An alternative size variable for allometric investigations in subadults

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ABSTRACT

Objectives Effective allometry research relies on appropriate size variables; however, two of the largest obstacles in subadult (ontogenetic) allometry research is small sample sizes and unknown dimensions. This study overcomes a barrier of ontogenetic allometry research by proposing alternative size variables that do not require additional calculations for use in subadult allometry research and retain general patterns among long bones when stature is used for size..

Materials and Methods Diaphyseal measurements, stature, and age were collected from computed tomography (CT) and full-body radiographic images for a sample of subadults between birth and 13 years from the United States (U.S., $n = 308$) and South Africa (Z.A., $n = 25$). Nineteen alternative size variables were evaluated using reduced-major-axis regression to identify the closest one-to-one relationship to stature. The applicability across samples was then evaluated using the selected alternative size variables.

Results Radius midshaft breadth (RMSB), femur midshaft breadth (FMSB), and the geometric mean of midshaft breadths (GM midshaft) yielded the closest isometric relationships to stature. Allometric relationships among long bones are maintained when using stature, FMSB, and GM midshaft as size variables for both the U.S. and Z.A. samples.

Discussion A large, modern dataset facilitated an investigation into alternative size variables that can be used for single-bone ontogenetic allometry. Generalizability of the model suggests FMSB and GM midshaft are persistent across populations. This methodology identifies alternative size variables appropriate for other allometry research and offers a robust approach even when historically relied upon size variables are unknown.

Keywords: skeletal allometry, limb proportions, subadult

1 INTRODUCTION

Allometry is the study of biological change in relation to size and produces proportional (size independent) measures suitable for comparison within and among groups under study (Bonner & Horn, 2000; Brown & West, 2000; Gayon, 2000; Huxley, 1932; Stevens, 2009). Allometry research is generally partitioned into one or more sub-categories (Gould, 1966; Klingenberg & Zimmermann, 1992): (a) static, which often involves group comparisons among the same age or life history stage; (b) evolutionary, which investigates change over time; and (c) ontogenetic, which evaluates the change in proportions through growth and development. In biological anthropology, skeletal limb allometry is used to explore questions of hominin evolution (e.g. Holliday, 1997; Holliday & Franciscus, 2009; Little, 2020), secular change (e.g. Jantz & Devlin, 2016; Jantz & Meadows Jantz, 2017; Meadows & Jantz, 1995), human variation (e.g. Auerbach, 2012; Livshits et al., 2002; Seguchi et al., 2017; Tilkens et al., 2007), and growth and development (e.g. Bareggi et al., 1996; Frelat & Mitteroecker, 2011; Temple et al., 2011; Waxenbaum et al., 2019). Huxley's (1932) allometry equation is used across disciplines, and in all three sub-categories, to explore bivariate relationships between the feature of interest (y) and a size variable (x):

$$y = bx^{\alpha} \tag{1}$$

1.1 Size Variables

The most common size variables across allometry research are body mass (Holliday & Franciscus, 2009; Ruff, 1991, 2002; Watkins & German, 1992; Yim et al., 2021) and a length measure, such as stature (Bogin & Baker, 2012; Buschang, 1982; Holliday, 1999; Meadows & Jantz, 1995). Unless working with a documented skeletal collection, which is not possible for paleoanthropologists and less common for bioarchaeologists, size variables are often calculated using linear regression methods (Elliott, Kurki, Weston, & Collard, 2016; Konigsberg et al., 1998; Lacoste Jeanson et al., 2017; Lundy, 1985), which may introduce sources of error because of incompatible reference samples or wide confidence intervals (Moore & Ross, 2012; Pelin & Duyar, 2003; Schaffer, 2016).

The geometric mean of measures under investigation (e.g. long bone lengths) has also been used as a size variable and does not require a linear regression calculation (Jungers et al., 1995; Sylvester et al., 2008; Temple et al., 2008). Yet, it has been shown that the geometric mean can produce a size variable *dependent on* the measures of interest and can also generate allometry coefficients that are difficult to interpret biologically (Auerbach & Sylvester, 2011; Coleman, 2008). For example, if an individual has a proportionally short femur, the geometric mean will be smaller than it should be, potentially inflating the calculation of positive and negative allometric relationships. Further, it is difficult to understand what a one-unit change in the geometric mean means in relation to changes in the length of a long bone; the geometric mean is not a tangible biological dimension.

