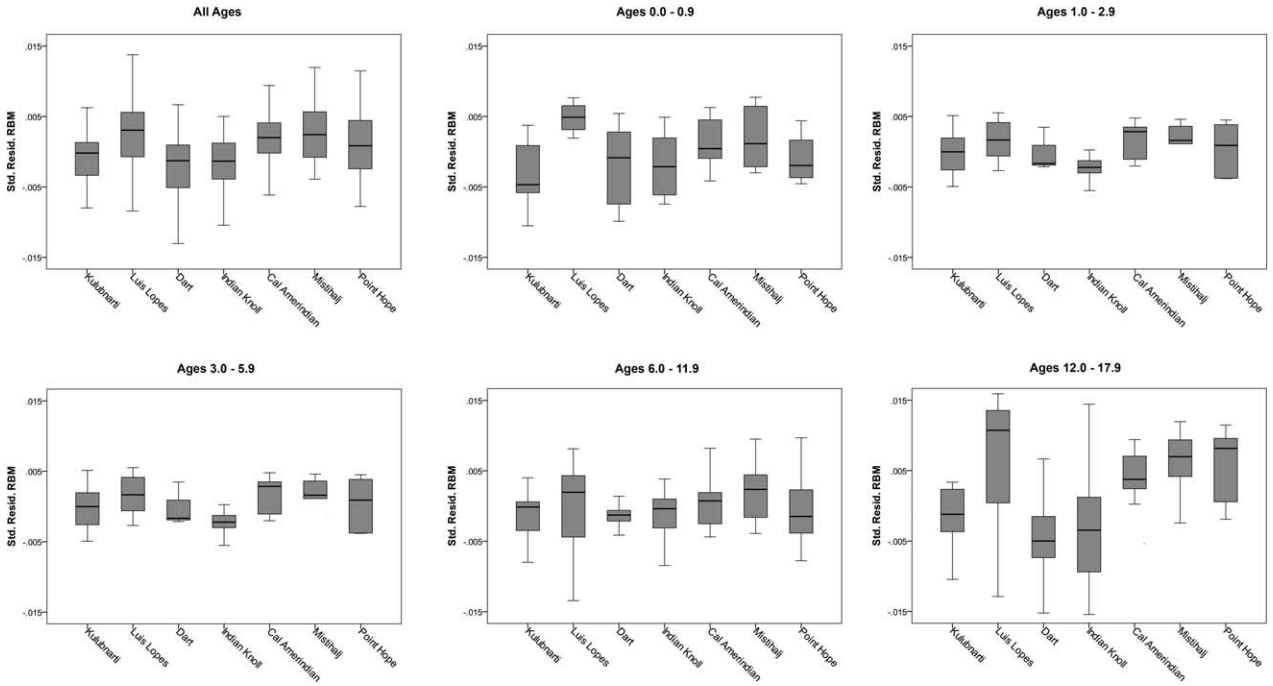

FIGURE 3 Boxplot distributions of age-standardized residuals of relative body mass (Std. Resid. RBM) for each sample in this study, across all age categories

6.2 | When do population differences in NSA and RBM emerge?

6.2.1 | Birth to 0.9 years

Results from one-way ANOVA tests reveal no significant sample differences in age- standardized residuals of NSA within the first year of life ($p = .108$). A significant sample difference in age-standardized RBM is detectable within the first year of life ($p = .019$). Posthoc comparison tests reveal that the Luis Lopes sample has significantly greater RBM than the Kulubnarti sample ($p = .038$). No other significant differences were observed ($p \geq .109$) (Table 5).

6.2.2 | 1–2.9 years

There is a significant difference ($p = .002$) in age-standardized NSA across the geographic samples, associated with the time at which independent walking is initiated. The Mistihalj, Luis Lopes, and California Amerindian samples have among the lowest NSA, and these significantly differ from the relatively high NSA of the Dart sample ($p \leq .028$). No significant differences were observed in RBM among geographic samples ($p = .692$) (Table 5).

6.2.3 | 3–5.9 years

No significant differences in age-standardized NSA were observed among geographic samples ($p = .097$) at the time in which a mature gait is established. Sample differences in age-standardized RBM are apparent ($p = .013$), however. The California Amerindian and Luis Lopes samples exhibit the greatest RBM, and these samples significantly differ from the relatively low age-standardized RBM of the Indian Knoll sample ($p \leq .041$) (Table 5).

6.2.4 | 6–11.9 years

Age-standardized NSA significantly differs among samples between 6 and 11.9 years of age ($p = .006$). The California Amerindian sample had the lowest NSA, which significantly differed from the Indian Knoll sample, which had the highest NSA ($p = .048$). No other geographic differences in age-standardized NSA were significant. Age-standardized RBM did not significantly differ among any sample within this age category ($p = .176$) (Table 5).

