

University of Nevada, Reno

# **Explorations into Appendicular Ontogeny using a Cross-Sectional, Contemporary U.S. Sample**

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by

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## Abstract

Investigations into the subadult skeleton have been restricted by sample availability in biological anthropology. Alternatively, the same source of longitudinal data has been repeatedly used, which does not reflect the variability of growth and development (*i.e.*, ontogeny) or the United States (U.S.) population. Small and/or homogenous samples have often resulted in limited or inappropriate modeling choices to investigate the growth and development and variation of the subadult skeleton. Recent technological advancements have made virtual anthropology possible. The use of computed tomography (CT) scans has opened the doors to increasing sample sizes of minority groups and in turn increasing the variation of skeletal information. One repository, the Subadult Virtual Anthropology Database (SVAD), has focused on increasing and diversifying subadult skeletal data to increase the possibilities of subadult research in biological anthropology. The articles in this (non)dissertation collection use the SVAD (M=610, F=416) and the Forensic Anthropology Data Bank (FDB; M=285, F=161) to evaluate three different perspectives of appendicular (*i.e.*, long bone) ontogeny: absolute, relative, and index. First, relative long bone lengths and nonlinear modeling are used as the first-ever evaluation of long bone growth through adult stabilization. Second, the brachial and crural indices are used to explore the chronological ontogenetic trajectories of each index and their ecogeographic patterns. Third, absolute long bone breadth and length measurements are used to create linear and nonlinear equations for estimating subadult stature for forensic application. In doing so, this is the first comprehensive collection of studies that explore three distinct perspectives of long

bone ontogeny and variation from the same source of subadult skeletal data, demonstrating the need for additional contemporary subadult samples and novel modeling approaches.

## **Dedication**

To my mother, Dr. Jane-Jane Lo.

You are my role model and number one fan.

Thank you for supporting my dreams.

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## Introduction

Appendicular ontogeny has been explored through three main lenses: absolute measures, relative measures, and indices. Each perspective has been used to explore aspects of long bone growth and diversity but are typically conducted within different anthropological niches. From absolute measurements, we know there is a strong relationship between long bone measurements and age, sex, and stature (*e.g.*, Gazarian, & Braillon, 2008; Brits, Bidmos, & Manger, 2017; López-Costas, Rissech, Tranco, & Turbón, 2012; Rissech, Márquez-Grant, & Turbón, 2013; Stull, Chu, Corron, & Price, 2022; Stull, L'Abbé, & Ousley, 2017). These theoretical relationships are used in forensic anthropology to estimate aspects of the biological profile. We also have a general understanding of the different growth trajectories and velocities of long bones (Maresh, 1943; Smith & Buschang, 2004, 2005; Völgyi et al., 2010), which have been used to diagnose atypical growth like stunting (*e.g.*, Schillaci, Sachdev, & Bhargava, 2012). Relative measurements using allometry or standardized means allow biological anthropologists to make inter- and intra-species comparisons. Using allometry, we know that hominins evolved to new environments (Holliday & Franciscus, 2009; Ruff, 1991; Trinkaus, 1981) and that distal elements scale at a greater rate than their proximal counterparts when size increases (Auerbach & Sylvester, 2011; Jantz & Jantz, 2017; Sylvester, Kramer, & Jungers, 2008); though these allometric relationships may not be static over ontogeny (Chu, Stull, & Sylvester, 2022). Standardized means and other statistical transformations have provided insight into morphological differences in long bone shape between populations (Frelat & Mitteroecker, 2011). From the brachial and

crural index, we know that upper and lower limb proportions roughly follow ecogeographic patterns, even at birth (Cowgill, Eleazer, Auerbach, Temple, & Okazaki, 2012; Temple, Okazaki, & Cowgill, 2011; Waxenbaum, Warren, Holliday, Byrd, & Cole, 2019) and that they are also important for mobility (Higgins & Ruff, 2011; Pietrobelli, Marchi, & Belcastro, 2022; Tallman, 2016).

The advantages of one perspective become the disadvantages of another. While absolute measurements are simple to interpret and easy to communicate, they can only be used to discuss difference in size. A long bone measured as 150mm should always measure as such – with some allowance for error. But given context, 150mm may be small for one population or age and it may be large in another population or age. While relative measures allow for within- and between-group comparisons of shape and relative size, they are especially difficult to quantify when size variables are not biologically interpretable (Auerbach & Sylvester, 2011; Chu et al., 2022; Coleman, 2008) or when transformed into log space (Gould, 1966; Huxley, 1932; R. J. Smith, 1993; Sprugel, 1983). For example, it is hard to fully appreciate what an  $x$  change in  $\log(\text{femur head diameter})$  is in relation to a single unit change in  $\log(\text{body mass})$ . Finally, intralimb indices have the same advantages to other relative measures but are often evaluated as a single value controlled for size instead of as an interaction between two long bone lengths (R. J. Smith, 2005). A brachial index of 90 does not fundamentally mean anything, without further context, beyond the proportional relationship of radius length compared to humerus length.



Long bones have relatively high levels (>50%) of preservation in most bioarchaeological and forensic contexts (Manifold, 2012, 2015) but continue to be underutilized in biological anthropology (Hoppa, 2000). In comparison to adults, the subadult skeleton has been under-studied because of small sample sizes, lack of diversity in available samples, and previous statistical and/or computational limitations (Stock et al., 2020). Given these limitations, no subadult reference sample has ever been used to evaluate all three methodological perspectives – absolute, relative, and index – for appendicular ontogeny. However, large-scale initiatives to increase the availability of subadult skeletal data through a virtual repository can alleviate many of the limitations of previous subadult long bone research (Stull & Corron, 2022).

Virtual anthropology provides alternatives to physical skeletal collections for obtaining skeletal information (Franklin & Blau, 2020; Uldin, 2017; Weber, 2015; Weber et al., 2001). Measurements and nonmetric scores collected using virtual modalities have been demonstrated to be reliable and precise, thus expanding the possibilities for skeletal research (Abegg et al., 2020; Colman et al., 2019; Corron et al., 2022; Corron, Marchal, Condemi, Chaumoitre, & Adalian, 2017; Stull, Tise, Ali, & Fowler, 2014). The Subadult Virtual Anthropology Database (SVAD) is one of the largest cross-sectional repositories of subadult data to date (Stull & Corron, 2022). Other repositories of contemporary skeletal data include the Bakeng se Africka digital repository (L'Abbé, Krüger, Theye, Hagg, & Sapo, 2021) and the New Mexico Decedent Image Database (Edgar et al., 2020). All three repositories share the goal of increasing representation of minority groups in biological anthropology and open access research.

Sample size limits the methodological options and validity of research (Button et al., 2013; Good & Hardin, 2006; Hackshaw, 2008; Kwak & Kim, 2017; Obertová & Stewart, 2020), while homogeneity of samples also prevents generalizability of research to new samples (Adalian, 2020; Kamper, 2020; Morellato et al., 2010; Song, Tang, & Wee, 2021). Small sample sizes in subadult reference samples in the past have resulted in methodological choices that have restricted the scope of long bone ontogeny in biological anthropology. Linear regression is not an appropriate method for modeling long bone growth, as multiple assumptions – such as linearity and equal variance (Allen, 1939; Yang, Tu, & Chen, 2019) – are violated in the relationship between long bone lengths and age (Stull et al., 2022; Stull, L'Abbé, & Ousley, 2014). Even so, linear regression has been used to model long bone growth (Maresh, 1955; Smith & Buschang, 2004) and linear models for estimating aspects of the biological profile remain prevalent (*e.g.*, Cardoso, Abrantes, & Humphrey, 2014; Rissech et al., 2013; Robbins Schug, Gupta, Cowgill, Sciulli, & Blatt, 2013; Schaefer, Scheuer, & Black, 2009). One argument for using linear regression over more appropriate nonlinear models is simplicity (Smith, 2007). When faced with nonlinear data, the choice to generate one or more linear equations is more common than using nonlinear alternatives (*e.g.*, Cardoso et al., 2014; Ruff, 2007). Recent technological advancements that have increased subadult sample size, variation, and availability are no longer restricted to inappropriate methodological choices. Instead, nonlinear models and nonparametric methods should be explored – or truly, adopted, in biological anthropological research to capture and predict the variability of long bone growth.

**The overarching goal of this collection of research is to use a large, demographically diverse, contemporary reference sample of subadults from the United States (U.S.) to bridge the gap between absolute, relative, and index perspectives of long bone ontogeny.** In doing so, biological anthropology may begin to understand past limitations and future directions of long bone ontogeny and gain a better understanding of the origins of human appendicular diversity. Three specific aims are pursued within this (non)dissertation:

**Specific Aim #1:** Bridge the gap between diaphyseal and maximum measurements in biological anthropology research. See **Chapter 2:** Expanding long bone ontogeny in biological anthropology.

**Specific Aim #2:** Contextualize the continuous ontogeny of the brachial and crural index using individual element changes and evaluate the ecogeographic positioning of a contemporary U.S. sample. See **Chapter 3:** Cross-sectional ontogeny of the brachial and crural index.

**Specific Aim #3:** Provide a method of subadult stature estimation that does not require other aspects of the biological profile and is trained on a contemporary U.S. sample for forensic application. See **Chapter 4:** Stature estimation of the subadult skeleton using a contemporary U.S. population.

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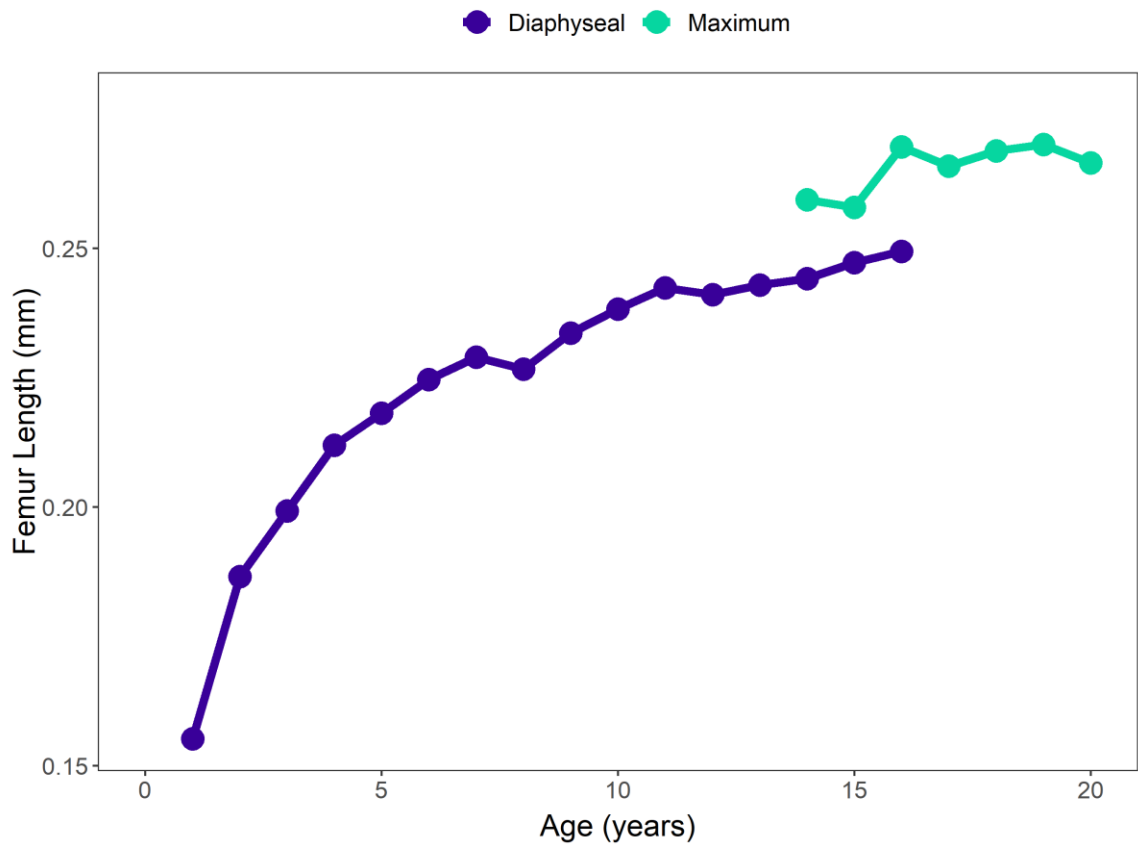
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# Chapter 1 - Expanding on long bone ontogeny in biological anthropology

## Introduction

Investigations into growth and development (*i.e.*, ontogeny) of the skeleton are imperative for understanding human skeletal variation. Findings from such research are applicable to forensic contexts (López-Costas, Rissech, Tranco, & Turbón, 2012; Rissech, Schaefer, & Malgosa, 2008; Smith, 2007; Stull, Cirillo, Cole, & Hulse, 2020; Stull, L'Abbé, & Ousley, 2014), understanding past populations (Cowgill, Eleazer, Auerbach, Temple, & Okazaki, 2012; Wescott, 2006), evolutionary investigations (Lacruz et al., 2015; Tallman, 2016), and even the living (Bogin, 2005; Bogin & Loucky, 1997; Bogin & Varela-Silva, 2010). Biological anthropologists have a slew of methods at their disposal for tracking growth and development, such as standardized dental development scoring (AlQahtani, Hector, & Liversidge, 2010; Demirjian, Goldstein, & Tanner, 1973; Moorrees, Fanning, & Hunt Jr., 1963) and tracking the appearance of ossification centers or occurrence of epiphyseal fusion (Moore-Jansen, Ousley, & Jantz, 1994; Stull & Corron, 2021). Each of these standardized methods encompasses the entire postnatal developmental trajectory of the features under investigation, from initial formation to final mature (*i.e.*, adult) stage. Appendicular bones are frequently used to study growth and development but the way their growth is quantified does not facilitate a complete picture of long bone growth. In contrast to the other developmental systems, appendicular bones have two different measurement definitions determined by broad stages of development: diaphyseal (*i.e.*, subadult / epiphysis-exclusive) versus maximum

(*i.e.*, adult / epiphysis-inclusive) measurements. The differing approaches to quantifying length have produced a development-based divide in long bone research, as the two definitions are rarely combined into a single analysis. When both types of measurements are considered, they are treated as separate samples, thus creating a break in the analysis (Figure 1.1).



**Figure 1.1** – Example of how diaphyseal and maximum measurements are treated as separate samples. Modified from Frelat and Mitteroecker (2011) using data from the present study.

It is important for long bone investigations to move beyond the tradition of keeping diaphyseal and maximum measurements separate so that the entire growth trajectory may be examined as a continuous biological process. This study provides an in-

depth examination of subadult and adult long bone measurements to quantify the entire ontogenetic trajectory and ultimately provide recommendations for future investigations of long bone ontogeny. In doing so, it is the first critical evaluation of the appropriateness and applicability of combining diaphyseal and maximum lengths into a single analysis, thus removing the divide between subadult and adult investigations using long bones.

### **Long bone ontogeny utility**

Long bone ontogeny has been used in many fields to make inferences about the human condition in the past and present. Biological anthropologists and human biologists have not only focused on individual long bone growth (Anderson, Green, & Messner, 1978; Bareggi et al., 1994; Buschang, 1982; Smith & Buschang, 2004, 2005), but also limb proportions to investigate the overall health and nutritional access of a population (Bielski & Welon, 1982; Bogin & MacVean, 1984; Bogin & Rios, 2003). From these lines of inquiry, we have a better understanding of the windows of growth sensitivity where most phenotypic diversity is introduced, as well as the differential effects of single- and multi-generational environmental change on size, but not proportion (Auerbach, 2012; Bogin, Smith, Orden, Varela Silva, & Loucky, 2002; Greulich, 1957; Kondo & Eto, 1975).

Human biologists are often interested in documenting typical long bone growth, thus necessitating longitudinal, homogenous samples (de Onis et al., 2012; Duggan, 2010; Schillaci, Sachdev, & Bhargava, 2012). Longitudinal studies are effective for estimating critical ontogenetic milestones, such as peak growth velocity (Eveleth & Tanner, 1990; Frelat & Mitteroecker, 2011; Healy, 1986; Smith & Buschang, 2004,

2005), but often lack the diversity reflective of an actual population due to small sample sizes and selection criteria meant to reduce variation (Eveleth & Tanner, 1990; Hauspie & Roelants, 2012).

In contrast, many biological anthropologists utilize the concept of typical population growth to generate methods for estimating aspects of the biological profile. For increased generalizability and applicability, cross-sectional data are often used in these research contexts to better encapsulate the breadth of human variation (Eveleth & Tanner, 1990; Hauspie & Roelants, 2012; Roberts, 1978). By utilizing cross-sectional samples, researchers can discuss population differences, or similarities, in mean absolute long bone growth and through the lens of population variation (Cardoso, Abrantes, & Humphrey, 2014; Facchini & Veschi, 2004; Smith, 2007; Stull, L'Abbé, et al., 2014).

While understanding the typical growth of an individual or group of individuals across ontogeny may be of greater importance for diagnosing atypical circumstances (Bogin & Varela-Silva, 2010; de Onis et al., 2012; Duggan, 2010; Stein et al., 2010), most biological anthropologists are interested in contextualizing long bone ontogeny within the breadth of human diversity, as well as that of non-human primates, and their shared lineages. However, exploring all of diversity at one time is either not feasible and/or involves too much information to produce interpretable results. Therefore, researchers limit diversity to better reveal and interpret underlying patterns. Diversity in biological anthropological examinations using long bones is accommodated through the use of population-specific (Brits, Bidmos, & Manger, 2017; Krüger, L'Abbé, & Stull, 2017; Rissech, Márquez-Grant, & Turbón, 2013; Sanabria-Medina, González-

Colmenares, Restrepo, & Rodríguez, 2016; Sullivan, Flavel, & Franklin, 2017; Y'Edynak, 1976), species-specific (Castanet et al., 2004; Holliday, 1999; Holly Smith, Crummett, & Brandt, 1994; Tallman, 2016) and global samples (Albanese, Tuck, Gomes, & Cardoso, 2016; Kenyhercz, Kiales, Stull, McCormick, & Cole, 2017). Often, subadult long bone investigations accommodate variation in growth rates across life history stages through restricted age ranges (Abrahamyan, Gazarian, & Braillon, 2008; Brits et al., 2017; Cardoso et al., 2014; Facchini & Veschi, 2004; Smith, 2007; Stull, L'Abbé, et al., 2014).