1.2 Ontogenetic Allometry

Ontogenetic allometry ideally uses longitudinal data for explorations of individual-level heterogeneity (e.g. Bareggi et al., 1996; Cheverud, 1982; Jungers & Fleagle, 1980; Pélabon et al., 2013). Due to sampling constraints, cross-sectional data covering multiple stages of growth and development may be used to approximate ontogenetic allometry patterns, sometimes referred to as *indirect ontogenetic allometry* (Brown & Vavrek, 2015; Gould, 1966; Klingenberg, 1998; Pélabon et al., 2013). Indirect ontogenetic allometry is commonly used for investigations of extant species (e.g. Brown & Vavrek, 2015; Goodwin et al., 2006; Padian & Horner, 2011) because of limitations in sample availability and is the framework used for the present study. This study aims to address the persistent problems in selecting an appropriate size variable for ontogenetic allometry research. Methods for estimating subadult body mass and stature are not accurate and therefore do not lead to valid results if incorporated into allometry research (Cowgill, 2018; Langley, 2017; Robbins et al., 2010; Yim et al., 2021). As an alternative, many subadult allometry studies investigating bivariate relationships continue to use the brachial or crural index (e.g. Bleuze et al., 2014; Cowgill, 2018; Frelat & Mitteroecker, 2011; Temple et al., 2011), in which the size variable is the proximal element. This region-specific method makes it difficult to interpret individual-level patterns of ontogenetic allometry. In addition, region-specific size variables make it difficult to observe the ontogeny of individual elements that make up these indices, which is important for linking ontogenetic allometry research to other aspects of biological anthropology, such as evolution and adult human variation. The present study proposes an alternative size variable for modern ontogenetic allometry investigations to overcome the current limitations of undocumented skeletal collections by demonstrating an analytical approach that is robust even when historically relied upon size variables are unknown.

2 MATERIALS AND METHODS

2.1 Samples

Two samples were used in the current study; one was used to identify alternative size variables and the other was used as an external test for inter-country applicability of the proposed alternative size variable. Diaphyseal data collected from computed tomography (CT) images of 308 subadults aged between birth and 13 years from the Subadult Virtual Anthropology Database (SVAD) (Figure 1) (Stull & Corron, 2021a, 2021b, 2022; Stull, Garvin, & Klales, 2020). These images were generated at the University of New Mexico Health Sciences Center, Office of the Medical Investigator and are part of the New Mexico Decedent Image Database (Berry & Edgar, 2021; Edgar et al., 2020) and are used to represent subadults from the United States (U.S.). Diaphyseal data from an additional sample of 25 subadults also aged between birth and 13 years-old and curated in the SVAD were used as the external test of the inter-country

applicability of the proposed alternative size variables identified with the U.S. sample. These data were originally collected from Lodox Statscan images (full-body radiographs) generated from the Red Cross War Memorial Children's Hospital in Cape Town, South Africa (Z.A.) (Stull et al., 2014). Age at death and stature were also recorded for both samples. Stature for the U.S. sample is represented as cadaveric stature at the time of intake at the medical examiner's office, whereas Z.A. stature was taken directly from full-body radiographs and include soft tissue for closer approximation to cadaveric stature (Stull, 2013). Both samples consist of pooled sex, as reliable methods of estimating sex from subadult remains have yet to be established (Cardoso & Saunders, 2008; Klales & Burns, 2017; Stull, Cirillo, et al., 2020; Stull & Godde, 2013).