6.2.5 | 12–17.9 years

No significant differences in age-standardized NSA were observed between geographic samples ($p = .350$) in this age category. Age-standardized RBM significantly differed between geographic samples ($p < .001$). Posthoc comparisons show that the Luis Lopes, Mistihalj, Point Hope and California Amerindian samples have significantly larger RBM compared to the Dart, Indian Knoll, and Kulubnarti samples ($p \leq .044$) at this age (Table 5).

6.3 | What is the pattern of relationship between NSA and RBM?

No significant relationship was found between age-standardized residuals of NSA and RBM ($r = -0.056$; $r^2 = 0.003$; $p = .244$; $n = 445$), samples pooled (Figure 4). When the study sample was divided by geographic sample and by age category, no significant relationship was observed in any geographic sample ($p \geq .123$), or any age category ($p \geq .108$). Table 6 shows the ordinal rankings of geographic samples by their age-standardized residual means for NSA and RBM, across all age categories.

7 | DISCUSSION

7.1 | Pattern of variation in NSA and RBM

Results indicate that populations significantly differ in both age-standardized NSA and RBM before skeletal maturity and that these differences are established early in life. Our results reveal two noteworthy trends regarding the pattern of variation in NSA and RBM both within and among samples.

First, as expected, there is a consistent trend of decreasing NSA and increasing RBM across the developmental span, and this pattern is experienced similarly *within* all geographic samples. The negative age-trend observed in NSA follows the expected pattern related to the shifting shear stresses experienced across the physeal surface associated with gait acquisition during development. Within each geographic sample, NSA is relatively high within the early years of life (birth to 2.9 years), during which time independent walking is initiated. Thereafter, there is a marked decrease in NSA at and around the time that a mature gait is established (3–5.9 years), with little further declination with advancing years. This consistent within-group trend of decreasing NSA is not surprising, given the remarkable consistency of developmental timing in the declination of NSA reported among ambulatory children in clinical and orthopaedic studies (Backman, 1957; Billings, 1954; Fabry et al., 1994; Garden, 1961; Hoaglund & Low, 1980; Humphry, 1889; Miller et al., 1993; Nordin & Frankel, 1980; Pick et al., 1941; Ribble et al., 2001; Reikeras et al., 1982, 1983; Sears, 1898; Shefelbine & Carter, 2004; Toogood et al., 2009).

RBM shows a similar, but opposite (positive) age-trend of increasing RBM across the developmental span, and follows the expected pattern related to the concomitant increase in both body mass and limb length with advancing age.

Second, patterns of variation in NSA and RBM are dissimilar *among* both geographic samples and age categories. There is little consistency in the ordinal ranking of NSA among geographic samples (Table 6). That is, populations that exhibit relatively high NSA in one age category do not necessarily retain their relatively high NSA in successive age categories. For instance, the Luis Lopes sample exhibits the highest NSA from birth to 0.9 years, the lowest NSA in the next age category (1–2.9 years), and then among the highest in the 3–5.9 age category. These results suggest that while populations differ with regard to NSA across ontogeny, these differences reflect differing mechanical loadings experienced during early gait acquisition and maturation, and that the degree of declination of NSA is likely similar among individuals with similar gait and ambulatory patterns.

In contrast to NSA, ordinal rankings (Table 6) of RBM reveal a remarkably consistent patterning among geographic samples across the developmental span, whereby geographic samples with relatively larger body proportions in youth retain their relatively larger body proportions in later years. In all five age categories, the Luis Lopes, Mistihalj, California Amerindian, and Point Hope individuals consistently rank higher in RBM than the Dart, Indian Knoll, and Kulubnarti samples. This suggests that RBM remains relatively consistent across ontogeny, likely reflecting developmental constraints and neutral and selective evolutionary processes rather than intrinsic and extrinsic factors pertaining to the mechanical environment.

7.2 | Developmental timing of group differences in NSA and RBM

There is considerable variation in age-standardized NSA among geographic samples within the early years of life up until the time that a mature gait is established (3–5.9 years). Thereafter, there is little variation among geographic samples, and this pattern is consistent with studies on the developmental declination of NSA. Although among-group differences in age-standardized NSA were significant in only two of the five age categories (1–2.9 and 6–11.9 years), examination of the sample distributions (Figure 2) across the age categories suggest that small within-age category sample sizes likely explain the lack of significance in the youngest age category (birth to 0.9 years), but are less likely the case in the latter two nonsignificant age categories (3–5.9 and 12–17.9 years). That is, while no significance was reached in these three age categories, a large degree of geographic variation is evident in the first age category while variation is markedly reduced in the latter two categories, despite having larger sample sizes.