### **Ontogeny Modeling Constraints and Considerations**

Growth is a relatively complex process to model, because different research approaches and age ranges result in different modeling choices. Recently, there is increased interest in modeling ontogeny in biological anthropology age estimation methods in ways that account for the nonlinear processes of growth (Konigsberg, Frankenberg, Sgheiza, & Liversidge, 2021; Sgheiza, 2022; Stull, Chu, Corron, & Price, 2022). While data quantifying the growth trajectories of long bones are not typically linear (Buschang, 1982; Maresh, 1970; Schillaci et al., 2012; Smith & Buschang, 2005), linear regressions are often adopted because of ease of use and interpretation (Smith, 2007), often sacrificing precision, and violating the statistical assumptions of these methods. Simple linear regression is also easy to calculate and interpret, making it ideal for methodological application. However, there are disadvantages to modeling long bone growth as a linear process. Primarily, the complexities of growth are lost because linear models imply that growth is a constant process without changes in slope (German & Meyers, 1989a, 1989b; Medawar, 1950). Humans undergo fluctuations in growth for

different parts of the body that can be readily observed through changes in velocity and on distance plots (Bogin, 2005; Cameron & Bogin, 2012; Eveleth & Tanner, 1990; Smith & Buschang, 2004, 2005). For example, the pubertal growth spurt provides the greatest postnatal peak in growth velocity and is considered a major source of phenotypic diversity that contributes to differences in body size and shape between the sexes (Bogin, 2005; Cameron, 2007; Cameron & Bogin, 2012). The pubertal growth spurt, and other periods of growth that introduce variation, would not be detectable with a linear model.

Other studies have applied nonlinear models to document long bone growth (J. L. Scheuer, Musgrave, & Evans, 1980; Stull, 2013; Stull, L'Abbé, et al., 2014). These methods are often better equipped to detect changes in growth velocity, or deviations in growth patterns, that can uncover periods of greater developmental plasticity and/or canalization. Younger individuals exhibit low levels of skeletal variation which increase with age (Konigsberg et al., 2021; Sgheiza, 2022; Stull, 2013; Stull, L'Abbé, et al., 2014), a pattern that would be undetectable with linear models. In biological anthropology, multivariate adaptive regression splines and basis splines (*e.g.*, Stull, 2013; Stull, L'Abbé, et al., 2014), power laws (*e.g.*, Stull et al., 2022; Stull, Price, Corron, & Chu, 2020), and logistic regression (*e.g.*, J. L. Scheuer et al., 1980) have been used to model the skeletal growth of long bones. The Gompertz curve (1825) has also been used as a method for modeling growth in humans (Cabana, Jolicoeur, & Michaud, 1993; Laird, Tyler, & Barton, 1965; Shohoji & Sasaki, 1984; Tanner, 1960). Sigmoidal curves, such as logistic regression and the Gompertz curve, have been shown to best reflect natural growth by being able to capture different periods of differential growth velocity (Nijhout, 2011; Nijhout & German, 2012).

Outside of biological anthropology, additional types of nonlinear curves are used to model growth, each selected to support specific research foci. For example, common methods of modeling growth in ecological studies include the von Bertalanffy growth curve (1938), which is an expansion on the traditional three-parameter exponential growth curve (*see section below: Nonlinear Growth and Final Adult Size*) to accommodate longitudinal data (Armstrong & Brooks, 2013). Nonlinear curve models with explicit asymptote parameters such as the three-parameter exponential growth curve, logistic regression, or Gompertz curve, allow for explicit investigations into the model-determined final value of the outcome variable (in this case, final adult size of long bone lengths) from which the predictor variable (in this case, age) can be calculated.

Studies of long bone growth in biological anthropology typically terminate at the initiation of epiphyseal fusion (*i.e.*, diaphyseal measurements) while human biology studies terminate around the legal age of majority, which is typically at age 18 (Bogin, 2013; Cameron, 1986; de Onis et al., 2012). Neither research agenda has traditionally taken the timing of stabilization at final adult size into account when assessing long bone growth. In other words, neither the onset of epiphyseal fusion or the legal age of majority is the final point of long bone growth; age of long bone epiphyseal fusion termination range between 14-22 years and the legal age of majority is variable across the world (Rösing et al., 2007; Schaefer, Scheuer, & Black, 2009; L. Scheuer & Black, 2000; Stull et al., 2022).

Currently, skeletal long bone measurement definitions are based on dichotomous stages of skeletal development. First, “subadult” measurements which are restricted to the



diaphyseal region prior to the onset of epiphyseal fusion processes. Second, “adult” measurements which include the epiphyses (heretofore, “maximum”) and are only applicable for individuals that have begun active epiphyseal fusion. Biological anthropologists do not mix “subadult” and “adult” skeletal measurements, as they fundamentally differ in definition and cannot be easily incorporated into a single technique, which therefore limits the types of research questions that can be explored using long bones. To the author’s knowledge, only a handful of studies – and specifically one researcher – have combined diaphyseal and maximum length measures together in a single method for individual linear (Primeau, Friis, Sejrsen, & Lynnerup, 2012, 2016) and nonlinear (Primeau et al., 2016) models in bioarchaeology to estimate age-at-death. The majority of subadult biological profile methods only use diaphyseal measurements (Lamer, Spake, & Cardoso, 2021; Stull, L’Abbé, et al., 2014; Stull, L’Abbé, & Ousley, 2017), truncate age ranges to limit the measurements (Cardoso et al., 2014; Smith, 2007), and/or have individual models for each chronological age that uses either diaphyseal or maximum measurements (Maresh, 1955, 1970; Ruff, 2007). Additionally, age distributions in long bone ontogeny research are often truncated around 12 to 16 years-old for the same reasons (Bleuze, Wheeler, Williams, & Dupras, 2014; Pujol, Rissech, Ventura, Badosa, & Turbón, 2014; Pujol, Rissech, Ventura, & Turbón, 2016; Smith & Buschang, 2005).

Overwhelmingly, there is an ongoing assumption or methodological approach that diaphyseal and maximum measurements cannot be included in the same model. The current underutilization of long bone dimensions in traditionally “subadult” methods because of epiphyseal fusion may be overlooking critical information about growth that

are excluded because of differences in definition and the perceived inability to combine these data types. To our knowledge, only two other studies have combined diaphyseal and maximum measurements into a single sample for estimating age on medieval subadult populations, but the ages were estimated, and the overall range explored was far narrower (*i.e.*, 3 to 13 years) than the age range explored in this study (Primeau et al., 2012, 2016). A formal evaluation and/or discussion on the appropriateness of combining the measurement definitions was not provided, although successful application of age-at-death estimation was achieved with no apparent differences in model performance when using diaphyseal or maximum length.

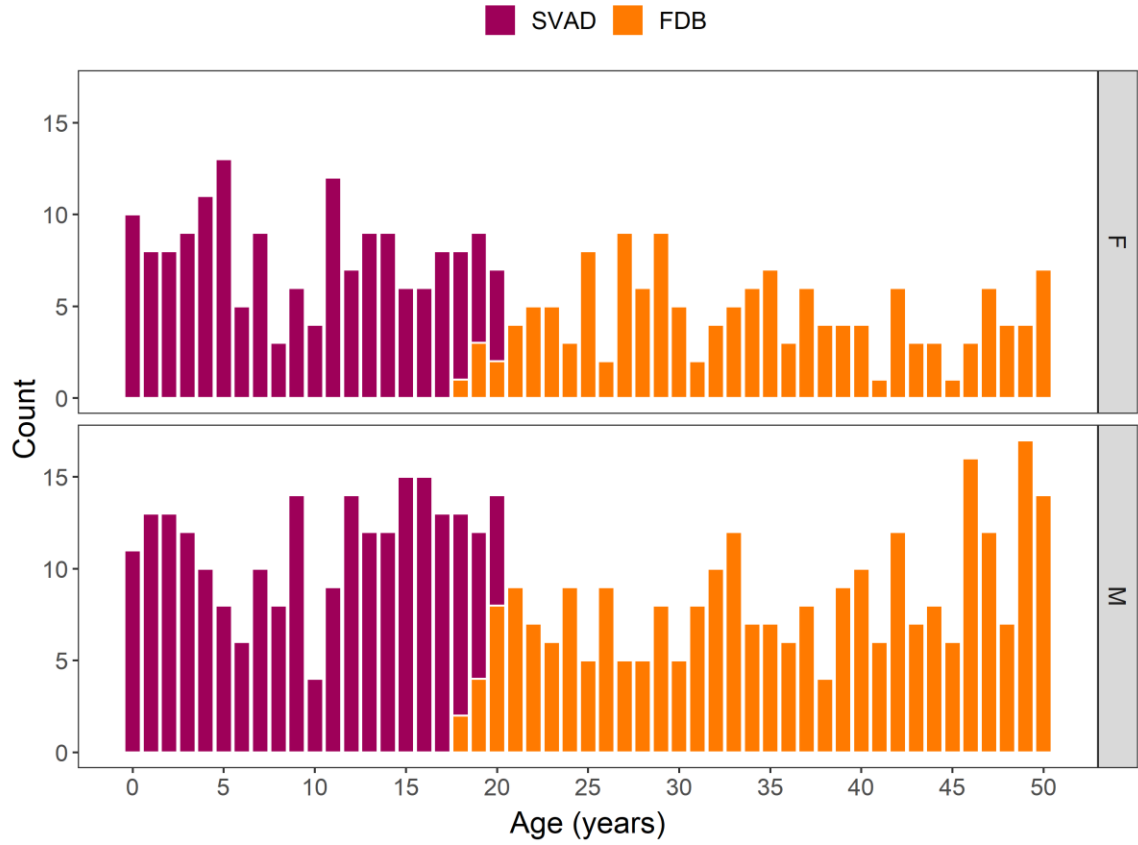
It is important to model and evaluate long bone ontogeny properly by following the growth trajectories through the end of maturation – thus necessitating the combination of diaphyseal and maximum measurements. In this study, we combine diaphyseal and maximum skeletal metrics, both through absolute and relative measures, and use nonlinear growth modeling to quantify the entire trajectory of long bone growth, to ultimately identify the timing of “adult” long bone stabilization. In doing so, this is one of the first studies to explore the entire ontogenetic trajectory of long bones from birth through adulthood.

## **Materials and Methods**

A sample of 798 individuals between the ages of birth and 20 years from the United States sample of the Subadult Virtual Anthropology Database ("SVAD", Stull & Corron, 2022) and between the ages of 18 and 50 years from the Forensic Anthropology Data Bank ("FDB", Jantz & Moore-Jansen, 1988) were used for the current investigation.

Both samples contributed almost equally to the combined sample (SVAD = 48%; FDB = 52%). Criteria for inclusion in the analysis included age between birth and 50 years-old, known stature, and at least one documented long bone length. To reduce sampling bias associated with imbalanced age classes, the original sample was down-sampled to include a maximum of 20 individuals per one-year age cohort when grouped by sex (Figure 1.2). Long bone lengths for the humerus, radius, ulna, femur, tibia, and fibula were measured either using diaphyseal (from Stull & Corron, 2021, 2022; Stull et al., 2014) or maximum definitions (Langley, Jantz, Ousley, & Jantz, 2016). Each bone of an individual was assessed for degree of epiphyseal fusion. Presence of active fusion (score 2) of both the proximal and distal epiphyses resulted in maximum lengths being taken.

A final total of 295 SVAD individuals had data collected following measuring protocols for either diaphyseal or maximum lengths and a final total of 413 FDB individuals with long bone data collected following the Data Collections Procedures for Forensic Skeletal Material 2.0 Manual or the previous FDB version (Langley et al., 2016; Moore-Jansen et al., 1994). Relative lengths were calculated by dividing absolute measurements by cadaveric (SVAD and FDB) stature or reported stature (FDB). Prior to analysis, assumptions of normality, linearity, homoskedasticity, and independence were checked on both the absolute and relative lengths. Data were found to be not normal, nonlinear, heteroskedastic, and not independent, leading to the use of non-parametric methods to prevent violating parametric assumptions. All analyses were conducted in R and RStudio (R Core Team, 2022; RStudio Team, 2022).



**Figure 1.2** - Final sample distribution by sex and chronological age.

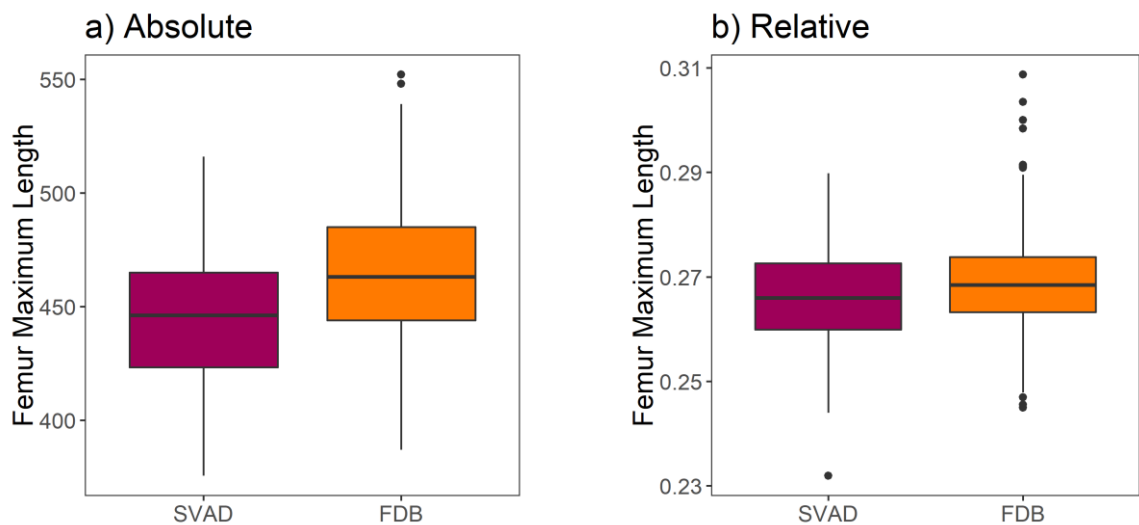
### Combining Sample Sources

It is necessary to consider potential errors when combining two data sources. In this situation there are concerns with data collected from different modalities and from different demographic compositions. Numerous publications have thoroughly evaluated the impact of modality, including both pre- and post-imaging parameters, on metric dimensions (Colman et al., 2019; Corron, Marchal, Condemi, Chaumoitre, & Adalian, 2017; Hishmat et al., 2015; Stull, Tise, Ali, & Fowler, 2014). Findings suggest there is a minimal ( $< 3\text{mm}$ ) measurement error in tests between modalities, and specifically between dry bone and CT scans (Stull, Tise, et al., 2014).

Of greater concern when combining the SVAD and FDB data are differences in demographic composition. The present U.S. sample from the SVAD largely originate from the New Mexico Decedent Identified Database (NMDID) which were compiled at the New Mexico Office of the Medical Investigator in Albuquerque, New Mexico (Berry & Edgar, 2021; Edgar et al., 2020), with a smaller sample originating from the Office of the Chief Medical Examiner for the State of Maryland located in Baltimore, Maryland. The FDB sample is largely from the state of Tennessee (Jantz & Moore-Jansen, 1988). The population composition of New Mexico, Baltimore, and Tennessee are vastly different and reflects the variability observed within the United States (U.S. Census Bureau, Population Estimates Program (PEP), 2021). In addition, birth years in the FDB span the 1900s, whereas the SVAD sample includes only individuals who were born within the last two decades (Jantz & Moore-Jansen, 1988; Stull et al., 2022; Stull & Corron, 2022). The effects of secular change have been documented in stature and limb proportions within the U.S. (Jantz, Jantz, & Devlin, 2016; Jantz & Jantz, 2017), which may be observed in the maximum lengths.