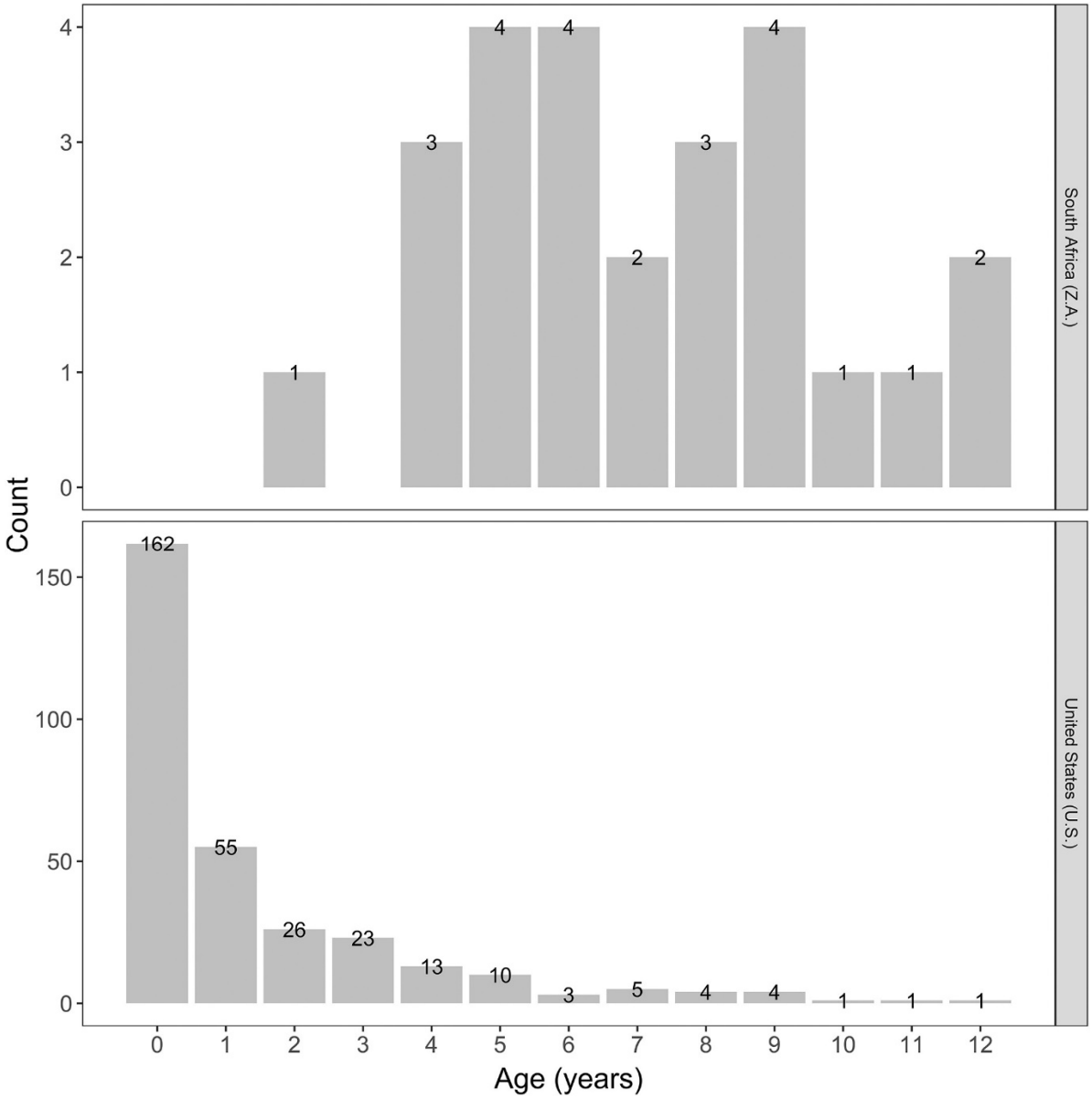

Figure 1. Sample age distributions by country

The U.S. and Z.A. have substantially different population histories (Mendes Fialho, 2017), ecogeographic locations (Cui et al., 2021), and socioeconomic structures (Assari & Moghani Lankarani, 2015; Moghani Lankarani et al., 2017), which make them good candidates for generalization of the proposed alternative size variable. Admittedly, the authors recognize the sampling biases in age and the lack of country-level diversity captured in the two samples. The U.S. sample is more representative of local population demographics in Albuquerque, New Mexico, than the entire country. Similarly, the Z.A. sample is more representative of local demographics of Cape Town than the entire country. While diversity and appropriate representation of larger countries/populations is normally considered paramount, in this situation, the identified size variables ideally should be – need to be – independent of extrinsic and intrinsic population-level and age-level characteristics. Therefore, while population and sampling biases exist, they should not impact the methodology.

2.2 Methodology

All computational analyses were conducted in R (R Core Team, 2021) and RStudio® (RStudio Team, 2020). The US sample was split into 10-folds (k = 10) for model development using the *caret* package in R (Kuhn, 2020). Each individual had a potential of 15 measurements collected from the medical images (i.e. CT or full-body radiographs), including both breadths and lengths (see Stull et al., 2014 for visualizations) (Table 1). All breadth measurements were evaluated as a potential alternative size variable (Table 2). Lengths were not included as potential alternatives because Auerbach and Sylvester (2011) previously showed the biologically confounding results of using the geometric mean of long bone lengths in allometric research. In contrast, the use of the geometric mean of long bone breadths as a size variable has not yet been tested to the knowledge of the authors. Exploring breadth measures also prevents biologically difficult interpretations of allometry coefficients created by using the same measures for both the numerator and denominator (e.g. FDL/FDL will always equal 1).

Table 1. Measurement definitions and abbreviations for each dimension, as published by Stull et al. (2014) and Stull and Corron (2021a). See original publication for visualizations and commentary/advice

Measurement	Long bone	Abbreviation	Definition and suggested comments
Diaphyseal length	Humerus, Radius, Femur, Tibia	HDL, RDL, FDL, and TDL	The maximum distance between the most proximal edge of the diaphysis to the most distal edge of the diaphysis.
Proximal breadth	Humerus, Radius, Tibia	HPB, RPB, and TPB	The distance between the most medial and lateral edges of the proximal diaphysis when the element is viewed in anatomical position.
Midshaft breadth	Humerus, Radius, Femur, Tibia	HMSB, RMSB, FMSB, and TMSB	The distance between the most medial and lateral edges at midshaft, perpendicular to the long axis of the bone, when the bone is in anatomical position.
Distal breadth	Humerus, Radius, Femur, Tibia	HDB, RDB, FDB, and TDB	The distance between the most medial and lateral points on the distal diaphysis, when the element is viewed in anatomical position.

Table 2. Alternative size variables tested in the present analysis

Breadth measurements	Region-specific geometric mean	Bone-specific geometric mean
HPB, HDB, and HMSB	All	Humerus
RPB, RDB, and RMSB	Proximal	Radius
FDB, FMSB	Midshaft	Femur
TPB, TDB, and TMSB	Distal	Tibia

Because the US sample consists of all complete cases (all 15 potential measurements available), the authors tested the use of the geometric mean using different combinations of breadth measurements (Table 2): all breadths (“All”), proximal breadths (“Proximal”), midshaft breadths (“Midshaft”), distal breadths (“Distal”), femur breadths (“Femur”), tibia breadths (“Tibia”), humerus breadths (“Humerus”), and radius breadths (“Radius”). The geometric mean (GM) is calculated as the *n*th root of the product of all *i* variables (Equation (2)):

$$\mathrm{GM} = \sqrt[i]{x_1 x_2 \cdots x_i} \quad (2)$$

In total, 19 alternative size variables consisting of breadths and geometric mean calculations, were tested. All measures were subsequently transformed into natural-log space, as recommended by Huxley (1932) to transform the power-law equation (Equation (1)) to a linear equation (Equation 3):

$$\ln(y) = \alpha \ln(x) + \ln(b) \quad (3)$$

Mardia (1970) and Henze and Zirkler (1990) tests and the visualization of a multivariate Chi-square quantile–quantile ("Q-Q") plot (Rani Das & Rahmatullah Imon, 2016; Stine, 2017) were used to evaluate multivariate normality using the *MVN* package (Kormaz et al., 2014). Correlation coefficients were calculated using Kendall's tau, which does not assume a normal data distribution, between stature and all potential size variables to identify the best alternative.