The lack of variation in NSA among the immature geographic samples in later years might seem contradictory to the vast range of variation commonly reported in adult NSA in other studies (Garden, 1961; Hoaglund & Low, 1980; Humphry, 1889; Inman, 1947; Parsons, 1914, 1915; Reikeras & Hoiseth, 1982; Reikeras et al., 1982, 1983). On the contrary, while NSA varies greatly among human populations, and mammalian taxa as a whole, within-group variation is reported to be relatively greater than among-group variation (Gilligan et al., 2013; Gilligan, 2010; Wilson & Geiger, 2015) and likely reflects intrapopulational (or intraspecific) differences in activity and postural behaviors that vary widely between individuals.

There is considerable variation in age-standardized RBM among geographic samples. Significant among-group differences were detectable in three of the five age categories: birth–0.9, 3–5.9, and 12–17.9 years. The lack of significant differences in RBM across two of the age categories (1–2.9 and 6–11.9 years) might seem erroneous, given the substantial body of evidence that body proportions *do vary* significantly throughout development (Buschang, 1982; Cowgill, Eleazer, Auerbach, Temple, & Okazaki, 2012; Feldesman, 1992; Hansman, 1970; Jungers, Cole, & Owsley, 1988; Maresh, 1959; Ruff & Walker, 1993; Ruff, 2007). Our results, however, likely reflect sample size bias among these age categories.

7.3 | Pattern of relationship between NSA and RBM

Since the proximal femur is influenced by pelvic configurations (Ruff, 1995), it has been hypothesized that populations from differing climatic regions might place different bending stresses along the femoral neck, thereby resulting in differing adult NSA (Hay, 1996; Weaver, 2003). Our results, however, do not support this hypothesis. No significant relationship was found between age-standardized NSA and RBM during development, for any sample ($p \geq .124$), or any age category

TABLE 5 ANOVA posthoc group comparisons for standardized residuals of NSA and RBM across all age categories

Ages Pooled	NSA	N	Kulubnarti	Luis Lopes	Dart	Indian Knoll	Cal. Amerindian	Mistihalj	Point Hope
				Age-standardized residuals of NSA (*N* = 451)					
	Kulubnarti	99							
	Luis Lopes	46	<0.001**						
	Dart	66		<0.000**			0.003[a]		
	Indian Knoll	94		<0.000**			0.020[a]		
	Cal. Amerindian	86	0.003[a]		<0.001**	<0.001**			
	Mistihalj	49	0.001**		<0.001**	<0.001**			
	Point Hope	56	0.048[a]		<0.001**	0.004[a]			
				Age-standardized residuals of RBM (*N* = 445)					
0–0.9 years	NSA	N	Kulubnarti	Luis Lopes	Dart	Indian Knoll	Cal. Amerindian	Mistihalj	Point Hope
				Age -standardized residuals of NSA (*N* = 73)					
	Kulubnarti	13							
	Luis Lopes	5	0.038[a]						
	Dart	12							
	Indian Knoll	15							
	Cal. Amerindian	15							
	Mistihalj	8							
	Point Hope	5							
				Age-standardized residuals of RBM (*N* = 63)					
1–2.9 years	NSA	N	Kulubnarti	Luis Lopes	Dart	Indian Knoll	Cal. Amerindian	Mistihalj	Point Hope
				Age-standardized residuals of NSA (*N* = 81)					
	Kulubnarti	14							
	Luis Lopes	6			0.028[a]				
	Dart	14					0.007[a]	0.009[a]	
	Indian Knoll	14							
	Cal. Amerindian	16							
	Mistihalj	10							
	Point Hope	7							
				Age-standardized residuals of RBM (*N* = 70)					
3–5.9 years	NSA	N	Kulubnarti	Luis Lopes	Dart	Indian Knoll	Cal. Amerindian	Mistihalj	Point Hope
				Age-standardized residuals of NSA (*N* = 79)					
	Kulubnarti	25							
	Luis Lopes	8							
	Dart	4							
	Indian Knoll	14		0.041[a]					
	Cal. Amerindian	11				0.018[a]			
	Mistihalj	8							
	Point Hope	9							

(Continues)

TABLE 5 (Continued)