To establish whether the SVAD and FDB samples can be combined for this study, Mann-Whitney U tests were performed to test for statistically significant differences in mean long bone lengths between SVAD and FDB. Comparisons were made between individuals who were measured for maximum length and were between 18 and 20 years-old; these were the only overlapping ages in both samples. This test was done for absolute lengths as well as relative lengths. Statistically significant differences ( $p < 0.05$ ) between absolute maximum lengths were observed in overlapping age cohorts (18-20 years) from the SVAD and FDB samples (Figure 1.3a). Unfortunately, this is not entirely

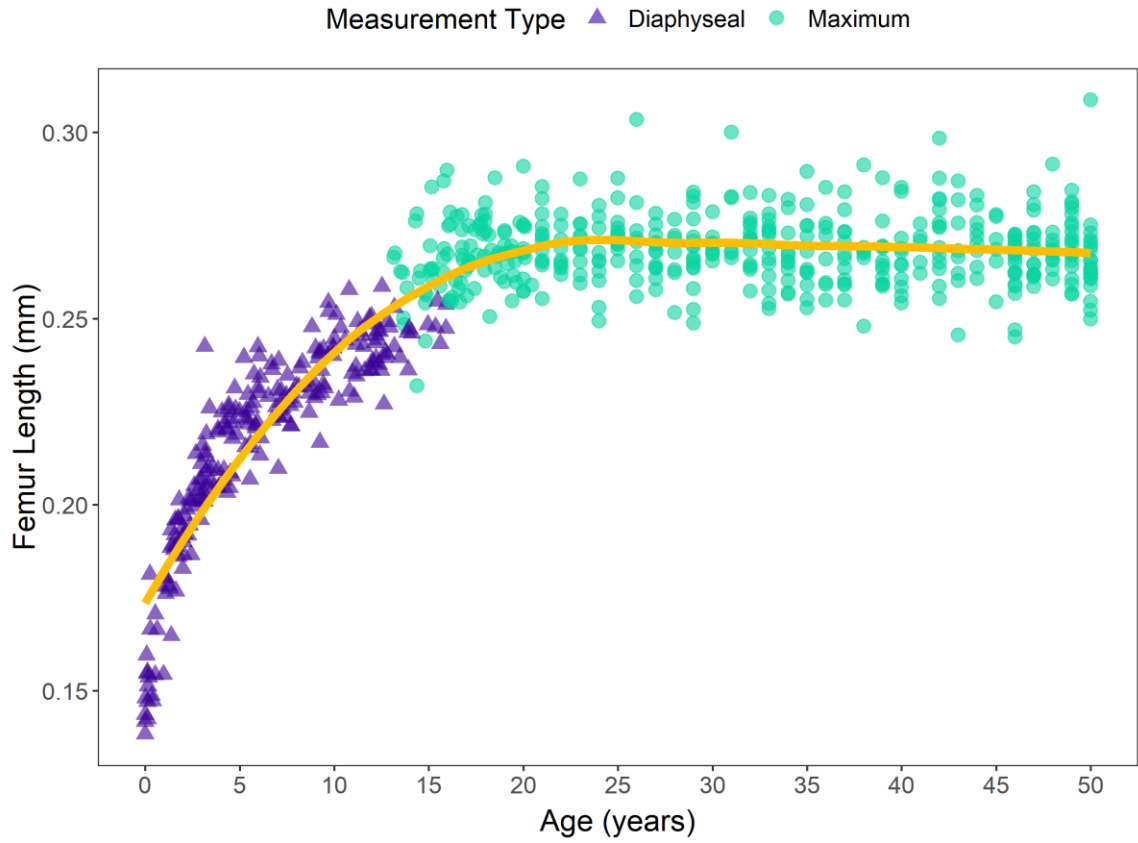
unexpected as population differences in long bone lengths in the United States have directed researchers to develop population-specific methods using long bone lengths to estimate aspects of the biological profile (Ousley & Jantz, 2013; Shields, 2007; Wilson, Herrmann, & Jantz, 2010). Results likely reflect the population-level differences in long bone lengths that have been previously documented. In contrast, there were no statistically significant differences in relative maximum lengths between sample sources for the overlapping ages (Figure 1.3b). Subsequently, relative measurements were used to ensure continuity in cross-sectional growth trajectory modeling; it offers the additional benefit of demonstrating the utility of shape in cross-population studies by removing the effects of size (Aiello, 1992; Cabana et al., 1993; Seguchi, Quintyn, Yonemoto, & Takamuku, 2017).



**Figure 1.3** - Boxplots demonstrating a) significant absolute and b) nonsignificant relative differences in femur length between sample sources for overlapping ages (18-20).

### Nonlinear Growth and Final Adult Size

Nonlinear growth was modeled using a three-parameter asymptotic exponential equation (Table 1.1). Visual assessment of relative long bone length ontogeny with combined diaphyseal and maximum lengths (Figure 1.4) suggested the use of a three-parameter asymptotic exponential function over a logistic or Gompertz (1825) function because of the lack of sigmoidal relationship between age and relative long bone length. The three-parameter asymptotic exponential equation approximates long bone growth ( $y$ ) over age ( $x$ ), while also providing the asymptote ( $\alpha$ ), which in this context represents final adult size or the value at which the curve stabilizes. In the exponential growth equation, the lower asymptote ( $b$ ) and growth rate ( $c$ ) are also calculated. An added benefit of the first nonlinear equation is that it can be solved for  $x$  (Table 1.1) to identify the age at which adult relative size ( $\alpha$ ) has stabilized.



**Figure 1.4** – Ontogeny of relative femur length. Diaphyseal dimensions are purple triangles and maximum dimensions are green circles.

<b>Table 1.1</b> – Equations used to 1) model nonlinear continuous long bone ontogeny and 2) calculate the age of adult size stabilization.	
$y = \alpha - be^{-cx}$	Eq. 1
$x = \frac{\ln(-y + \alpha) - \ln(b)}{-c}$	Eq. 2

The growth trajectory for the relative length of each long bone was modeled using Equations 1 and 2 using a bootstrap ( $n=500$ ) approach by sex. The *stats* (R Core Team, 2022) and *nlstools* (Baty et al., 2015) packages in R were used for bootstrapping. A 95% confidence interval was generated for both relative adult size and the age at which

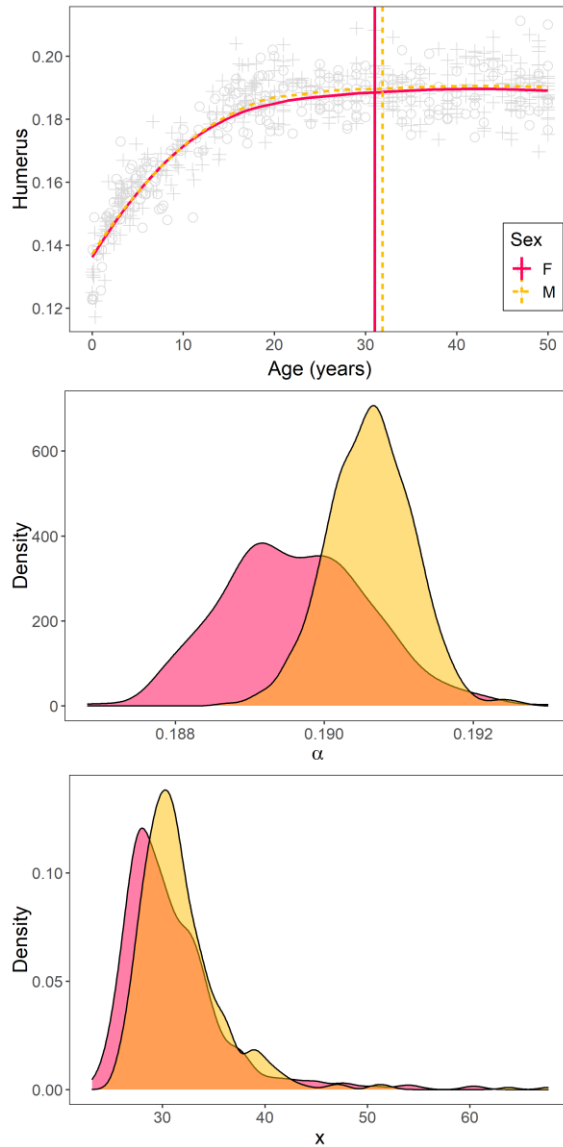


relative adult size is stabilized using the density distributions from the bootstrapped models. The mean simulated growth trajectory of each long bone is visualized by sex as well as the densities of all bootstrapped estimates of relative size ( $\alpha$ ) and age ( $x$ ).

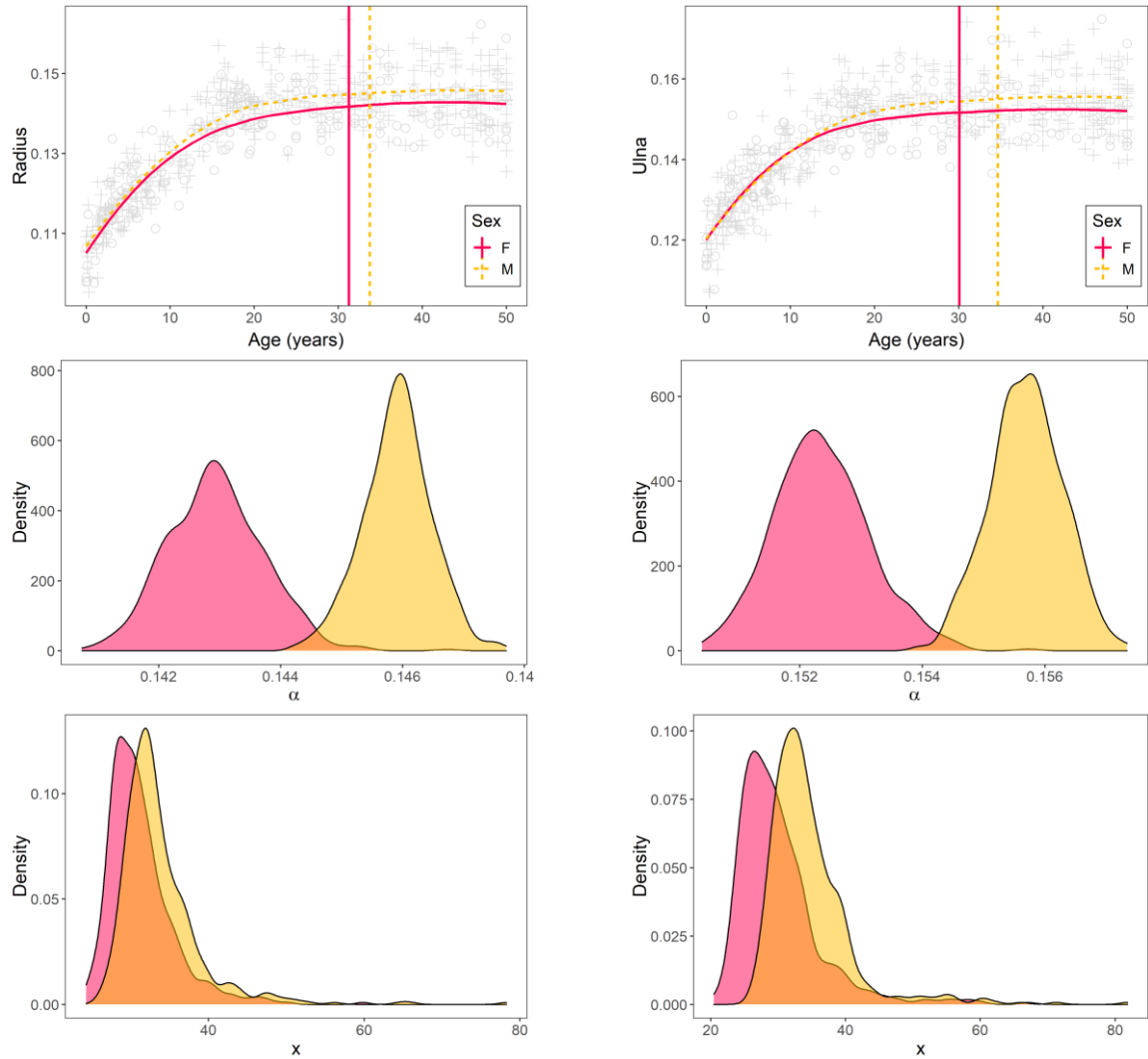
## Results

Nonlinear model parameters for each long bone length model by sex are provided in Table 1.2 and Figures 1.5-1.8 visualize the results of the nonlinear modeling by sex. Proximal elements of the upper and lower limb (Figures 1.5 and 1.7) demonstrate less variation compared to the distal elements in the upper and lower limb in relative adult size (Figures 1.6 and 1.8). The same observations are not only true for the asymptote of relative size ( $\alpha$ ), but also the timing of stabilization as well. The age when relative adult size stabilizes is consistently younger for females than males (Table 1.2). Still, the difference in age of stabilization is more pronounced for proximal elements than distal elements. Looking into the age at stabilization a bit deeper reveals that both male and female tibia and fibula reach adult size earliest (at the youngest ages). In contrast, males and females vary for later stabilizing elements. The remaining order of stabilization for females from youngest to oldest is ulna, femur, humerus, radius. For males, the order of stabilization is humerus, femur, radius, ulna.

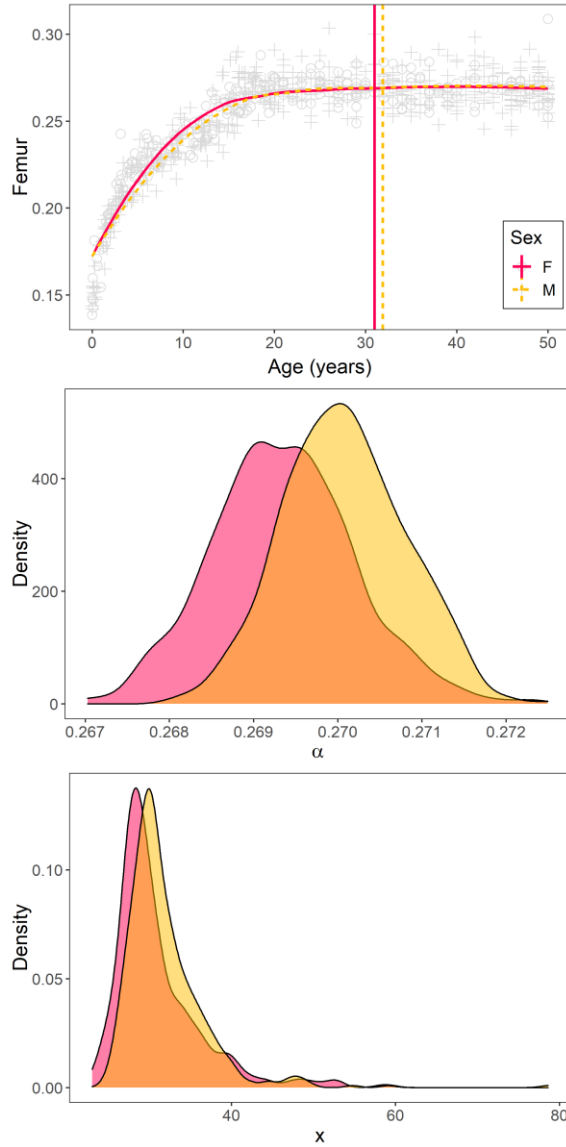




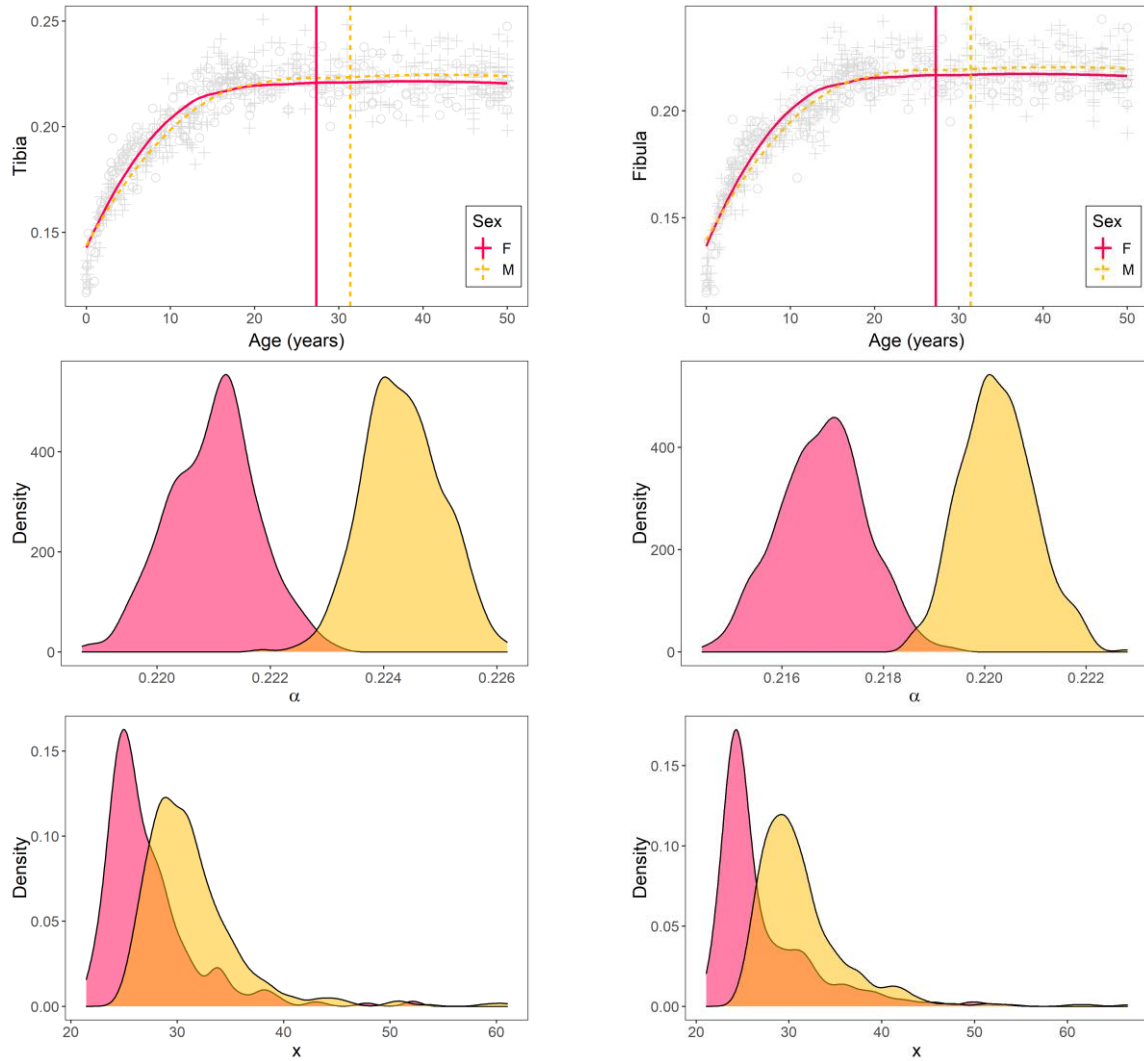
**Figure 1.5** - Growth trajectory (top) and density distributions of final relative adult size (middle) and age at relative adult size stabilization (bottom) for femur humerus length. Females are represented in pink, and males are in yellow. The vertical lines in the top plot demonstrate the little-to-no difference in timing of relative adult size stabilization between females (solid) and males (dashed).



**Figure 1.6** - Growth trajectory (top) and density distributions of relative adult size (middle) and age at relative adult size stabilization (bottom) for radius length (left) and ulna length (right). Females are represented in pink, and males are in yellow. The vertical lines in the top plot demonstrate the difference in timing of relative adult size stabilization between females (solid) and males (dashed).



**Figure 1.7** – Growth trajectory (top) and density distributions of final relative adult size (middle) and age at relative adult size stabilization (bottom) for femur humerus length. Females are represented in pink, and males are in yellow. The vertical lines in the top plot demonstrate the little-to-no difference in timing of relative adult size stabilization between females (solid) and males (dashed).



**Figure 1.8** - Growth trajectory (top) and density distributions of relative adult size (middle) and age at relative adult size stabilization (bottom) for tibia maximum length (left) and fibula length (right). Females are represented in pink, and males are in yellow. The vertical lines in the top plot demonstrate the difference in timing of relative adult size stabilization between females (solid) and males (dashed).