Reduced-major-axis (RMA) regression was used for model construction, meaning that alternative size variables (*y*) were regressed on stature (*x*) (Equation (4), as an example). RMA is a common regression method used in biological anthropology because it assumes equal levels of error for both *x* and *y* (Aiello, 1992; Sjøvold, 1990), and is most appropriately used when the variables are significantly correlated and there is a large sample size (Smith, 2009). RMA models were generated using the *lmodel2* package (Legendre, 2018).

$$\ln(humerus\ distal\ breadth) = \alpha \ln(stature) + \ln(b) \quad (4)$$

All models were first built using the US training sample. Slope (α, "allometry coefficient") and intercept (*b*) corresponding to each RMA equation were stored for subsequent analyses. After all models were generated, the slopes of all potential alternative size variables were evaluated to see which was closest to one, representing a one-to-one scaling relationship between the size variable and stature. The selected alternative size variable was then applied to the U.S. and Z.A. test samples for model evaluation.

To test the biological validity of the proposed alternative size variable, diaphyseal lengths of the humerus, radius, femur, and tibia were regressed against stature, the selected alternative size variables, and GM of diaphyseal lengths as size variables. The allometric relationship between long bone lengths was visualized to explore whether the same pattern was observed using subadult measures, thus providing evidence that the selected alternative size variables are appropriate for allometry research (Auerbach & Sylvester, 2011).

3 RESULTS

Results of the Mardia and Henze–Zirkler tests ($p < 0.05$ for both) and Q–Q plot visualization indicated significant deviation from multivariate normality (Figure 2). Therefore, nonparametric statistical tests and modeling techniques were chosen for the subsequent analyses. Kendall's tau correlations between stature and alternative size variables yielded correlation values ranging between 0.80 and 0.87 (Table 3).