Ages Pooled	NSA	N	Kulubnarti	Luis Lopes	Dart	Indian Knoll	Cal. Amerindian	Mistihalj	Point Hope
				Age-standardized residuals of RBM (*N* = 66)					
6–11.9 years	NSA	N	Kulubnarti	Luis Lopes	Dart	Indian Knoll	Cal. Amerindian	Mistihalj	Point Hope
				Age-standardized residuals of NSA (*N* = 147)					
	Kulubnarti	29							
	Luis Lopes	16							
	Dart	11							
	Indian Knoll	31					0.048[a]		
	Cal. Amerindian	24							
	Mistihalj	15							
	Point Hope	21							
				Age-standardized residuals of RBM (*N* = 137)					
12–7.9 years	NSA	N	Kulubnarti	Luis Lopes	Dart	Indian Knoll	Cal. Amerindian	Mistihalj	Point Hope
				Age-standardized residuals of NSA (*N* = 116)					
	Kulubnarti	18							
	Luis Lopes	11	0.008[a]						
	Dart	25		<0.010**					
	Indian Knoll	20		0.001**					
	Cal. Amerindian	20			<0.001**	0.013[a]			
	Mistihalj	8	0.044[a]		<0.001**	0.011[a]			
	Point Hope	14	0.020[a]		<0.001**	0.003[a]			
				Age-standardized residuals of RBM (N=109)					

[a]Significance at p = .05; ** Significance at p = .001; Nonsignificant values are omitted.

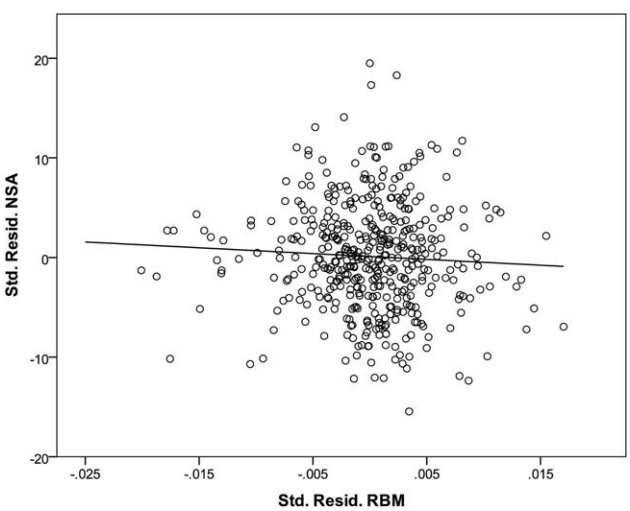

FIGURE 4 Age-standardized residuals of neck-shaft angle (Std. Resid. NSA) on age-standardized residuals of relative body mass (Std. Resid. RBM), ages and samples pooled ($n = 445$; $r^2 = 0.003$; $p = .244$)

($p \geq .108$) (Figure 4). While it is clear that RBM increases and NSA decreases with advancing age, once the effects of age are controlled by examination of age-standardized residuals, no significant relationship exists between NSA and RBM.

Comparison of the ordinal rankings of geographic samples across ontogeny reveals that populations with relatively larger body proportions do not necessarily have lower NSA, or vice versa (Table 6). For example, we would predict that the Kulubnarti sample, which had the lowest RBM within the first year of life, to have had among the highest NSA in this study. However, the Kulubnarti have the lowest NSA at this age. Similarly, the Luis Lopes sample has a significantly larger RBM compared to the Kulubnarti at this age, but does not significantly differ in NSA from this sample. If changes in body proportions influence the declination of NSA, then we would have expected to observe greater concomitance between these two features along the developmental span. This suggests that regardless of differences in body proportions between populations, the degree of declination of the NSA is presumably similar among individuals with similar gait and ambulatory behaviors. Support for this finding may be found in the observance of relatively higher NSA observed among suspensory anthropoids and

TABLE 6 Relative ranking of mean standardized residuals for NSA and RBM across all age categories