## Discussion

The entire trajectory of long bone growth has not been fully evaluated through maturation. Through the integration of diaphyseal and maximum lengths into a single sample for analyses, the present study approached the novel task of exploring the entire ontogenetic trajectory of long bone length and identifying the stabilization of relative

adult size variation. The differences in definition between diaphyseal and maximum lengths means that once epiphyseal fusion has begun, typically around 10 to 13 years (Schaefer et al., 2009; L. Scheuer & Black, 2000; Stull et al., 2022), diaphyseal dimensions are no longer collected and the scope of the research utilizing that data ends. Previously, research utilizing epiphyseal fusion as a cut off for study inclusion has truncated the upper ages available for analysis in research using long bone dimensions. Similarly, individuals with active epiphyseal fusion are not included in research using maximum lengths.

This is the first study to combine long bone lengths from such a wide range of chronological ages from the entire lifespan into the same model. Diaphyseal and maximum lengths were able to be combined only when the effects of size were removed by dividing lengths by stature. The need to calculate standardize by size reiterates the impact of size on skeletal variation, somewhat supporting the hesitance of past research to combine the two types of measurement definitions (Figure 1.1). Differing demographic composition of the two samples (SVAD and FDB) in the current study may have attributed to the significant differences in absolute measures (Figure 1.3a). Inter-population variation in long bone size has been demonstrated both in ontogeny (Jantz & Owsley, 1984; Lovejoy, Russell, & Harrison, 1990; Pinhasi, Teschler-nicola, Knaus, & Shaw, 2005) and through the proliferation of population-specific methods using long bones (Brits et al., 2017; Pinhasi, Timpson, Thomas, & Šlaus, 2014; Rissech et al., 2013; Sanabria-Medina et al., 2016). Standardizing measurements, whether through PCA, log-transforms, or dividing by body size, have been commonly used for cross-population and cross-species comparisons (Aiello, 1992; Cheverud, 1982; Gonzalez, Perez, & Bernal,

2011; Jolicoeur, 1984; Klingenberg & Zimmermann, 1992). Therefore, it is unsurprising that no significant differences were found in the relative length measures between sample sources (Figure 1.3b), despite potential differences in population distribution.

The flexibility of nonlinear models can capture the rapid growth of the first life history stage (infancy, 0-3 years) followed by the gradual decrease in growth trajectory through childhood and adolescence into adulthood (Bogin, 2005; Cameron & Bogin, 2012). True growth velocity cannot be modeled without longitudinal data (Cameron, 1986; Eveleth & Tanner, 1990; Healy, 1986). It is therefore untenable to explore the true age of individual adult size stabilization because we do not have the type of data needed to evaluate a growth velocity of 0. Instead, the present study provides a more realistic picture of the stabilization of relative adult size variation in a contemporary U.S. population. The cross-sectional sample used in this study is beneficial to providing an idea of the breadth of variation over ontogeny into adulthood (Hauspie & Roelants, 2012; Stull, L'Abbé, et al., 2014). The age of relative adult size stabilization, for males and females, found in this study ranges from 27 to 34 years (Table 1.2). Given our knowledge of epiphyseal fusion completing in long bones between 14 and 22 years old (L. Scheuer & Black, 2000; Stull et al., 2022), age range for adult stabilization can be viewed with skepticism. However, we believe that the prematurely truncated age ranges associated with limited sample ability - and a previous misconception about the discrete grouping of subadults and adults - may have led to this erroneous skepticism. For example, a recent publication by Stull and colleagues (2022) presented the age ranges of each epiphyseal fusion and dental development stage. The maximum age for the final stage of each



variable was 22 years – not because that age is precisely when epiphyseal fusion or dental development is complete, but because that is the oldest individual in their sample.

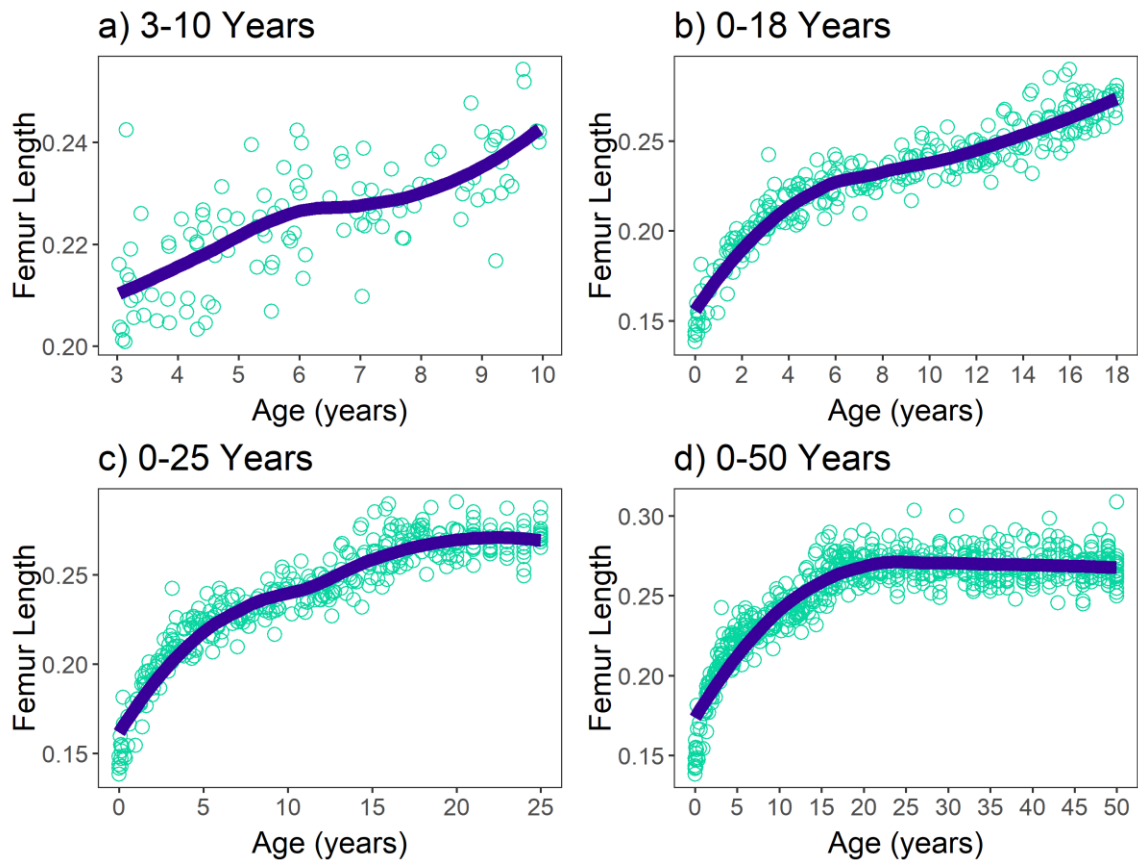
Females were found to stabilize earlier than males in all long bone lengths, with the distal elements demonstrating a wider age difference of stabilization than the proximal elements. These trends are consistent with the sexually dimorphic trends of ontogeny (Bogin, 2005; Duren, Seselj, Froehle, Nahhas, & Sherwood, 2013; Eveleth & Tanner, 1990; Humphrey, 1998; L. Scheuer & Black, 2000; Stull et al., 2022) and strengthen the outcomes of the nonlinear models. Patterns of adult stabilization also differ between the sexes in the upper limb. In females, the ulna stabilizes first, followed by the humerus and radius stabilizing around the same age. In males, the humerus stabilizes first, followed by the radius, then ulna (Table 1, Figures 1.5-1.6). Sexual dimorphism of the order of stabilization were not detected in the lower limb, as the distal elements (tibia and fibula) stabilize before the femur for both males and females (Table 1.2, Figures 1.7-1.8). Elements of the upper limb stabilize after the lower limb (Table 1.2), which is in line with the Law of Developmental Direction (Jackson & Morris, 1914) that describes energy expenditure on regions of the body closest to the brain (Bogin & Varela-Silva, 2010; C. W. Kuzawa et al., 2014; Christopher W. Kuzawa & Bragg, 2012; Little, 2020). Using longitudinal data, Smith and Buschang (2005) found similar patterns in order of peak velocity attainment, often associated with maturation, where elements of the lower limb reached peak height velocity earlier than elements of the upper limb.

## Implications of Sample Restrictions

Subadult and adult samples are often treated as discrete groups in biological anthropology, therefore method development for each designation has been distinct and dichotomous with very little overlap. However, the defining characteristics of adulthood may differ depending on the regions under examination – dental development, epiphyseal fusion, or chronological age (*e.g.*, age of majority). Each type of maturity or age indicator can result in different designations of an individual as a subadult or an adult. As we have demonstrated here, restricting samples based on certain ages or milestones of development has downstream consequences not only in modeling choices, but also on the potential outcomes of an ontogenetic study, including the interpretation of results. Long bone growth is inherently nonlinear; research using age restrictions to model growth using linear regression therefore oversimplifies the relationship between long bone measurements, chronological age, and skeletal maturity. Combining diaphyseal and maximum long bone measurements, instead of keeping them separate, allowed the current study to follow long bone ontogeny as a continuous biological process through the stabilization of adult size variation.

The relationship between age and long bone growth has been documented using linear (Cardoso et al., 2014; Primeau et al., 2012; Rissech et al., 2008; Smith & Buschang, 2004) and nonlinear methods (Buschang, 1982; Ives & Humphrey, 2017; Primeau et al., 2016; Smith & Buschang, 2005; Stull, L'Abbé, et al., 2014). Depending on the research agenda and the age ranges included, different types of models may be applied to the bivariate relationship. When thresholding the postnatal growth period into certain parts, the relationship between long bones and age may change (Figure 1.9), and

the true relationship may be obscured, especially at the tail ends of a truncated age range (Stull, L'Abbé, et al., 2014). Postnatal growth is complex and undergoes different stages that differentially affect the overall variability observed within a population (Chou, Iwasa, & Nakazawa, 2016; Eveleth & Tanner, 1990; Walker & Hamilton, 2008; Wells, 2017). Life history stages – infant, child, juvenile, adolescent, adult – all characterize nuanced differences in growth velocity, developmental changes over ontogeny, or allocation of resources (Bogin, 2005).



**Figure 1.9** – Demonstration of differences in modeling relationships between age and femur length based on age range.

It is certainly possible that by truncating age ranges, variation in the growth trajectory of different elements and regions (*e.g.*, epiphyses) may be missed and/or oversimplified. By combining diaphyseal and maximum lengths into a single analysis and using the three-parameter asymptotic exponential equation, the present study provides a more nuanced exploration into relative adult size, and other aspects of ontogeny. For example, the lower asymptote (*b*) and growth rate (*c*) parameters may be compared across results for other ontogeny research, either using the same bones and other reference samples or between the ontogenetic trajectories of other bones, for evaluations of initial postnatal size and different cross-sectional rates of growth. Certainly, we are not stating that this nonlinear equation is the most appropriate for modeling long bone ontogeny. Indeed, we invite the field to explore other options, such as a power law, the Gompertz curve (1825), or other equations that capture nonlinear relationships (German & Meyers, 1989a; Gliozzi, Guiot, Delsanto, & Iordache, 2012; Israelsohn, 1960; Laird et al., 1965; Nijhout & German, 2012, 2012; Stull et al., 2022) to support the specific needs and requirements of individual research agendas.

### **Relative Adult Size Stabilization**

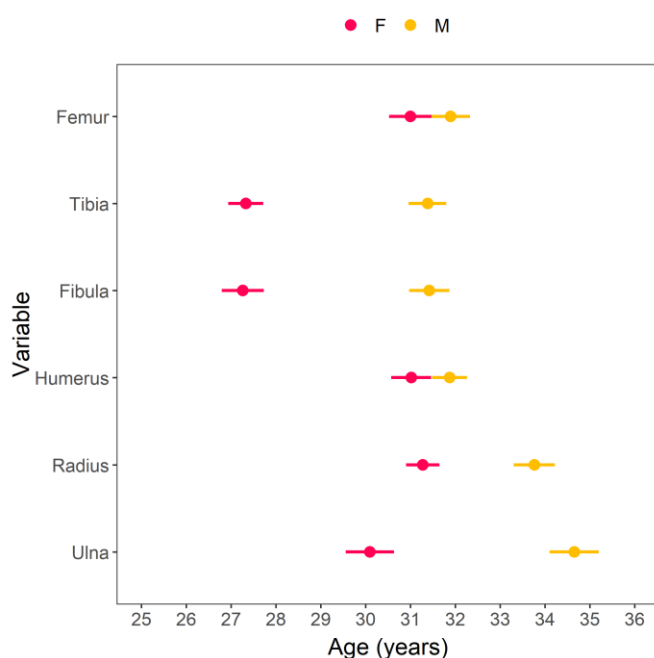
The current study suggests that pre-existing subadult methods may be expanded to include greater age ranges up until the age of adult size stabilization. In the present study, the age of final adult size for both males and females, and all long bone lengths (Table 1.2), is a full decade later than the age of legal majority at 18 years. Stull and colleagues (2022) recently published on a series of univariate and multivariate age estimation models for “subadults” using the mixed-cumulative-probit approach, which is an extension of transition analysis used for age estimation (Boldsen, Milner, Konigsberg,

& Wood, 2002; Getz, 2020; Kamnikar, Herrmann, & Plemons, 2018; Milner & Boldsen, 2012). Therein, they explain the pattern of missingness inherent in growth indicators, such as the reduction in diaphyseal dimension utility/collection after active fusion of long bone epiphyses (Stull et al., 2022). Results of the current study suggest that other dimensions, such as maximum length, may also enhance age estimation for older ages, where the current missingness of long bone measurement information results in much larger credible intervals (Stull et al., 2022). Beyond age estimation, knowing the value and age of relative adult size stabilization of long bone lengths is advantageous for all other methods presently relying on long bone lengths.

### Sexual Dimorphism

Sexual size dimorphism was also identified in both magnitude and timing of adult size variation stabilization, even with the removal of absolute size (Figure 1.10). Ontogenetic studies have identified sexual dimorphism not only in size (Brandt & Navas, 2013; Chou et al., 2016; Rensch, 1950; Stull et al., 2017), but also timing of epiphyseal fusion completion (Scheuer & Black, 2000; Stull et al., 2022). It is well known that rates of sexual size dimorphism vary across global populations (Krüger et al., 2017; Spradley & Jantz, 2011; Ubelaker & DeGaglia, 2017), and the extent to which the final adult size and age at final adult size may vary in the same manner. This has been one of the main arguments in support of population-specific methods. Therefore, differences in global rates of sexual size dimorphism, absolute size may not be very informative as a point of comparison among global populations. Because of this context, using relative lengths may be highly advantageous. In this study, termination to final adult long bone length was found in females to be 1 to 5 years ahead when compared to males. This result is

consistent with the general understanding that puberty occurs earlier in females than males and the downstream effects of puberty (*i.e.*, accelerated growth, epiphyseal fusion completion) also conclude earlier (Bogin, 2005; Chou et al., 2016; B Vizmanos & Martí-Henneberg, 2000; Barbara Vizmanos, Martí-Henneberg, Clivillé, Moreno, & Fernández-Ballart, 2001)



**Figure 1.10** – Comparison of sexual dimorphism in timing of relative adult size stabilization.

### Considerations to Research Design and Future Directions

This research used cross-sectional data from two demographically different sources: individuals aged birth to 20 years from the NMDID and individuals aged 18 to 50 from FDB. Therefore, the results may not be reflective of final adult size in a more demographically comparable sample. However, because the focus of this study was to explore the value and timing of relative adult size stabilization, restricting the evaluation

to relative long bone length ontogeny enabled the combination of diaphyseal and maximum lengths into a single analysis, resulting in a greater understanding of the timing of adult size stabilization. In addition, small sample sizes in critical periods of growth (ages 5-10), necessitated the downsampling of a much larger original dataset. It is possible that a resampling of the full data may slightly alter the outcomes of relative adult size and age of stabilization. Variation that may have affected the modeling of ontogeny, asymptote of relative adult size, and age of relative adult size stabilization may have been left out of the final sample, but the larger sample size ( $n > 500$ ) of the present study remains one of the largest in long bone ontogeny studies. Future inquiries utilizing data from the same sample source that encompasses the entirety of possible long bone ontogeny will be conducted. In addition, the ontogeny of other long bone dimensions (*i.e.*, breadths) should be explored to establish whether a similar combination of diaphyseal and maximum breadths is appropriate. Finally, future research with more diverse populations may help uncover the variation in timing of reaching final adult size, which is currently not well understood.

## **Conclusion**

The increasing accessibility to greater, more diverse samples of subadult skeletal information allows our field to delve deeper into the underlying processes that inform the overall adult phenotypic diversity of long bone size and shape. The abundance of methods in biological anthropology that rely on long bones is immense (*e.g.*, Albanese et al., 2016; Bidmos & Mazenganya, 2021; Curate et al., 2016; Krüger et al., 2017; Reynolds et al., 2018). Considering the recent push for a greater grounding of certain

sub-disciplines in theory (Ross & Pilloud, 2021; Winburn, Yim, & Stock, 2022), continuing inquiry into skeletal ontogeny remains an important research agenda. More proximate than theory, the current results emphasize the importance of understanding how research design and sampling impacts the historically foundational understanding of growth and development and more specifically, its completion. To summarize the results:

- Long bone ontogeny can be reasonably modeled using nonlinear methods
- Diaphyseal and maximum length measurements can be combined for analyses concerning birth to adulthood
- Sexual size dimorphism is retained even after standardized for size
- Relative adult size is similar between sexes, but is attained earlier for females than males
- Distal elements present with longer age discrepancies than their proximal counterparts

The present study demonstrated that nonlinear modeling techniques can be used to better understand the full ontogenetic trajectory of long bone lengths from birth to adulthood. Additionally, the results demonstrate that diaphyseal and maximum measurements can be combined in a single analysis if standardized into a relative metric that takes current body size (*i.e.*, stature) into account. Importantly, the results of this study have provided greater insight into the timing and mean value of relative adult size stabilization in a modern U.S. sample. Implications of this research include a re-evaluation of the partitioning of diaphyseal and epiphyses-inclusive methods in biological anthropology.