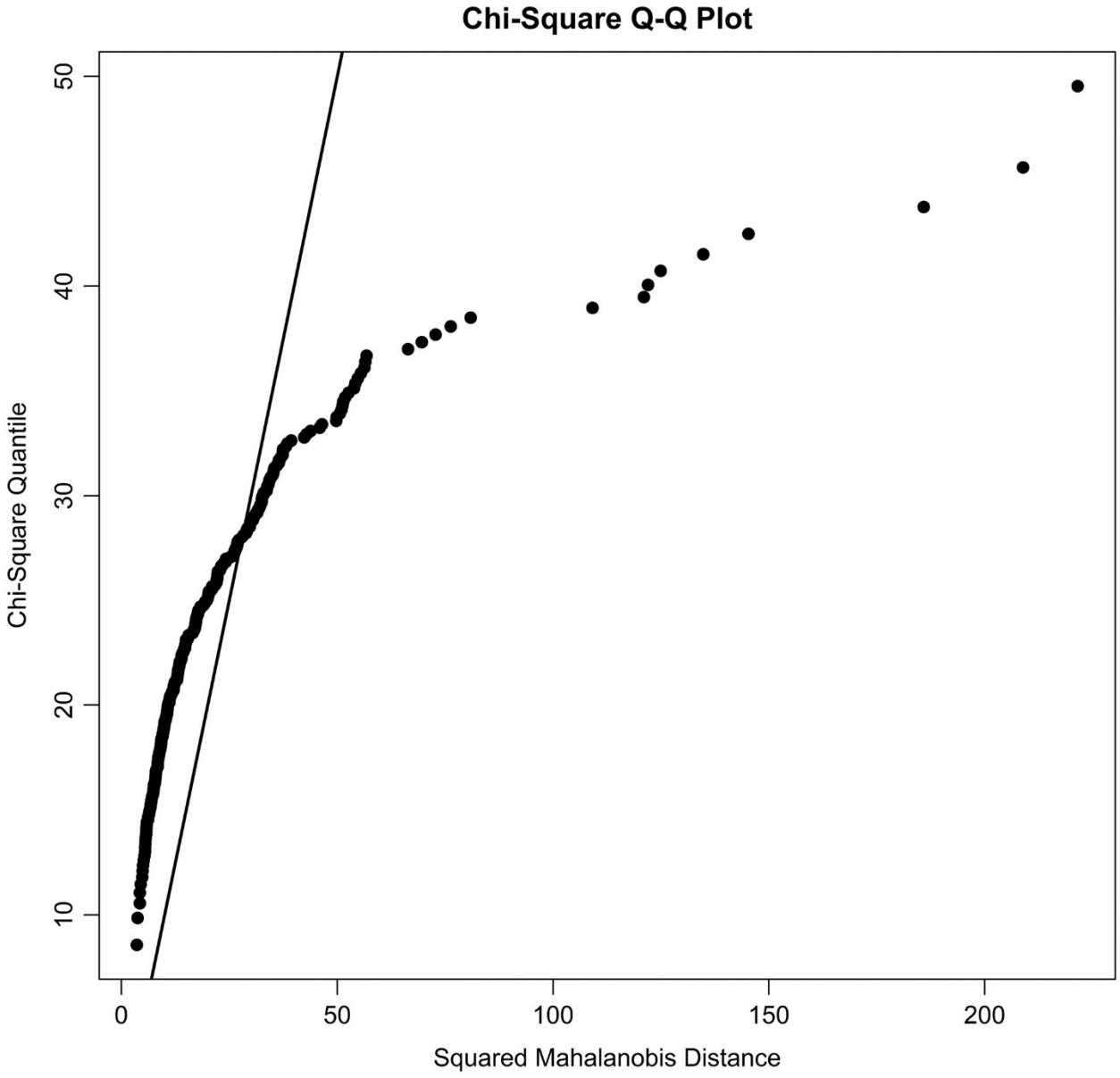

Figure 2. Chi-square Q–Q plot to visualize multivariate normality. The solid black line represents multivariate normality, and the deviation of the pattern of filled circles indicates non-normality of the U.S. data

Table 3. Allometry coefficients (*α*) and correlations (*r*) generated from the respective RMA models ranked by allometry coefficient distance to 1.00

Alternative size variable	Allometry coefficient (α)	Correlation with stature (r)
Radius midshaft breadth	0.99	0.80
Femur midshaft breadth	1.01	0.84
GM midshaft breadths	1.01	0.84
Humerus distal breadth	0.98	0.85
Radius proximal breadth	0.97	0.81
GM Humerus breadths	1.03	0.85
Tibia midshaft breadth	1.03	0.81
GM all breadths	1.05	0.86
Humerus proximal breadth	1.05	0.82
GM Radius breadths	0.95	0.83
Radius distal breadth	0.93	0.80
GM distal breadths	1.07	0.86
GM proximal breadths	1.08	0.85
Humerus midshaft breadth	1.08	0.82
GM Femur breadths	1.09	0.87
GM Tibia breadths	1.16	0.86
Femur distal breadth	1.18	0.87
Tibia distal breadth	1.21	0.85
Tibia proximal breadth	1.26	0.86

Allometry coefficients from each linear regression model are also summarized in Table 3. General trends do not indicate that geometric mean measures outperform single breadth measurements. Using RMA, RMSB presented with the closest (to the ten-thousandth decimal) one-to-one linear relationship with stature in natural-log space, followed by FMSB and the GM of all midshaft breadths (“GM midshaft breadths” in

Table 3, Figure 3). The Kendall's tau correlation between stature and the alternative size variables are 0.80, 0.84, and 0.84, respectively. Note how the size variables with the slope closest to one do not necessarily have the strongest correlation with stature in natural-log space (Table 3).