All Ages	Birth–0.9	1–2.9	3–5.9	6–11.9	12–17.9
		Age-standardized residuals of NSA			
1) Cal Amerindian[A]	1) Kulubnarti	1) Mistihalj[A]	1) Cal Amerindian	1) Cal Amerindian[A]	1) Indian Knoll
2) Point Hope	2) Point Hope	2) Luis Lopes[A]	2) Point Hope	2) Kulubnarti	2) Cal Amerindian
3) Kulubnarti	3) Mistihalj	3) Cal Amerindian[A]	3) Mistihalj	3) Point Hope	3) Luis Lopes
4) Mistihalj	4) Cal Amerindian	4) Kulubnarti	4) Kulubnarti	4) Mistihaljh	4) Mistihalj
5) Luis Lopes	5) Dart	5) Indian Knoll	5) Dart	5) Dart	5) Dart
6) Indian Knoll[B]	6) Indian Knoll	6) Point Hope	6) Luis Lopes	6) Luis Lopes	6) Point Hope
7) Dart[B]	7) Luis Lopes	7) Dart[B]	7) Indian Knoll	7) Indian Knoll[B]	7) Kulubnarti
		Age-standardized residuals of RBM			
1) Luis Lopes[A]	1) Luis Lopes[A]	1) Cal Amerindian	1) Cal Amerindian[A]	1) Luis Lopes	1) Luis Lopes[A]
2) Point Hope[A]	2) Mistihalj	2) Mistihalj	2) Luis Lopes[A]	2) Point Hope	2) Mistihalj[A]
3) Cal Amerindian[A]	3) Cal Amerindian	3) Point Hope	3) Mistihalj	3) Cal Amerindian	3) Point Hope[A]
4) Mistihalj[A]	4) Point Hope	4) Luis Lopes	4) Point Hope	4) Mistihalj	4) Cal Amerindian[A]
5) Dart[B]	5) Dart	5) Dart	5) Kulubnarti	5) Dart	5) Dart[B]
6) Indian Knoll[B]	6) Indian Knoll	6) Kulubnarti	6) Dart	6) Indian Knoll	6) Indian Knoll[B]
7) Kulubnarti[B]	7) Kulubnarti[B]	7) Indian Knoll	7) Indian Knoll[B]	7) Kulubnarti	7) Kulubnarti[B]

Age standardized residuals of NSA are listed from lowest to highest; Age standardized residuals of RBM are listed from highest to lowest. Superscript A samples significantly differ from superscript B samples.

other mammals, such as hystricomorphs and sloths, compared to generalized quadrupeds. The higher NSA observed within these locomotor groups are presumed to enhance hip abduction in the performance of their locomotor and postural behaviors, despite a wide range of body proportions observed among these taxa (Almécija et al., 2013; Fleagle, 1976; Fleagle & Meldrum, 1988; Hammond, 2014; Harrison, 1986; Jenkins & Camazine, 1977; MacLatchy, Gebo, Kityo, & Pilbeam, 2000; Rose, 1983; Turvey, Grady, & Rye, 2006; Walker, 1974; Ward, Walker, Teaford, & Odhiambo, 1993; White, 1993; Wilson & Geiger, 2015). Taken as a whole, results suggest that while both NSA and RBM change over the course of ontogeny, changes in RBM during development do not directly drive changes in the declination of NSA, and suggest that these two measures are responsive to differing stimuli, such as nutrition, activity levels, hormones, or ecogeographic principles. Given the scarcity of immature skeletal collections, it is possible that the seven samples used here, which span tropical and arctic climates, do not represent sufficient geographic variation to detect any potential relationship. Previous studies using these same samples (Cowgill et al., 2012; Cowgill, 2008, 2010), however, have detected marked climatic variation, so this seems unlikely.

8 | CONCLUSIONS

We examined the pattern of relationship between NSA and RBM over the course of ontogeny in a geographically diverse sample of immature Holocene remains. Analytical results indicate that populations differ with regard to NSA and RBM before skeletal maturity, and that these differences are detectable at or before the first year of life. NSA differs among populations throughout the developmental landmarks of independent walking and mature gait acquisition. Thereafter, the angle is "fixed," reaching adult values with little further declination in advancing years. While population differences in age-standardized NSA were detectable in some samples and in some age categories, the relative ranking among samples was highly variable. This suggests that regardless of differences in body proportions between populations, the degree of declination of the NSA is presumably similar among individuals with similar gait and ambulatory behaviors. Conversely, population differences in RBM differ significantly from birth and these differences remain consistent throughout the developmental years, suggesting that RBM is strongly dictated by ecogeographic principles.

While both NSA and RBM change along the course of development, no statistical relationship between age-standardized NSA and RBM was found. Individuals that exhibit relatively greater RBM do not necessarily exhibit lower NSA. While caution is warranted in drawing specific sample- and age-related inferences due to relatively small sample sizes when the study sample is subdivided into these subgroups, the overall pooled study sample is robust ($n = 445$). Changes in RBM during development do not directly drive changes in declination of NSA, and it is likely that these two measures are responsive to differing stimuli, such as nutrition, activity levels, hormones, or ecogeographic variables. Any potential relationship between NSA and RBM is likely more complex and multifactorial, reflecting the combined effects of

body size, musculature, and activity level. A large sample of immature remains with known body mass and body proportions is required to further test this relationship.

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How to cite this article: Child SL, Cowgill LW. Femoral neck-shaft angle and climate-induced body proportions. *Am J Phys Anthropol*. 2017;164:720-735. https://doi.org/10.1002/ajpa.23311