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## **Chapter 2 - Cross-sectional Ontogeny of the Brachial and Crural Indices**

### **Introduction**

Allometry is the study of change in shape with respect to change in absolute size (Schmidt-Nielsen, 1984). Allometry is used to evaluate limb proportions (or plant equivalents) across and within species (Ibáñez & O'Higgins, 2011; Klingenberg & Zimmermann, 1992; Niklas, 2004; Norberg, 1981), and within species (Aiello, 1992; Frynta, Baudyšová, Hradcová, Faltusová, & Kratochvíl, 2012; Gould, 1966; Kaliontzopoulou, Carretero, & Llorente, 2007). Adopting an allometric perspective in biological anthropological research allows for the evaluation of phenotypic variation in traits without the direct effects of size and is applicable for comparisons across hominin, bioarchaeological, and contemporary skeletal samples. While size variables in human allometry research are commonly body mass (Holliday & Franciscus, 2009; Ruff, 1991, 2002; Watkins & German, 1992; Yim et al., 2021) or stature (Bogin & Baker, 2012; Buschang, 1982; Holliday, 1999; R. L. Jantz & Jantz, 2017; Meadows & Jantz, 1995), other allometric investigations have used anatomically region-specific perspectives.

Intralimb indices, such as the brachial or crural index, are commonly used in biological anthropology. The brachial index is calculated as the radius divided by the humerus times 100 (Davenport, 1934). The crural index is calculated as the tibia divided by the femur times 100 (Davenport, 1933). Similar to traditional allometric analyses, these ratios represent the relationship between the distal and proximal elements of the limb, where the proximal element is often treated as the size variable, therefore removing

the need to estimate body mass or stature from limited skeletal information (Chu & Stull, 2020; Chu, Stull, & Sylvester, 2022). These indices have been used to infer hominin evolution and migration patterns (Holliday, 1999; Holliday & Franciscus, 2009; Richmond, Aiello, & Wood, 2002; Shang, Tong, Zhang, Chen, & Trinkaus, 2007), explore the population history of modern groups (Seguchi, Quintyn, Yonemoto, & Takamuku, 2017; Temple, Auerbach, Nakatsukasa, Sciulli, & Larsen, 2008), and document the patterning of modern humans in adults (Auerbach, 2012; Betti, Cramon-Taubadel, & Lycett, 2012; Betti, Lycett, von Cramon-Taubadel, & Pearson, 2015), as well as subadults (Cowgill, Eleazer, Auerbach, Temple, & Okazaki, 2012; Temple, Okazaki, & Cowgill, 2011; Waxenbaum, Warren, Holliday, Byrd, & Cole, 2019). Thus far in anthropological literature, researchers have hypothesized that the brachial and crural indices require up to 20k years to shift under the selective pressures of new environments (Holliday, 1999). Thus, an intermediate index value of a group of individuals between the expected target environment and the supposed origin environment could signal a migration – and a resulting shift of the phenotypic peak (Holliday, 1999; Seguchi et al., 2017; Temple et al., 2008; Temple & Matsumura, 2011; Trinkaus, 1981). Additionally, other researchers have further demonstrated that when populations move to new environments, their absolute size may change by more than a few centimeters, but their relative measures (*i.e.*, proportions) are retained (Bogin & Loucky, 1997; Bogin & Rios, 2003; Bogin, Smith, Orden, Varela Silva, & Loucky, 2002; Greulich, 1957; Kondo & Eto, 1975). Yet in more modern research contexts, secular change in the brachial and crural indices have increased over the span of 140 years in a sample from the United States ("U.S.", Bogin, 2013; Jantz, Jantz, & Devlin, 2016; Jantz



& Jantz, 2017; Meadows & Jantz, 1995). This is directly in contrast to Holliday's (1999) hypothesis that the brachial and crural indices of groups persist for thousands of years.

Global variation of intralimb indices might be explained through more complex processes than adaptation to cold or warm climates (Roseman & Auerbach, 2015; Savell, Auerbach, & Roseman, 2016). A recent study by Savell and colleagues (2022) demonstrated weaker correlations between postcranial lengths and temperature (Allen's rule, 1877) in comparison to common measures of body size (Bergmann's rule, 1847). The authors also suggest that population history may have a greater influence on the skeletal measures under investigation than proxies for climate, such as minimum average temperature or latitude, which has previously been suggested (Pomeroy, Stock, & Wells, 2021; von Cramon-Taubadel, Stock, & Pinhasi, 2013). Conversely, Betti and colleagues (2015) found that intralimb indices follow latitudinal patterns along traditional ecogeographic expectations even when accounting for neutral variation guided by population history. While brachial and crural indices have been shown to follow Allen's rule in the past, recent research has produced differing perspectives on the extent to which natural environmental factors (e.g., temperature, climate, latitude, and altitude) affect variation in limb proportions. These findings could also alter the current hypothesis that it takes upwards of 20k years for the brachial and crural indices to evolve (Garcia, 2015; Holliday, 1999; King, 2010). One way to investigate sources of phenotypic variation is through the lens of growth and development (*i.e.*, ontogeny). Final adult size, shape, and variation stem from intrinsic and extrinsic factors experienced during ontogeny.

The postnatal ontogenetic trajectory of brachial and crural indices has been explored through an ecogeographic lens, suggesting that the latitudinal patterning of intralimb indices is present at birth (Cowgill et al., 2012; Temple et al., 2011) and that the upper limb (brachial index) may be more environmentally sensitive than the lower limb (crural index) (Bleuze, Wheeler, Williams, & Dupras, 2014). Despite methodological differences in the construction of age categories, several authors have found consistent patterns in the brachial index across ontogeny (Bleuze, Wheeler, Williams, et al., 2014; Cowgill et al., 2012; Temple et al., 2011): a high index at birth followed by a decrease during the intermediate ages (~3 to 10 years) and ending with an increase in index for adults. In contrast, different trajectories are described among the studies for the crural index. Temple and colleagues (2011) describe a reduced parabolic trajectory compared to the brachial index, with the adults still demonstrating higher index values than the intermediate ages. Cowgill and colleagues (2012) demonstrate the crural index as decreasing into adulthood. A similar trajectory is found by Bleuze and colleagues (2014), although the stabilization of a lower crural index occurs before the adult age category.

Regardless of how the fluctuations in the brachial or crural index are quantified, we know that the brachial and crural indices change over ontogeny. The sources of fluctuations across ontogeny have been suggested to align with normal fluctuations in proximal and distal elements (Bleuze, Wheeler, Williams, et al., 2014), although this has not been directly investigated. Further, general differences in the adult brachial and crural indices have often been attributed to greater variation in the distal elements (Holliday & Franciscus, 2009). However, it has also been suggested that individual long bone lengths and intralimb indices are independent (Auerbach & Sylvester, 2011) – meaning that

variation in the proximal elements should also be considered when discussing differences in intralimb indices.

Thus, it is important for further inquiry into both the patterns of growth for intralimb indices and their individual elements to glean information on whether changes in the proximal or distal elements drive fluctuations in index value. Additionally, small, bioarchaeological samples with imprecise demographic information - such as age, stature, or wide temporal origins – have further hindered in-depth explorations into the driving forces behind intralimb index fluctuations (Chu et al., 2022). The following study uses a large contemporary sample of subadults from the U.S. to demonstrate the utility of contextualizing growth trajectories of intralimb indices with the relative growth trajectories of individual long bone lengths. In doing so, sources of variation such as sexual dimorphism and population differences are explored.

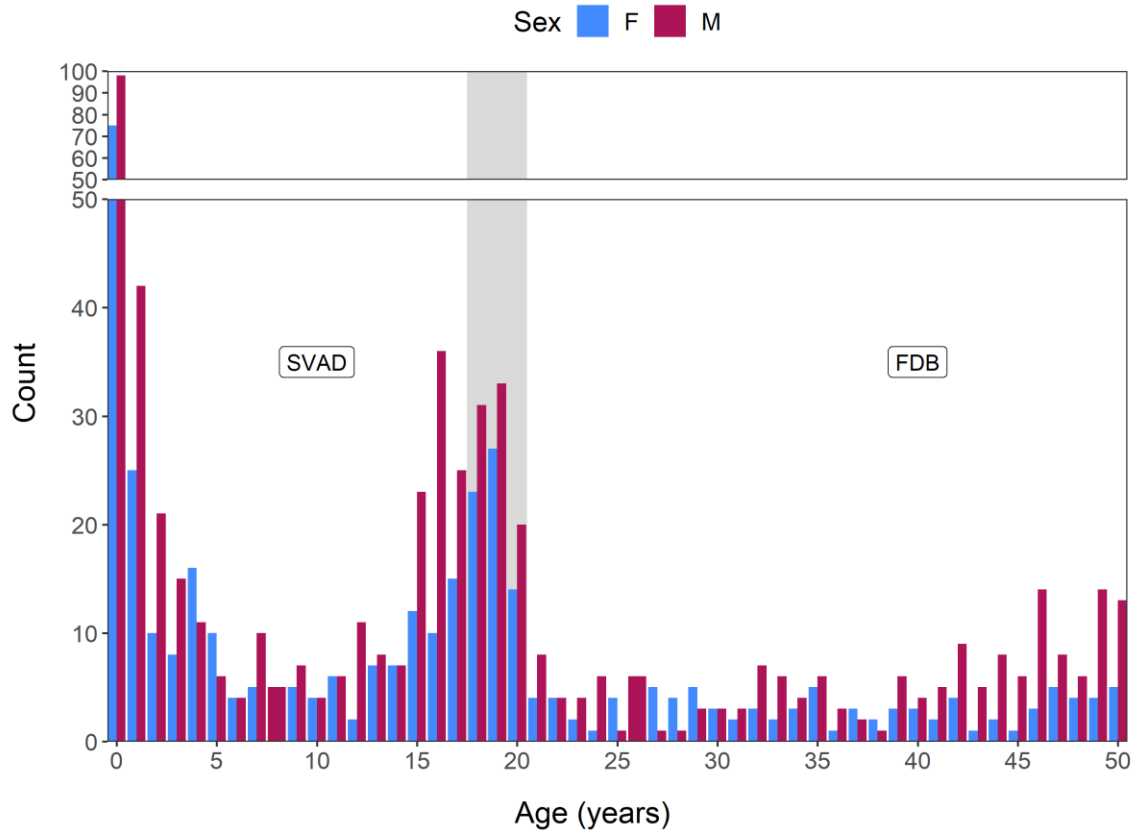
## **Materials & Methods**

### **Sample**

The sample includes 965 individuals from the U.S. aged from birth to 50 years-old from two sources. Individuals from the Subadult Virtual Anthropology Database ("SVAD", Stull & Corron, 2022) comprise most of the postnatal growth portion of the data, whereas individuals from the Forensic Anthropology Data Bank ("FDB", Jantz & Moore-Jansen, 1988) represent the tail end of postnatal growth and final adult size (Figure 2.1). Age, sex, stature, and the diaphyseal or maximum lengths (Langley, Jantz, Ousley, & Jantz, 2016; Moore-Jansen, Ousley, & Jantz, 1994; Stull & Corron, 2021; Stull, L'Abbé, & Ousley, 2014) of the femur, tibia, humerus, and radius were retained for

analyses. Intralimb indices were calculated, using length measurements, as the distal element divided by the proximal element for the upper (brachial) and lower (crural) limb, then multiplied by 100. Relative measures of all length measurements were also calculated by dividing lengths by stature. All absolute measures are in millimeters and relative measures are technically ratios.

Because intralimb indices are thought to require thousands of years to shift evolutionary peaks (Garcia, 2015; Holliday, 1999; King, 2010) and have been used to infer population history migration patterns (Bleuze, Wheeler, Dupras, Williams, & El Molto, 2014; Temple et al., 2008; Temple & Matsumura, 2011), social race and ethnicity designations (referred to here as “population designations”) were also retained as additional demographic information from each sample source. In the SVAD sample, individuals have both social race categories based on recent U.S. Census designations, as well as Hispanic ethnicity information. Thus, race and Hispanic ethnicity were combined to denote population. The FDB includes Hispanic ethnicity as part of a single race column, kept as population. Because of differences in population sample sizes, only the following populations were retained (Table 2.1): Amerindian (“AmI”), white (“W”), and white Hispanic (“WH”). The SVAD and FDB samples included in this study originate from states (New Mexico and Tennessee, respectively) that sit around 35°N latitude.



**Figure 2.1** – Sample distribution colored by sex. The grey area indicates the region of overlap between sample sources (SVAD, FDB). Note that the y-axis has a break between 50 to 100 to better highlight that sample sizes are only greater than 50 for age=0.

<b>Table 2.1</b> – Demographic breakdown of the data by sample source. Abbreviations: Amerindian (“AmI”), white (“W”), and white Hispanic (“WH”).						
	Age Range	Sex		Social Race/Ethnicity		
		Males	Females	AmI	W	WH
<b>SVAD</b>	0-20	408	268	156	244	276
<b>FDB</b>	18-50	182	107	0	288	1

## Statistical Analyses

Initial assumption checks prior to analysis demonstrated non-normality in the intralimb indices and a nonlinear relationship between intralimb indices and age.

Therefore, nonparametric tests and nonlinear modeling techniques were selected for all analyses. Fluctuations in intralimb ontogeny have been demonstrated using boxplots

(Cowgill et al., 2012; Temple et al., 2011), scatter and line plots (Frelat & Mitteroecker, 2011; Waxenbaum et al., 2019), and quadratic regression (Bleuze, Wheeler, Dupras, et al., 2014). Because the current sample is large enough to explore further, a Kruskal-Wallis and post-hoc Dunn's test using a Holm's correction for repeated comparisons (Holm, 1979) was used to test for significant differences in the brachial or crural index by chronological age using single-year cohorts from birth to 50 years. Brachial and crural indices have also been shown to be sexually dimorphic in adults (Bleuze, Wheeler, Dupras, et al., 2014; Bleuze, Wheeler, Williams, et al., 2014; Holliday, 1999; Jantz et al., 2016). Therefore, Mann-Whitney *U* and Kruskal-Wallis statistics were used to test whether there are statistically significant differences in the brachial or crural index between sexes using pooled, by sample source, by population, and by chronological age cohort (single year) data subsets from zero birth to 50 years. In addition, Kruskal-Wallis tests were used to explore differences in the intralimb indices between the sample populations. Post-hoc tests were used, when applicable, to further tease apart group differences.

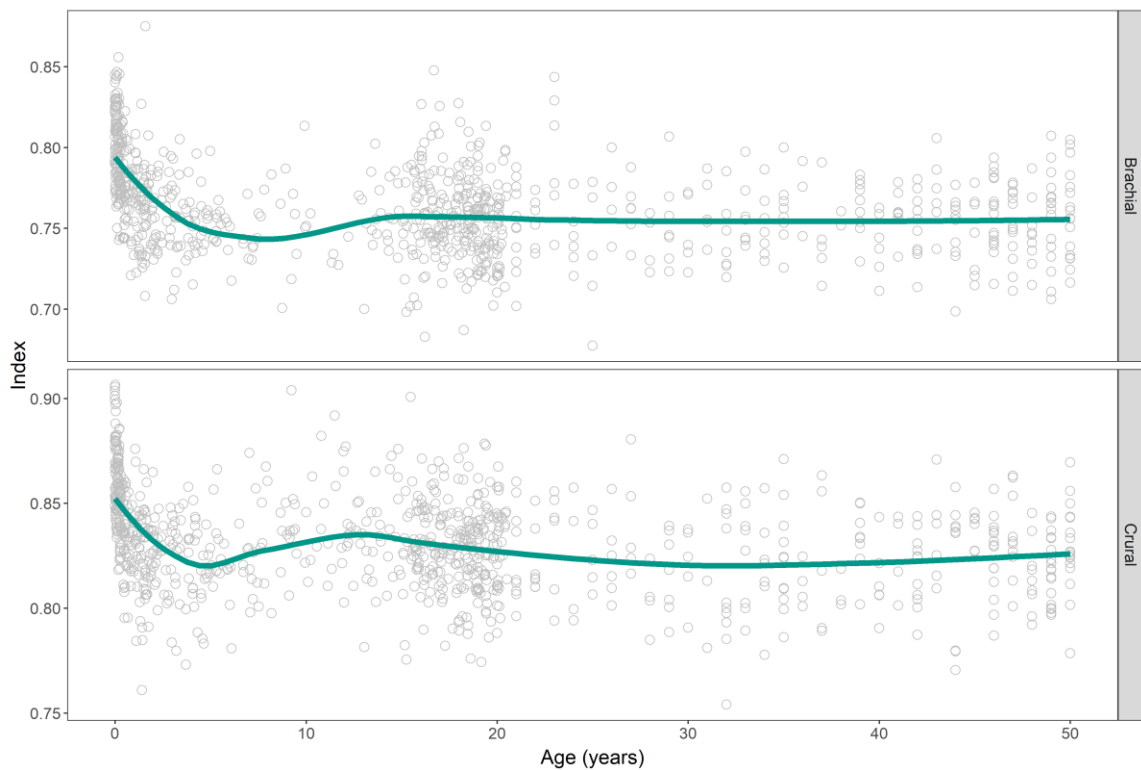
The ontogeny of each intralimb index and individual long bone was visualized using local polynomial regression fit ("loess", Cleveland & Loader, 1996) with a smoothing factor of 0.5 ( $\alpha$ , R Core Team, 2022), which represents the proportion of nearest data points used to generate the localized fit. This allows for detection of subtle changes in the overall ontogenetic trajectory of each individual long bone and the intralimb index without over- or under-fitting the data. Changes in the trajectory of the brachial or crural index are then contextualized within changes of the proximal and distal elements.

Finally, the data from the current study were compared to previously published subadult intralimb ontogeny research by Cowgill and colleagues (2012), which includes eight bioarchaeological populations. Specifically, the mean and 95% intervals were calculated for the current data by the following age cohorts, 0.0-2.9, 3.0-9.9, 10.0-17.9, 18+ (Adult). The data were visualized together by order of latitude to determine whether the present contemporary US sample follows the canonized ecogeographic patterns from Allen's rule. All analyses were conducted using R and RStudio (R Core Team, 2022; RStudio Team, 2022).