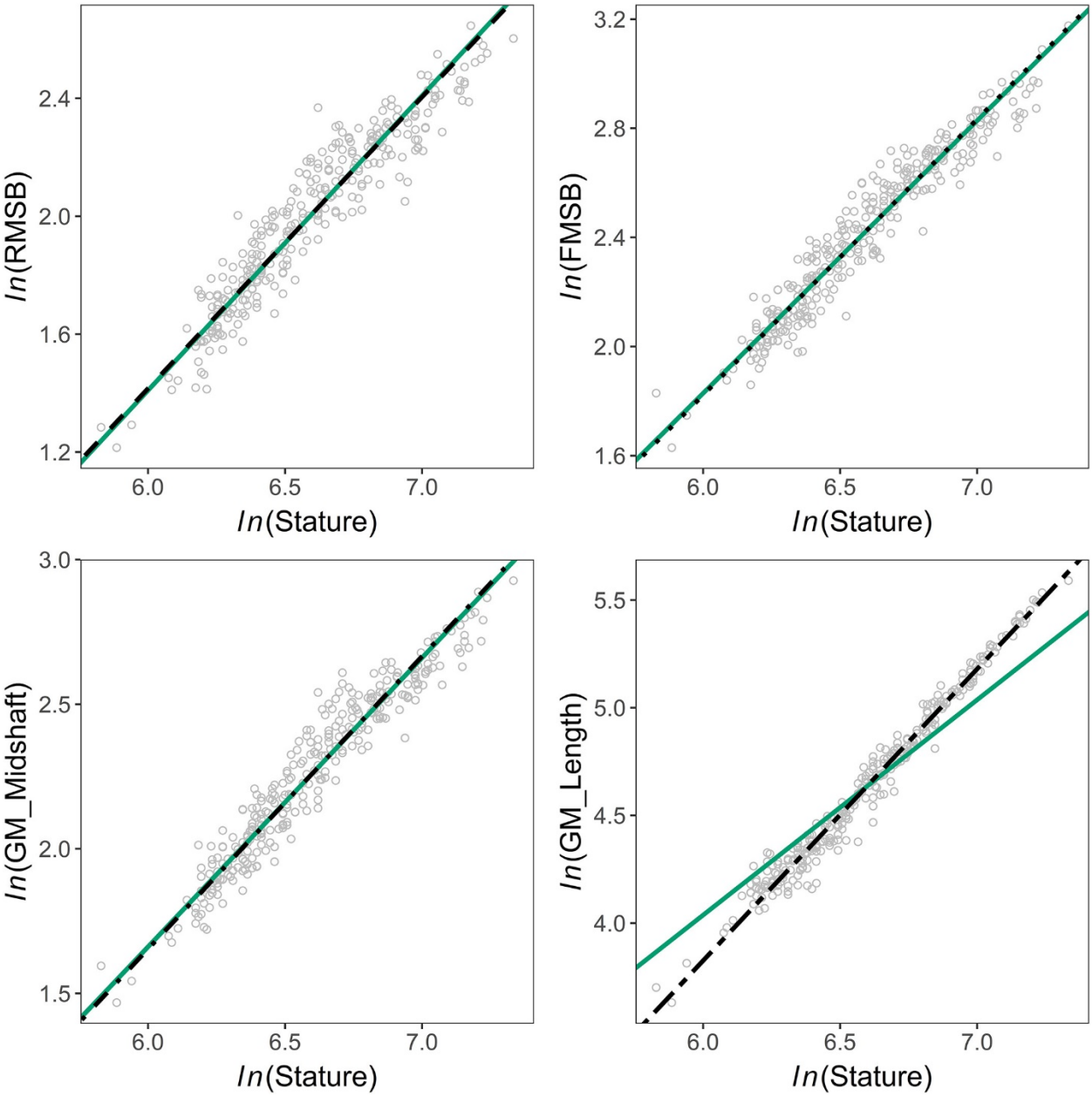

Figure 3. Bivariate relationship between stature (*x*) and alternative size variables (*y*) in log-normal space. The solid green line represents isometry. Note the magnitude and directionality of the black, nonsolid line crossing the isometry line

When comparing the allometry coefficient relationships among long bone diaphyseal lengths using the US sample, all three alternative size variables present with

the similar magnitudes of inter-long bone relationships (Figure 4a) and the GM of diaphyseal lengths shows negative allometry of the upper limb. When applied to the Z.A. sample, FMSB and the GM of midshaft breadths demonstrate the closest inter-long bone relationship to stature and RMSB and GM of diaphyseal lengths show negative allometry of the upper limb (Figure 4b).

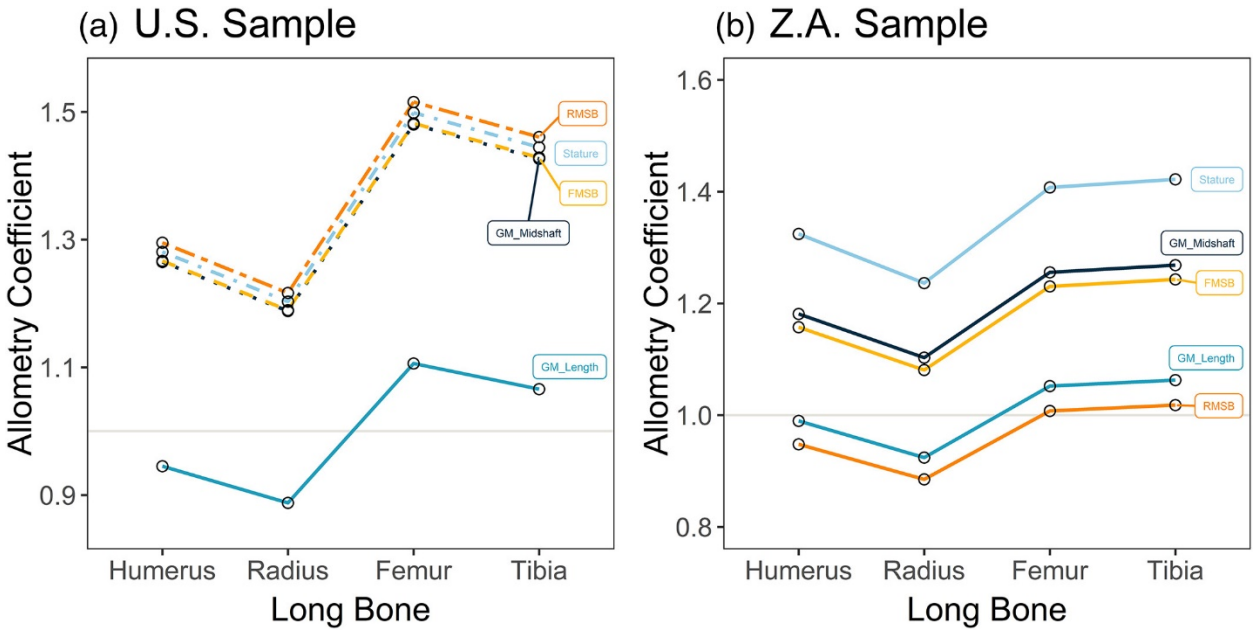

Figure 4. Inter-long bone allometric relationships. The solid gray line across slope = 1.0 represents isometry

Figure 5 provides a comparison between the allometric relationships of long bones for an adult sample from Auerbach and Sylvester (2011) and subadults from the present study. Allometric relationships from the present study depict greater positive allometry for the proximal elements compared to the distal elements as well a distinct separation between the allometry coefficients of the upper and lower limbs, with the lower limbs showing overall greater positive allometry compared to the upper limbs. This allometric relationship of long bones is not in conjunction with those reported by Auerbach and Sylvester (2011), which depict greater positive allometry of the distal elements compared to the proximal elements and overlap of the allometry coefficients between the upper and lower limbs.