## Results

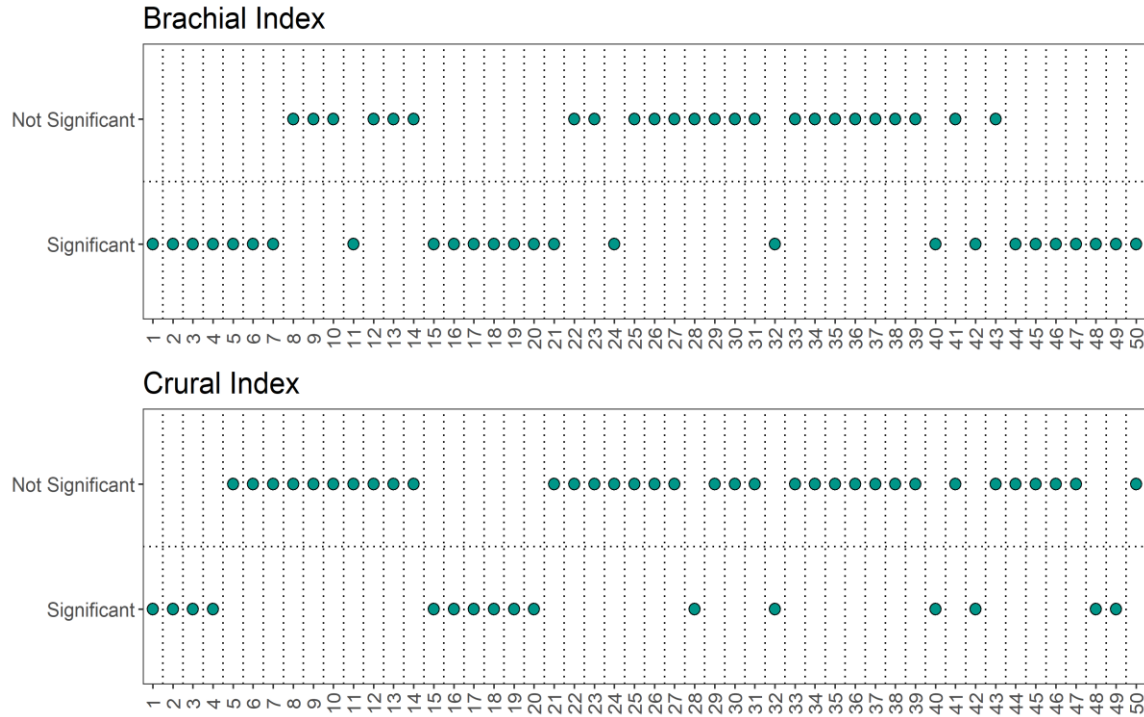
Fluctuations in the ontogeny of the brachial and crural indices and the amount of variability at birth are shown in Figure 2.2. The maximum value for both indices occurs at birth, followed by fluctuation that ends in stabilization around age 12 for the crural index and age 15 for the brachial index. The brachial index has a more gradual U-shaped trend than the crural index, potentially because of the longer duration until stabilization. Full pairwise comparisons (Kruskal-Wallis and Dunn's test) of median brachial and crural indices between age cohorts yielded statistically significant index differences only at birth (age=0); 26 of 50 single chronological ages were significant for the brachial index while 16 of 50 single chronological ages were significant for the crural index (Figure 2.3). Significant differences in brachial index between birth and age cohorts 1-7 are in line with the duration of index decrease observed in Figure 2.2. After age 7, there are no discernible patterns between significant and not significant age cohorts, even after stabilization of the brachial index around age 15. Between birth and age 20, the crural

index has more patterned results from significance testing. Significant differences between birth and age cohorts 1-4 follow with the decrease in crural index in Figure 2.2, whereas the not significant differences between birth and age cohorts 5-14 are in line with the increase and onset of stabilization. Significant differences between birth and age cohorts 15-20/21 for the crural and brachial index coincide with the onset of stabilization in both indices. Significance reported in Figure 2.3 generally aligns with changes in sample size apparent in Figure 2.2. Therefore, some skepticism towards significant results, especially between ages 5 to 10 for the brachial index – is warranted.



**Figure 2.2** – Ontogenetic trajectory of the brachial (top) and crural (bottom) index from birth to 50 years using pooled sex and population.





**Figure 2.3** – Significance results of the post-hoc Dunn's test of comparisons between birth (age=0) and other age cohorts for the brachial (top) and crural (bottom) index using pooled sex and population.

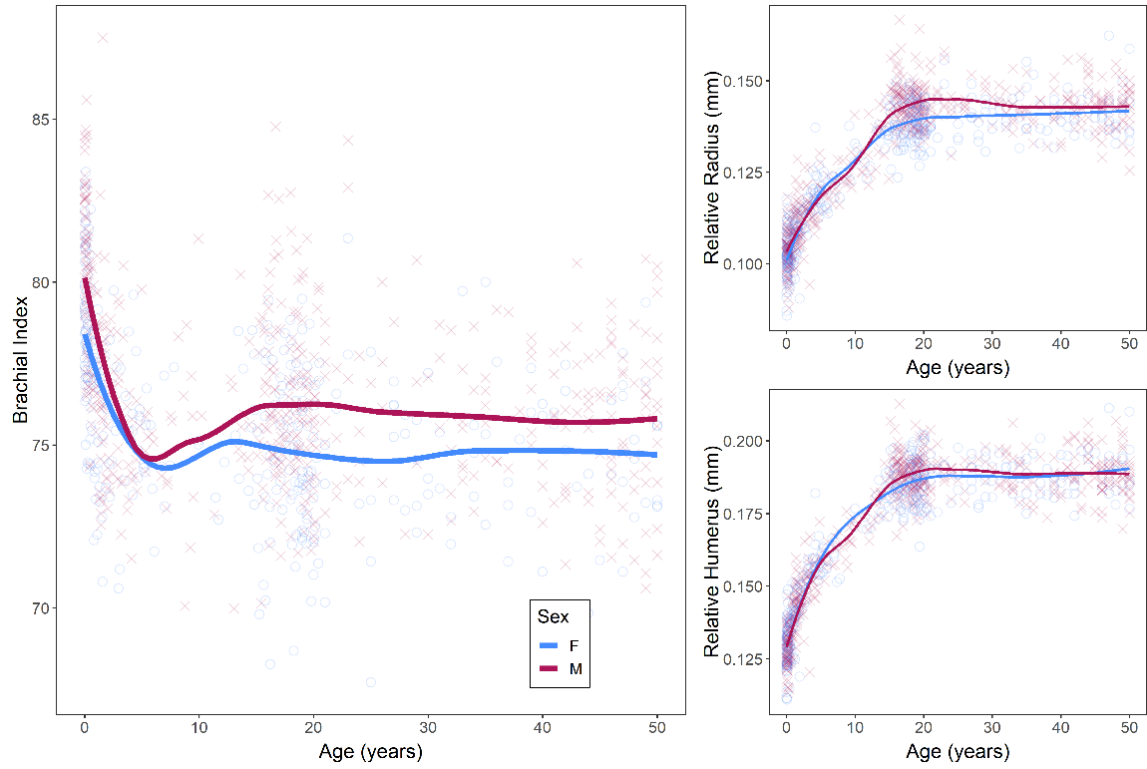
Results of the Mann-Whitney U tests for differences in median brachial and crural indices between sexes are summarized in Table 2.2 by data subsets. In general, sexual dimorphism was detected in both intralimb indices for pooled data and FDB and SVAD exclusive subsets. In addition, sex differences were significantly different for the brachial index of W and WH exclusive subsets, and sex differences were significantly different for the crural index of AmI and W exclusive subsets.

<b>Table 2.2</b> – Results of Mann-Whitney U tests for sexual dimorphism in the brachial and crural indices among sample subsets.						
	<b>Brachial Index</b>			<b>Crural Index</b>		
	<i>Median</i>		<i>p-value</i>	<i>Median</i>		<i>p-value</i>
	M	F		M	F	
<b>Pooled Data</b>	0.764	0.756	< 0.001	0.834	0.828	< 0.05
<b>FDB Only</b>	0.760	0.748	< 0.001	0.827	0.816	< 0.05
<b>SVAD Only</b>	0.766	0.761	< 0.001	0.835	0.831	< 0.05

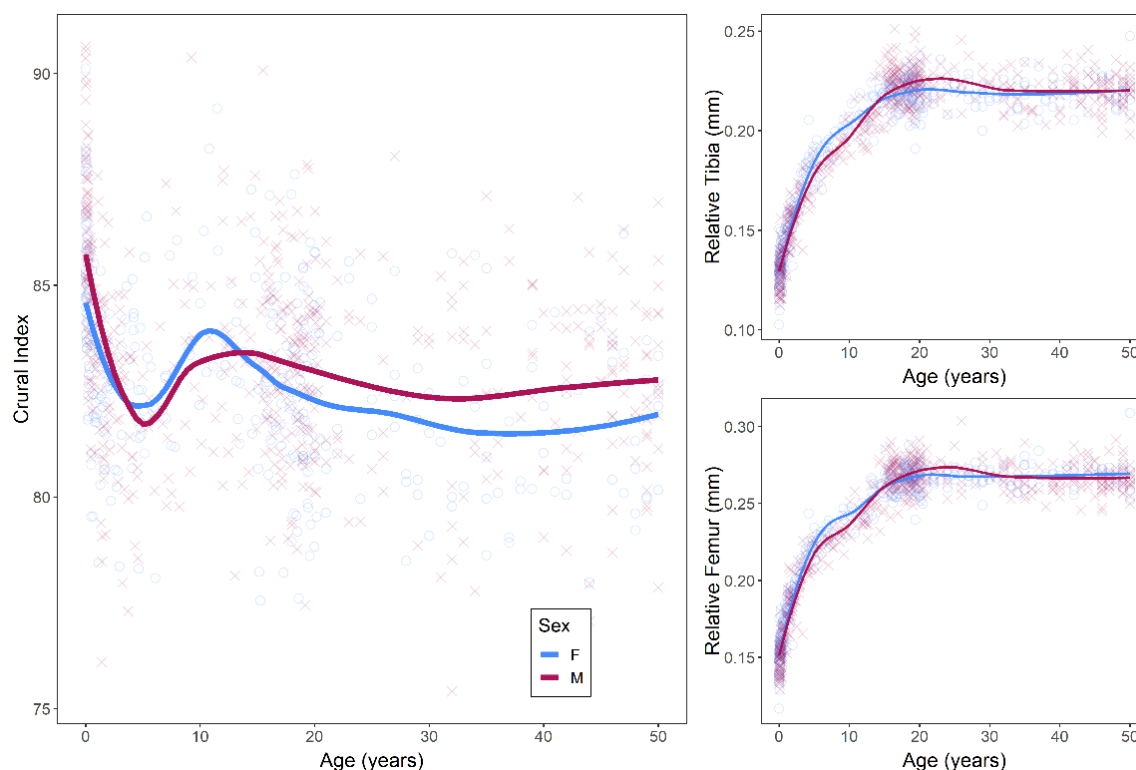
<b>W Only</b>	0.761	0.751	< 0.001	0.831	0.824	< 0.05
<b>WH Only</b>	0.765	0.755	< 0.05	0.835	0.829	0.06
<b>AmI Only</b>	0.772	0.773	0.30	0.837	0.833	< 0.05

Mann-Whitney U tests by chronological age by single year cohorts only reported statistically significant differences between sexes in the brachial index at age 21, and significant differences in the crural index at ages 15, 21, and 48 years. Because there appears to be no patterning to these significant results, it is most likely an artifact of sample size and/or sample composition, which is an inherent limitation of cross-sectional, observational data (R. J. Smith, 2019).

The cross-sectional ontogeny of the brachial or crural index, as well as for the individual relative growth (lengths standardized by stature) of the elements, were visualized by sex (Figures 2.4-2.5). Size differences between males and females in the upper limb are primarily because of relatively shorter radius lengths, whereas the humerus presents with relatively low levels of sexual dimorphism. Greater dimorphism in the brachial index begins around 5 years-old, where a markedly greater relative humerus length is responsible for a greater decrease in the female brachial index compared to males. For the lower limb, the ontogenetic trajectories of both sexes seem to be quite similar until a remarkable divergence around age 20 years, which again can be attributed mainly to greater differences in relative tibia length, with males being larger, compared to relative femur length. Of note, the ontogenetic trajectories of the lower limb elements appear to hinge and stabilize ~3 years earlier in females than in males. In contrast, the upper limb elements appear to stabilize at more similar times but are relatively smaller in females.



**Figure 2.4** – Cross-sectional ontogeny of the brachial index (left), distal element (top-right), and proximal element (bottom-right), colored by sex.



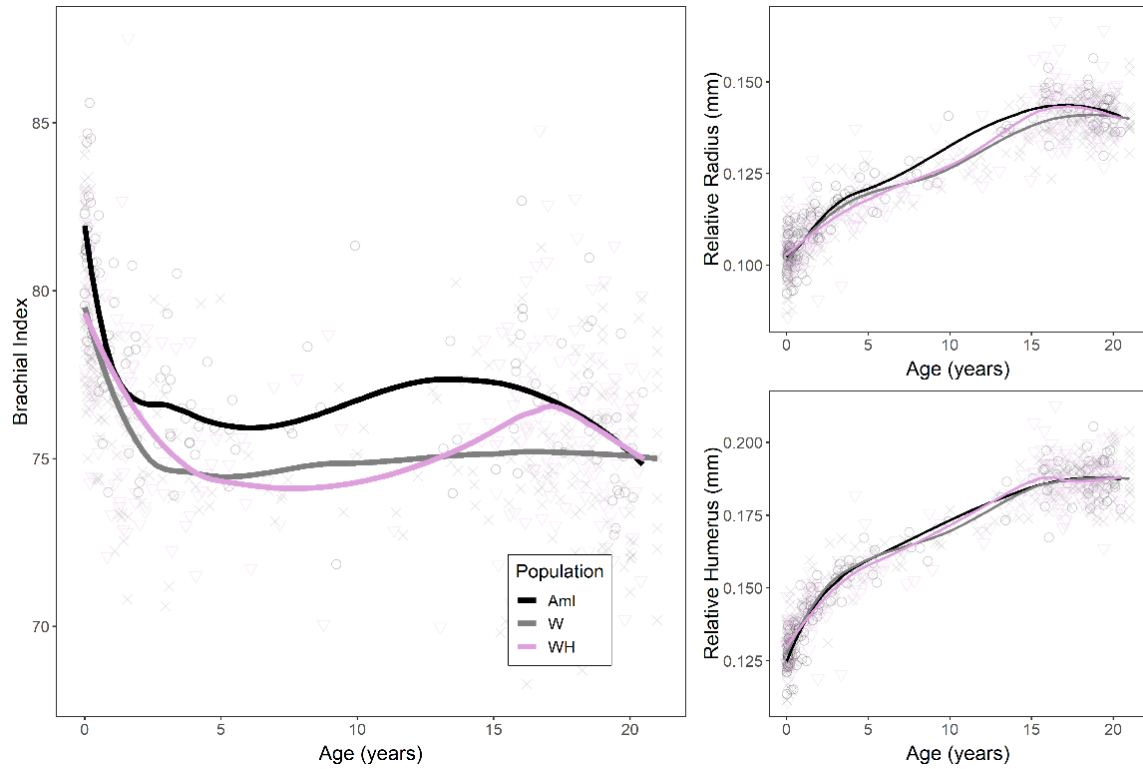
**Figure 2.5** – Cross-sectional ontogeny of the crural index (left), distal element (top-right), and proximal element (bottom-right), colored by sex.

Kruskal-Wallis and post-hoc Dunn's tests exploring population differences in the brachial or crural index found statistically significant differences ( $p < 0.05$ ) in both indices for the pooled sample. In contrast, the SVAD sample only yielded statistically significant differences between populations in the brachial index. There was not an FDB-only sample analysis conducted because of the lack of population diversity in the present FDB sample. For both the pooled and SVAD-specific analyses of the brachial index, the Amerindian group was separated from the white and white Hispanic groups. In contrast, the pooled crural index analysis demonstrated overlap in the white Hispanic group but distinct indices for the Amerindian and white groups. P-values for the Dunn's tests are summarized in Table 2.3.

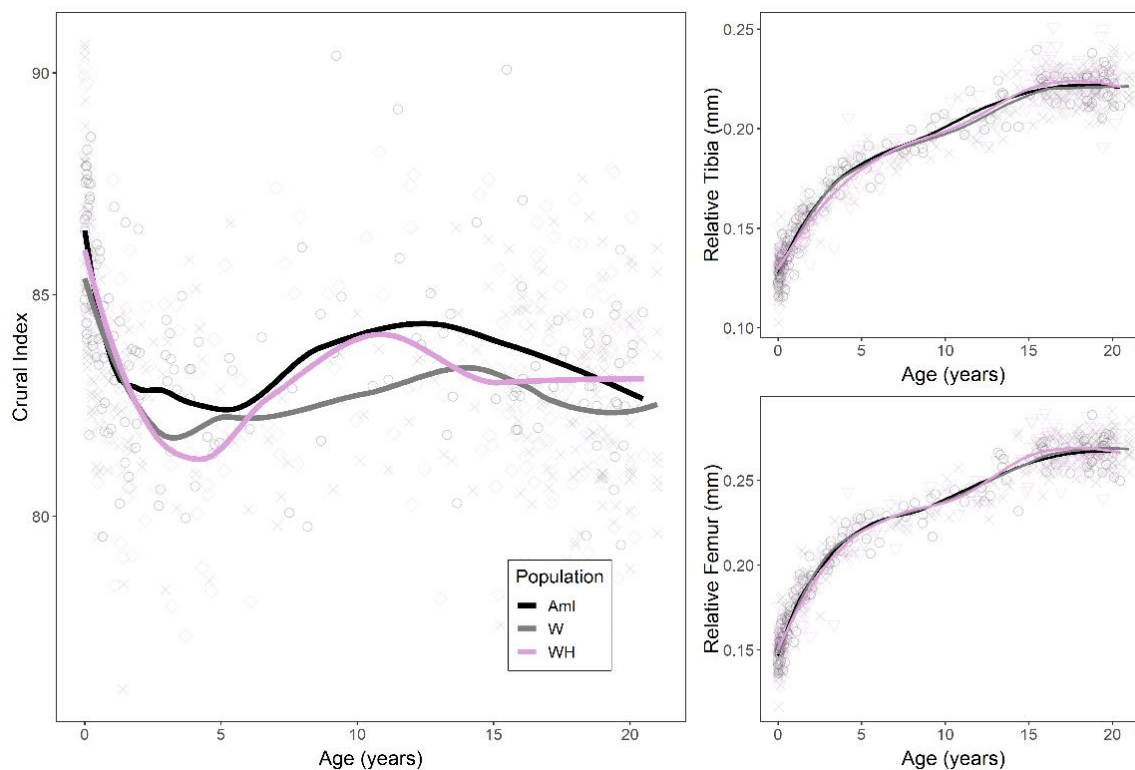
<b>Table 2.3</b> – Results of the post-hoc Dunn’s test of comparisons between sample populations for the pooled and SVAD-specific analyses, separated by brachial index and crural index. Significant relationships are denoted with an asterisk. While the p-value threshold remained at 0.05, the criteria for rejection of the null hypothesis was adjusted to 0.025 in accordance with Holm’s correction for multiple comparisons.		
<b>Comparison</b>	<b>Brachial Index</b>	<b>Crural Index</b>
<i>Pooled Data</i>		
AmI – W	0.0000*	0.0000*
AmI – WH	0.0000*	0.0478
W – WH	0.0330	0.0022*
<i>SVAD Specific Data</i>		
AmI – W	0.0002*	0.1233
AmI – WH	0.0001*	0.1525
W – WH	0.3899	0.4769

The cross-sectional ontogeny of the intralimb indices and individual elements were also visualized by sample population (Figures 2.6-2.7). In general, the Amerindian (AmI) group presented with higher brachial and crural indices over the entire ontogenetic period (birth to 21 years), which seems to be attributed to a larger relative radius length in the upper limb compared to the other groups; this pattern is less apparent in the lower limb. Relative radius and humerus lengths are similar in the white and white Hispanic groups until around age 4 years, where the white Hispanic group index dips below the white group index. Of significance, this decrease in the brachial index for the white Hispanic group appears to be attributed to a much greater increase in relative length of the humerus at that age, instead of the radius. Another point of trajectory deviation in the white Hispanic group occurs around age 13, where the brachial index becomes larger than that of the white group. This deviation aligns with greater difference in relative radius length around that age. Regarding crural index ontogeny, there appears to be much less deviations in individual element growth trajectory, although it may be observed that fluctuations in the white Hispanic group are most likely because of minor increases in

relative femur length. The overall smaller crural index of the white group also appears to be because of a relatively shorter tibia.



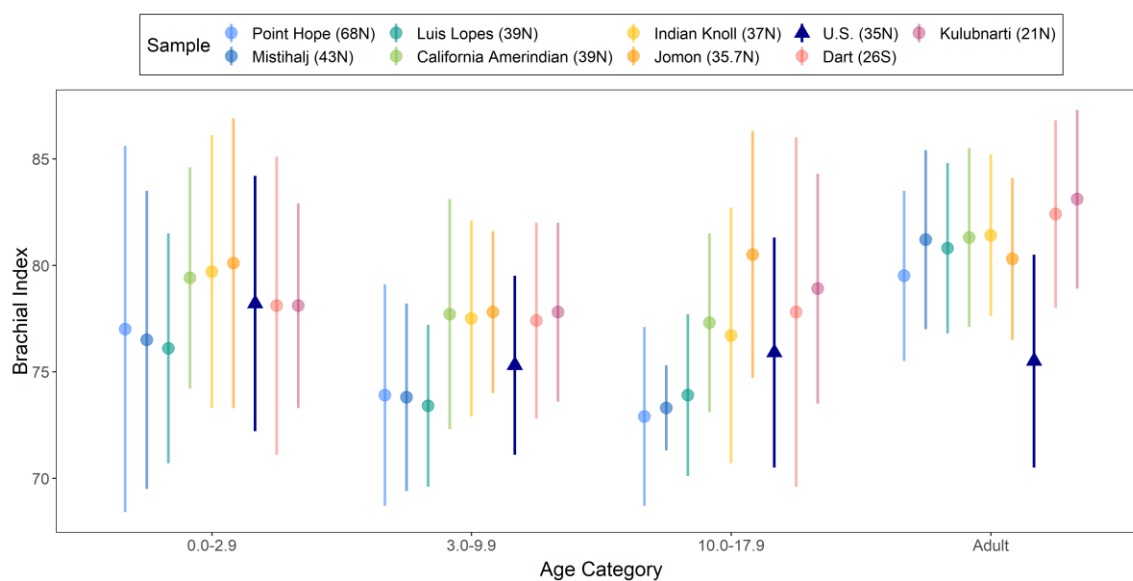
**Figure 2.6** – Cross-sectional ontogeny of the brachial index colored by population.



**Figure 2.7** – Cross-sectional ontogeny of the crural index colored by population.

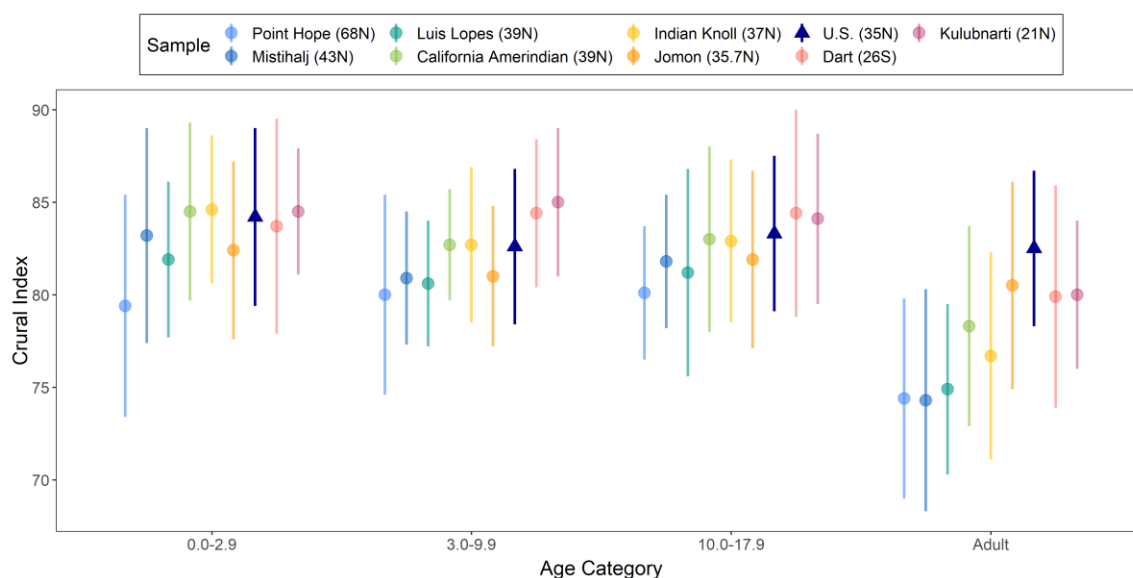
The mean and standard deviation for brachial and crural indices of the pooled data (Figures 2.8-2.9) by age cohorts were plotted against the data published by Cowgill and colleagues (2012). There is a distinct difference in the adult brachial index of the contemporary adult sample compared to the Cowgill and colleagues' adult samples. Excluding the adult sample, both the brachial and crural indices of the contemporary U.S. sample fall within general ecogeographic pattern expected based on latitude. When teasing apart the contemporary U.S. sample further by population, the adult samples maintain positions that are not congruent with the bioarchaeological data (Figures 2.10-2.11). Slight differences in the mean and spread of the brachial and crural indices of each U.S. population does further support the results of the Kruskal-Wallis tests by population: there is more variance between populations in the brachial index compared to the crural

index. In the upper limb, the Amerindian (“AmI”) group maintains a higher brachial index from the other two contemporary populations (“W”, “WH”) across age categories until adulthood.

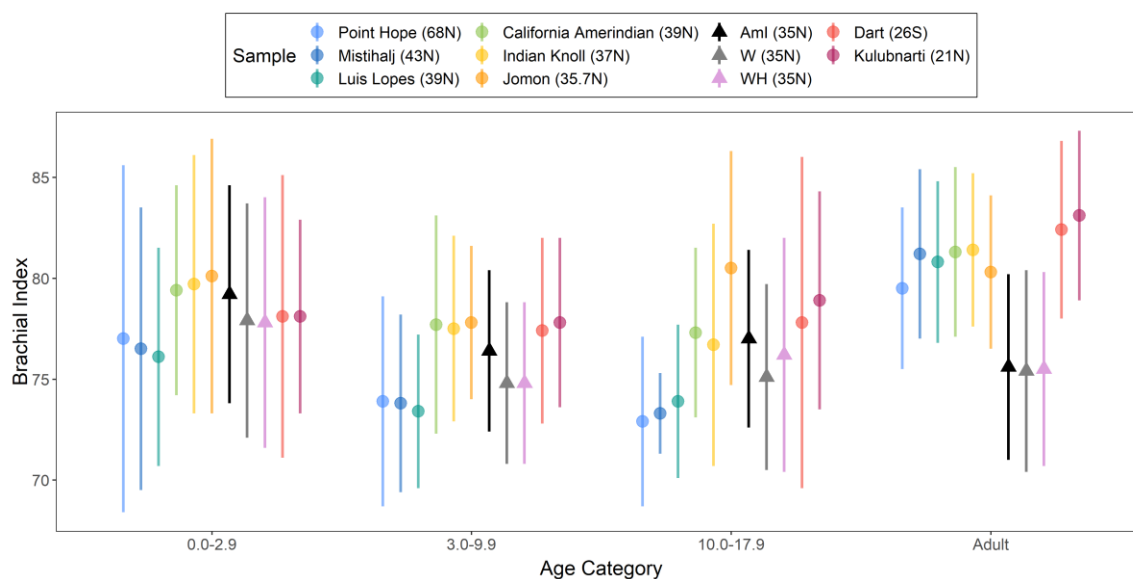


**Figure 2.8** – Mean and 95% interval of the brachial index by age category, colored by sample. Cowgill and colleagues (2012) have filled circles, the present contemporary sample has a filled triangle. Samples are ordered from highest to lowest latitude within age categories.

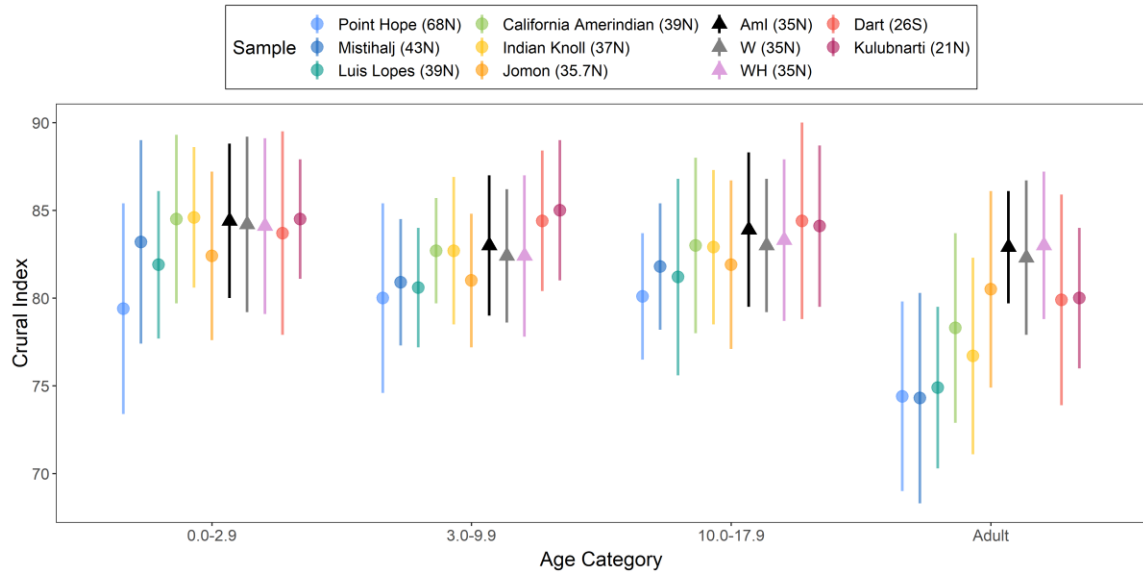




**Figure 2.9** - Mean and 95% interval of the crural index by age category, colored by sample. Cowgill and colleagues (2012) have filled circles, the present contemporary sample has a filled triangle. Samples are ordered from highest to lowest latitude within age categories.



**Figure 2.10** - Mean and 95% interval of the brachial index by age category, colored by population. Cowgill and colleagues (2012) have filled circles, the present contemporary populations have filled triangles. Populations are ordered from highest to lowest latitude within age categories.



**Figure 2.11** - Mean and 95% interval of the crural index by age category, colored by population. Cowgill and colleagues (2012) have filled circles, the present contemporary populations have filled triangles. Populations are ordered from highest to lowest latitude within age categories.

## Discussion

The current study is one of the first to contextualize postnatal intralimb ontogeny with individual long bone growth to uncover the element-level sources of fluctuation observed in previous studies (Bleuze, Wheeler, Williams, et al., 2014; Cowgill et al., 2012; Temple et al., 2011). Before diving into the potential influences on index variation, an in-depth evaluation of the brachial and crural indices is imperative for understanding why these indices roughly follow Allen's (1877) rule (*e.g.*, Cho et al., 2022; Holliday, 1999; Temple & Matsumura, 2011). The intralimb indices are allometry coefficients, when allometry is moved into log space and the relationship is made linear, insofar as they follow the allometry definition of change in one element relative to a unit change of size (Aiello, 1992; Brown & West, 2000; Fleagle, 1985; Gould, 1966; Huxley, 1932; Thompson, 1917). Equations for the brachial index and crural index can therefore be

interpreted as the proximal elements being size variables and the distal elements as the element under investigation (Table 2.4). From this perspective, the humerus serves as a statistical constraint that controls for size (R. J. Smith, 2005). The only difference is between allometry coefficients in logged space and the intralimb indices are the additional multiplication by 100, which turns the indices from proportions (represented as decimals) into percentages.

**Table 2.4** – Equations for the brachial and crural indices.

Brachial Index	$\frac{\text{radius length}}{\text{humerus length}} \times 100$
Crural Index	$\frac{\text{tibia length}}{\text{femur length}} \times 100$

Retaining only the decimal form of the ratio between distal and proximal element and multiplying by 100 changes the interpretation of the brachial or crural index from “the relationship between distal and proximal length” to “the distal length is  $x$  percent of the proximal length”. These two interpretations are fundamentally different. Using the second interpretation, where the proximal element only serves to remove effects of size, it is logical that ecogeographic differences in the brachial or crural index between populations means the distal element is either smaller or larger. This interpretation requires the proximal element (humerus or femur) to remain constant when conducting cross-population comparisons, which is biologically untrue. The variability of the human form is more amenable to treating the brachial or crural index as a ratio, otherwise thought of as a fraction (R. J. Smith, 2005). For example, if one population has an index of 80 (or 0.8) and two other populations have an index of 75 (or 0.75), there are an

infinite number of distal and proximal element combinations that can result in the same index (Equation 1).

**Equation 1** – Example of the effects of a change in the distal or proximal length on an index.

Starting from:  $\frac{80\text{mm}}{100\text{mm}} \times 100 = 80$ , to achieve an index of 75:

1) a change in the distal element:  $\frac{75\text{mm}}{100\text{mm}} \times 100 = 75$ , or

2) a change in the proximal element:  $\frac{80\text{mm}}{106.66\overline{6}\text{mm}} \times 100 = 75$

As provided in the example above, a change in either the distal or proximal element achieves the same result. There are an infinite number of denominator/numerator x 100 combinations to achieve an index of 75 – in addition to what was presented in Equation 1 - although the biomechanical demands of the upper and lower limb certainly must constrain the possibilities. But allowing for the possibility of the distal or proximal element to exhibit variation, and the independence of the indices and absolute lengths (Auerbach & Sylvester, 2011), is how the intralimb indices should be approached when considering the ecogeographic (or otherwise influenced) patterning of limb proportions.