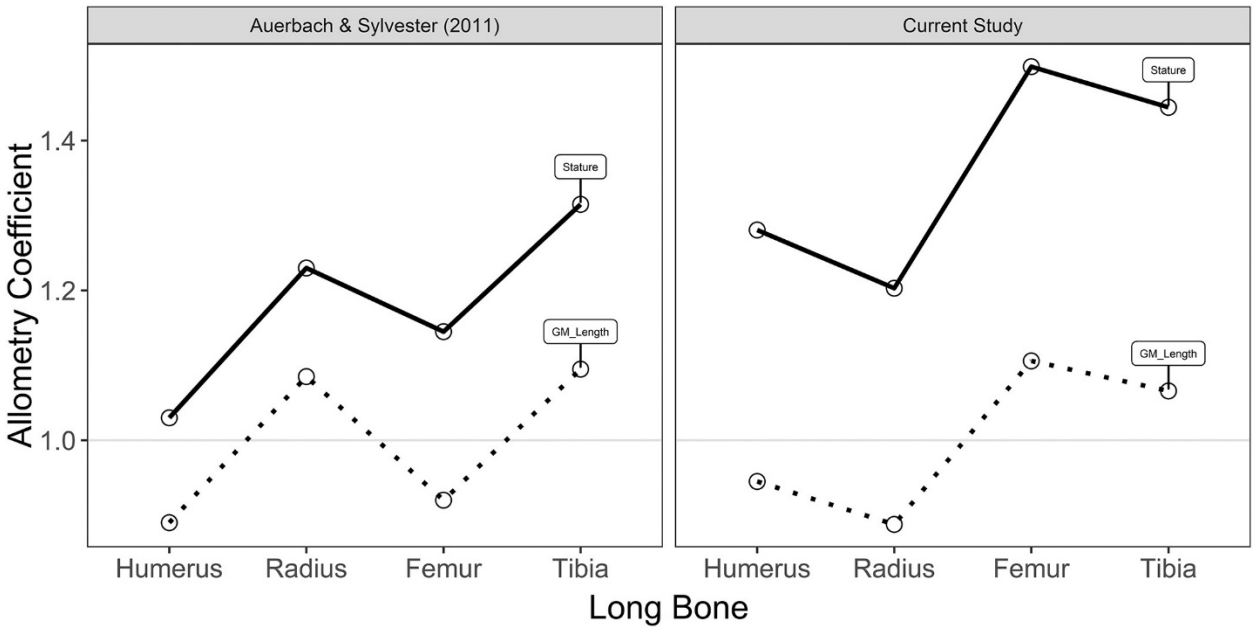

Figure 5. Allometry coefficient relationships between long bone diaphyseal lengths from averaged coefficients from Auerbach and Sylvester (2011) on the left and the current study on the right. The solid gray line across slope = 1.0 represents isometry

4 DISCUSSION

Results of this study demonstrate FMSB and the GM of midshaft breadths as the best alternative size variables to stature for subadult allometry research across two geographically diverse samples. The main criteria used in this study to deem a size variable suitable for ontogenetic allometry research include (1) having the closest one-to-one bivariate relationship to stature to approximate isometric relationships with stature that therefore, (2) produces similar allometric relationships between long bones when using stature as the size variable, and (3) is applicable to more than a single sample population. These three criteria will be explored in detail below.

4.1 (Almost) Isometric

Results of this study demonstrate that FMSB and GM midshaft breadths are the best alternative size variables to stature for subadult allometry research across two geographically diverse samples. Choosing an appropriate size variable is important to identify deviations from *isometry* (Fox et al., 2021; Jungers et al., 1995; Jungers & German, 1981), as all positive or negative allometric relationships are inferred based on departures from a slope of one for stature in logarithmic space and represent a biological change in relation to size. Thus, the methodology of this research focused more on finding the closest isometric relationship between alternative size variables and stature instead of relying on correlation. As is demonstrated in Table 3, no correlations between stature and potential alternative size variables fall below 0.80. There are

imperceptible differences in allometric relationship among the three proposed alternative size variables RMSB, FMSB, and GM midshaft breadths with stature (Figure 3). In contrast, GM diaphyseal length has a strong positive allometric relationship with stature (coefficient = 1.36, Figure 3), which further suggests against using GM diaphyseal length as an alternative size variable when stature is unavailable for both adult and subadult studies.

4.2 Allometric Relationships

Allometry coefficients of the humerus, radius, femur, and tibia were plotted using stature, FMSB, RMSB, GM of midshaft breadth, and GM of diaphyseal length (Figure 4). Note that while the general pattern between long bones is also demonstrated by GM diaphyseal length, the same instance of negative allometry for some elements that Auerbach and Sylvester (2011) demonstrated (see Figure 5) is reproduced when using a subadult sample.

The allometry coefficients for males and females reported by Auerbach and Sylvester (2011) were averaged and plotted against the coefficients generated by the current study using stature and GM of diaphyseal length as the size variables (Figure 5). The general pattern of allometry coefficients for long bones in this study presents with proximal elements as more positively allometric than their distal counterparts. This observation is the opposite of what was reported in Auerbach and Sylvester (2011), though this may be due to a comparison between a static and ontogenetic allometry approach. Further, this observation deviates from findings by Buschang (1982) that showed the tibia to be more positively allometric than the femur in subadults aged between 2 months and 11 years. These differences in allometric patterning of long bones demonstrates the importance of identifying alternative size variables suitable for *ontogenetic* (i.e. growth and development) allometry research, as we may now begin to explore the underlying causes of fluctuating intralimb (i.e. brachial and crural) proportions reported by previous subadult allometry studies (Bleuze et al., 2014; Cowgill, 2018; Frelat & Mitteroecker, 2011; Temple et al., 2011) over the entire human growth period.

4.3 Cross-sample Application

The final criterion for choosing an appropriate alternative size variable to stature in ontogenetic allometry research was the applicability of the size variable to other samples. Figure 4b demonstrates that FMSB and GM midshaft breadths, when used as a size variable, produce the most-similar inter-long bone allometric relationships to that of stature. Greater distance of the allometry coefficients from the stature coefficients observed in the Z.A. sample (Figure 4b) may be either be because of population differences or differences in the sample distribution of ages. While this sampling bias should still be considered, the persistence of FMSB and GM of midshaft breadths having the closest relationship to stature further demonstrates the generalizability of FMSB to samples from other countries. The multi-sample applicability of FMSB and GM

midshaft breadths demonstrated in this study allows for the direct comparison of ontogenetic allometry coefficients and trajectories among the U.S. and Z.A. samples. Such comparisons may then be used to evaluate periods of similarity and differences in growth and development among populations and provide evidence for potential effects of intrinsic and extrinsic factors on human variation.

5 CONCLUSION

Skeletal allometry research has one obstacle that has persisted through time and impacts all types of allometry research: using stature to quantify body size. First, stature is not commonly available in skeletal remains *or* accurately estimated, and second, the geometric mean of the long bone lengths has been commonly used instead of stature in static allometry research, producing allometric relationships that may be misleading or hard to interpret (e.g. negative allometry of the upper limb). Subadult allometry research has been primarily limited to brachial and crural indices because of small sample size and unknown stature. However, these indices cannot provide the detailed, long bone-specific information needed to understand certain processes of growth and development, such as the establishment of allometric relationships and/or maturation of body proportions. Questions regarding periods of developmental plasticity and/or canalization of long bone growth may be pursued, and the differential effects of maturation events, such as the pubertal growth spurt on the relative growth of long bones, may also be explored. The present study provides an alternative size variable to further research in subadult allometry to allow for a deeper interpretation of the development and relationship of intralimb (i.e. brachial and crural) proportions found in the previous subadult allometry studies (Bleuze et al., 2014; Cowgill, 2018; Frelat & Mitteroecker, 2011; Temple et al., 2011).

The current study utilizes a newly developed, freely available database (SVAD) to explore alternative size variables and determine that FMSB and GM midshaft breadths yield the closest one-to-one relationship with stature. This novel research has broad impacts in paleoanthropology, bioarchaeology, and research involving modern human variation by providing a valid skeletal measure to use, rather than estimating stature, in human skeletal allometry research. Additional areas of inquiry into the potential biomechanical and/or evolutionary constraints on the relative development of long bones can also be investigated using alternative size variables. Body mass was not used in this study as it is even less accurately reported and less accurately estimated than stature in subadults. Because stature and body mass do not scale isometrically (Bogin, 2005), future investigations should be pursued to understand the differences in allometry inferences generated by both size variables. Future research is needed to explore these questions, and the present methodology could be conducted on a large adult sample with known stature to establish alternative size variables for use in adult skeletal allometry research. Importantly, the current study demonstrates that these alternative size variables are not population or geographically dependent and

should be universally applicable. However, an additional validation study using larger test samples and diverse samples would be beneficial. Such steps may help better clarify questions of secular change and the evolution of body proportions.

AUTHOR CONTRIBUTIONS

Elaine Y. Chu: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); project administration (lead); visualization (lead); writing – original draft (lead). **Kyra E. Stull:** Conceptualization (supporting); formal analysis (supporting); methodology (supporting); resources (lead); software (lead); supervision (lead); visualization (supporting); writing – review and editing (equal). **Adam D. Sylvester:** Formal analysis (supporting); methodology (supporting); supervision (supporting); visualization (supporting); writing – review and editing (equal).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo as the Subadult Virtual Anthropology Database at 10.5281/zenodo.6481478. A research compendium to fully replicate the results is available at http://rpubs.com/elainechu/subadult_sv_2022.

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