To the author's knowledge, only one other study has compared relative long bone growth of the lower limb to the crural index, conducted by Frelat and Mitteroecker (2011), and the upper limb (*i.e.*, brachial index) has not been studied as extensively. An increase in sample size of the current study allows for more in-depth investigations into the ontogenetic trajectories of intralimb indices. In this study, fluctuations found in the ontogenetic trajectory of the brachial and crural indices in a contemporary sample from the United States were found not to be solely because of the radius and tibia, which have

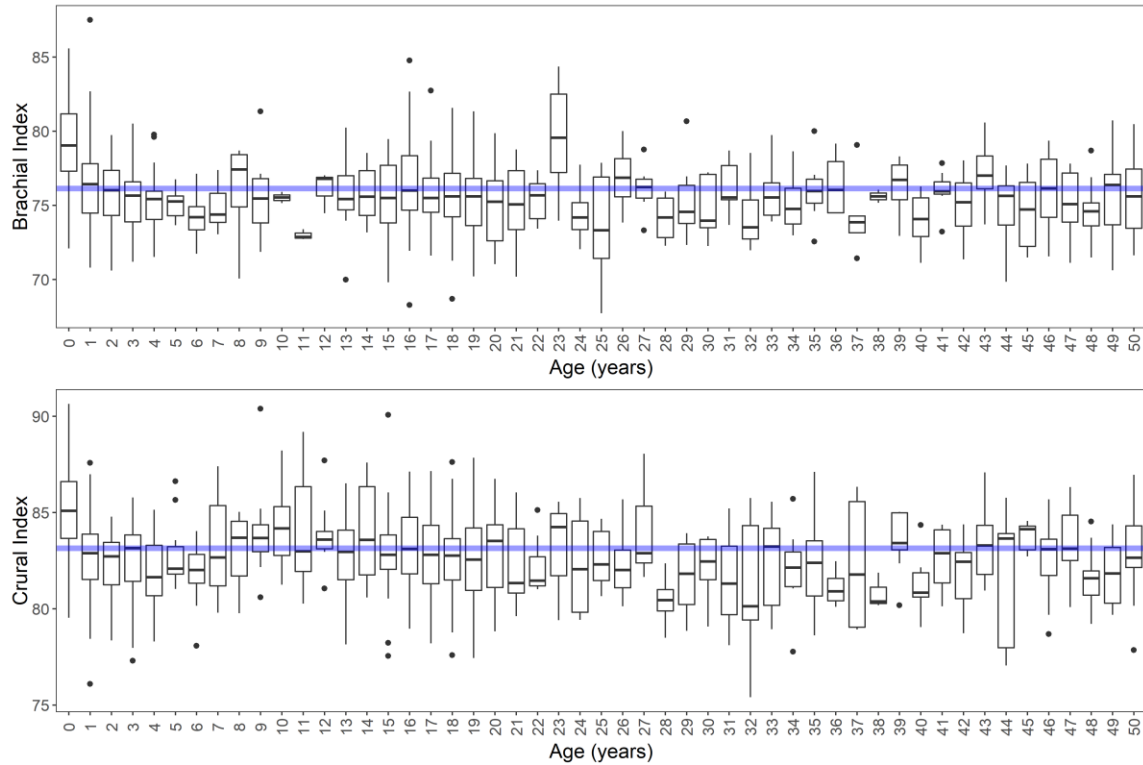
commonly been used to explain differences in ecogeographic changes in the intralimb indices (Cowgill et al., 2012; Holliday & Ruff, 2001; Waxenbaum et al., 2019). Sexual dimorphism of the brachial and crural indices were detected when separating by sample source or population, but not detected in single age cohorts (except for ages 15, 21, and 48). The significance observed in more generalized subsets but not in in-depth subsets may be because of sample size and/or sample bias (R. J. Smith, 2019).

Comparisons with previous postnatal intralimb ontogeny data demonstrate deviations to the classic understanding of ecogeographic patterning of the brachial and crural indices for not only the contemporary U.S. sample used in the present study, but also previous data, suggesting other factors outside of latitude may influence proportional limb lengths. In fact, the results of this study align with other recent publications demonstrating a greater need to expand current understandings of global limb variation beyond classic proxies for environment such as latitude or temperature. Population history assuming environmental selection (Cho et al., 2022; Savell et al., 2016, 2022) and the effects of secular change on limb proportions (Jantz et al., 2016) have both been previously suggested as additional sources of global intralimb proportion patterning, which will be explored in the discussion below.

### **The Brachial and Crural Indices**

The ontogenetic trajectories of each individual long bone length are variable (S. L. Smith & Buschang, 2004, 2005). Fluctuations observed in the intralimb indices across ontogeny therefore cannot be solely the result of changes in the distal elements, as the proximal elements are also actively growing. Loess lines presenting the ontogenetic

trajectories of the brachial and crural indices in the present study demonstrate the different fluctuations of the intralimb indices occurring until stabilization in conjunction with the individual relative trajectories of the proximal and distal elements (Figures 2.4-2.7). Significant differences of the brachial and crural indices are present over ontogeny, especially between the first four years of life where the loess lines display steep trajectory changes (Figures 2.2 and 2.3), which coincides with the rapid deceleration of growth in the first life history stage (Bogin, 2005; Cameron & Bogin, 2012). Subsequent variation in the significance of the brachial or crural index between birth and other age cohorts (Figure 2.3) may be because both indices are at their maximum at birth, whereas stabilization of each index is somewhat intermediate within the observed fluctuations (Figures 2.2, 2.4-2.7). An alternative perspective is that the indices at each age include so much variation that they cannot be teased apart using traditional hypothesis testing methods (see Figure 2.12 for variance and fluctuations).



**Figure 2.12** – Boxplots of the brachial (top) and crural (bottom) index by single-year age cohorts for the U.S. sample. The straight blue line is the median index value for the entire sample across all ages.

Results from this study further support the importance of appreciating not only the full ontogenetic trajectory of the brachial and crural indices, but also the relative growth trajectories of individual elements contributing to the indices. The brachial or crural index, by way of definition, inherently collapses a lot of human variation. Fluctuations observed in the trajectory of the indices over ontogeny observed here (Figures 2.2, 2.4-2.7) and shifts in variance (Figure 2.12) cannot be further investigated without teasing apart potential contributors to phenotypic variation.

### **Sexual Dimorphism**

All subsets of data tested - except for AmI in the upper limb, WH in lower limb, and single-year age cohorts - demonstrated sexual dimorphism of the brachial and crural

indices (Table 2.2). Lack of significance in the AmI population for the brachial index and the WH population for the crural index may be because of differing levels of sexual dimorphism observed globally (Kenyhercz, Klales, Stull, McCormick, & Cole, 2017; Ubelaker & DeGaglia, 2017). Absence of significant sex differences in the indices within single-year age cohorts, including ages 30-50, was surprising given that they have been proven to be sexually dimorphic in adult populations (Bleuze, Wheeler, Dupras, et al., 2014; Cho et al., 2022; Jantz et al., 2016). Small sample sizes at each chronological age for most of the FDB sample (Figure 2.1) may be masking the overall sexual dimorphism of the indices observed when taking the full sample into account (Table 2.2). Regardless of significance, the ontogenetic trajectories of males and females in the intralimb indices are demonstrated in Figures 2.4 and 2.5, and stabilization of sexual dimorphism for the brachial and crural indices is achieved by age 20.

Fluctuations in brachial index trajectory by sex occur at different ages because of changes in the humerus and/or the radius (Figure 2.4), which demonstrates how the indices may change in response to more than the lengthening or shortening of the distal element. Most of the sexual dimorphism observed after age 20 in the brachial index can be attributed to a steeper ontogenetic trajectory of the radius in males compared to females. Fluctuations in the crural index trajectory are largely from rapid changes in the relative trajectory of the tibia and femur at different times. Between the ages of 5-10, females exhibit a relatively larger tibia and femur, resulting in a greater crural index than males. After 10, the steeper ontogenetic slope of males in both the tibia and femur, paired with a decrease in slope in the female trajectories, results in the male crural index being greater than the female index by age 20. As such, the sexual dimorphism observed in



both index trajectories are similarly driven by steeper relative growth of the long bones at birth with an earlier plateauing of growth for the females compared to the males. These observations are in line with the different timings of puberty and maturity between sexes demonstrated in growth and development studies (Cameron & Bogin, 2012; Granados, Gebremariam, & Lee, 2015; Stull, Chu, Corron, & Price, 2022).

### **Ecogeographic Patterns**

The sample used in the present study does not contain enough latitude and temperature variation to explore correlations or modeling relationships between such variables and the intralimb indices. Instead, within-U.S. population results demonstrated that there are statistically significant differences in the both the brachial and crural indices among Amerindian, white, and white Hispanic groups in the United States. These differences are apparent in the growth trajectories of intralimb indices as well as the relative long bone elements (Figures 2.6 and 2.7). Trajectories of the crural index appear to fluctuate in much greater magnitude and the positionality of each population was not maintained over ontogeny, in contrast to what was previously demonstrated by Frelat and Mitteroecker (2011). Loess lines are sensitive to sample size, which was not constant through ontogeny, subsequently potentially causing artificially inflated fluctuations in the data. In addition, the two samples used by Frelat and Mitteroecker (2011) are from two different continents, making them geographically distinct and resulting in potentially less shared population history than the contemporary U.S. sample used in this study. In contrast, there is large genetic and craniometric overlap in individuals who are reported to be Native American (here, “Amerindian”), Hispanic, and white (Algee-Hewitt, 2016).

Direct comparison using the mean and 95% intervals of intralimb indices of the present U.S. sample with data published by Cowgill and colleagues (2012) reveals distinct ecogeographic, and potentially temporal, patterns across ontogeny (Figures 2.8-2.11). The brachial and crural indices of the present contemporary sample (with combined populations) generally fall within the conceptual ecogeographical patterning of the bioarchaeological samples across age categories (Figures 2.8 and 2.9). However, the adult category of the U.S. sample has a much lower brachial index and an uncharacteristically high crural index compared to the bioarchaeological samples. The intralimb index ranges of the contemporary adult sample fall within those observed by Jantz and colleagues (2016) in their investigation of secular change in European Americans over the past 150 years, thus legitimizing the brachial and crural indices of the adult category.

Greater attention to the ecogeographic positioning of all samples reveals that there are marked differences in the intralimb indices between Luis Lopes and California Amerindian samples, although they are from the same latitude (Figures 2.9 and 2.10). These two samples, momentarily disregarding the contemporary U.S. sample, potentially confound the ecogeographic patterning concept, as Luis Lopes clusters with higher latitude groups (Point Hope and Mistihalj), and California Amerindian sample clusters with the more temperate groups (Indian Knoll and Jomon, for the most part). While the general positioning of each bioarchaeological sample remains consistent across age categories, as previously demonstrated (Cowgill et al., 2012), a slightly different approach to visualizing the brachial and crural indices – using point and 95% intervals instead of boxplots and plotting by age category instead of by sample – uncover patterns

that were not previously considered. Contextualizing these two samples from Cowgill and colleagues (2012) with the present study populations may provide insight as to the different ontogenetic patterns observed in the contemporary sample compared to the comparative samples (Figures 2.10 and 2.11). The contemporary U.S. sample populations used at present - Amerindian, white, and white Hispanic - all fall intermediately between cold and more temperate climate bioarchaeology groups, except for their final adult samples. From an ecogeographic perspective, this pattern is to be expected since they originate from ~35°N. Nevertheless, we acknowledge that the comparisons between the current contemporary U.S. sample and bioarchaeological samples from Cowgill and colleagues (2012) may not be entirely appropriate, given a few factors detailed below.

**Environmental Factors of Growth.** There is no current consensus as to the extent to which environmental factors, such as temperature, affect body proportions (Betti et al., 2012; Pomeroy et al., 2021; Roseman & Auerbach, 2015; Savell et al., 2022). The effect of cold temperatures on resting metabolic rate and total lower limb length has demonstrated Allen's rule in experimental contexts (Serrat, 2013; Tilkens, Wall-Scheffler, Weaver, & Steudel-Numbers, 2007). Further, the ecogeographic patterning of the brachial and crural indices has been previously demonstrated in skeletal samples (Auerbach, 2012; Cho et al., 2022; Cowgill et al., 2012; King, 2010; Temple et al., 2011). Many of these studies included long-term temperature data to calculate correlations between index and minimum, maximum, and average temperature. In doing so, temperatures after 1989 or 1990 are not included because of unprecedented increases in temperature over approximately the last 30 years and the unknown effects on limb ontogeny. The marked difference in mean and 95% interval positioning of the brachial

and crural indices for the contemporary U.S. sample and populations (Figures 2.8-2.11) may be because of the unknown effects of global warming on the ontogeny of individual long bones and their indices.

**Population History.** Population history could have a greater influence on intralimb index variation than ecogeographic studies suggest. Savell and colleagues (2022) recently found little-to-no temperature-driven effects on long bone lengths, although distal elements appeared to shorten with higher latitudes while proximal elements either increased or remained neutral. Their findings give greater credit to stabilizing selection over environmentally driven changes in limb length, providing greater credence to non-latitudinal effects, such as population structure, population history, or other aspects of stabilizing selection (Auerbach & Sylvester, 2011; Bogin et al., 2002; Kondo & Eto, 1975; Roseman & Auerbach, 2015). Body proportions of contemporary populations within the United States have been demonstrated to be different in adults and children (Fulwood, Abraham, & Johnson, 1981; Hamill, Johnston, & Lemeshow, 1973; Krogman, 1970). The maintenance of ancestral limb proportions in more recently migrated populations may explain the positioning of the contemporary populations among each other and the bioarchaeological samples (Figures 2.10 and 2.11), except for the adult age category. Of the three contemporary samples, the Amerindian group maintains the highest brachial and crural indices through adulthood, which is more in line with the California Amerindian or Indian Knoll samples. The white group almost consistently maintains the lowest indices through adulthood, which may be more in line with the Luis Lopes sample. Finally, the white Hispanic group maintains intermediate indices, again

perhaps suggesting genetic influences from both European and Hispanic population histories (Algee-Hewitt, 2017).

**Secular Change.** Changes to the allometric proportions of long bones have changed within the last 150 years (Jantz et al., 2016; Meadows & Jantz, 1995). One major difference between samples published by Cowgill and colleagues (2012) and the present study is temporality. Temporal composition of the bioarchaeological sample ranges from 6,415 BP to the 20<sup>th</sup> century (Cowgill et al., 2012, Table 2). In contrast, the present sample consists of individuals all born after 1990, apart from the FDB sample, of which individuals were born between 1905 and 1993, which is more comparable to the other 20<sup>th</sup> century populations (Dart and Luis Lopes) that Cowgill incorporated into the comparisons. Secular changes may be captured in the bioarchaeological samples, as both the California Amerindian and Indian Knoll groups temporally span thousands of years and the Luis Lopes sample, as an example, is comprised of a single century (see Table 2 in Cowgill et al., 2012). The contemporary U.S. populations are all born within the last two decades, apart from the adult FDB sample. The growth trajectories presented in the current study, based on shorter temporal spans, and known demographic information, are much more likely to reflect the current ontogenetic trajectory of contemporary humans compared to their bioarchaeological comparative counterparts.

## **Conclusion**

The brachial and crural indices are two of the only metrics that can be compared across hominin, bioarchaeological, and contemporary skeletal samples. While standardizing by size - either dividing by body mass or stature - is also possible, most

skeletal samples do not have known body size measurements to use; estimating body size inherently adds additional uncertainties or error to the analyses. Anatomical region-specific measures, such as the brachial and crural indices, are therefore an important source of data for biological anthropologists, often overlooked in many avenues of research. Without proper investigation and understanding of how these intralimb indices are affected by population history, environment, and time, these measures in biological anthropological inquiry will remain under-utilized. The positioning of the brachial and crural indices in relation to geographically distinct samples is established early in ontogeny. Yet the contemporary sample of the present study demonstrates stabilization of the brachial and crural indices to adult proportions much earlier than bioarchaeological samples.

Indeed, the brachial and crural indices have been far less explored in the context of modern, contemporary human variation (Garcia, 2015). Biological anthropologists often argue that it takes tens- or hundreds- of thousands of years for intralimb indices to evolve to new environments (Garcia, 2015; Holliday, 1997; King, 2010). Yet secular change in stature has been demonstrated to significantly alter the brachial and crural indices (Jantz et al., 2016; Jantz & Jantz, 2017) and secular change in stature has been documented across the globe (Bertsatos & Chovalopoulou, 2018; Bogin, 2013; Larnkjaer, Attrup Schrøder, Maria Schmidt, Hørby Jørgensen, & Fleischer Michaelsen, 2007; Myburgh, Staub, Rühli, Smith, & Steyn, 2017; Shin, Oh, Kim, & Hwang, 2012). Here, we identify that contemporary U.S. populations follow expected ecogeographic patterns, although their overall ontogenetic trajectories differ from the comparative bioarchaeological samples. Certainly, more comprehensive investigations into the

differential effects of genetic control, global warming, and secular change on contemporary human proportions can glean important information on human variability and why their ontogenetic trajectories do not reflect those of past populations. Not only may these future findings provide insights into the multifactorial contributors to growth and development, but also help contextualize rapid changes in body proportions used to infer past human conditions regarding migration patterns (Auerbach, 2012; Seguchi et al., 2017; Temple & Matsumura, 2011) and evolutionary adaptations to new environments (Holliday, 1997, 1999; Ruff, 1991, 1994; Trinkaus, 1981).

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## **Chapter 3 - Stature estimation of the subadult skeleton using a contemporary U.S. population**

### **Introduction**

Stature is used in biological anthropology to discuss body size evolution (Dingwall, Hatala, Wunderlich, & Richmond, 2013; Holliday & Franciscus, 2009; Ruff, 2002; Will, Pablos, & Stock, 2017), evaluate human variation (Eveleth & Tanner, 1990; Gustafsson & Lindenfors, 2009), assess health and nutrition or socioeconomic status (Morgan, 2000; Perkins, Subramanian, Davey Smith, & Özaltin, 2016; Temple, 2008; Vercellotti et al., 2014), diagnose atypical growth (de Onis et al., 2012; Duggan, 2010; Natale & Rajagopalan, 2014; Topor, Feldman, Bauchner, & Cohen, 2010), and assist in forensic identification (Albanese, Tuck, Gomes, & Cardoso, 2016; Konigsberg, Hens, Jantz, & Jungers, 1998; Krishan, Kanchan, Menezes, & Ghosh, 2012; Langley, 2017; Wilson, Herrmann, & Jantz, 2010). Methods for estimating stature using the skeleton have been split into two types: anatomical and mathematic (Dwight, 1894; Lundy, 1985). The anatomical method uses all bones that contribute to stature with a soft-tissue correction (Fully, 1956; Raxter, Auerbach, & Ruff, 2006). Numerous validations of the anatomical method have demonstrated high accuracy (Langley et al., 2018; Niskanen, Maijanen, McCarthy, & Junno, 2013) – even in subadult groups (Brits, Manger, & Bidmos, 2018). Mathematical methods for estimating stature traditionally use one or more elements in a regression formula to estimate stature (Lundy, 1985). Even with less precision, mathematical methods for estimating stature have persisted in the biological anthropological literature because of ease of use, applicability on incomplete skeletons,

and reliability of results (Duyar & Pelin, 2003; Formicola, 1993; Lundy, 1985; Maijanen, 2009; Mays, 2016).

A handful of methods for estimating stature from immature skeletal remains currently exist (Abrahamyan, Gazarian, & Braillon, 2008; Brits, Bidmos, & Manger, 2017; Brits et al., 2018; Feldesman, 1992; Robbins Schug, Gupta, Cowgill, Sciulli, & Blatt, 2013; Ruff, 2007; Smith, 2007) (Table 3.1). Research included in Table 3.1 contributed substantially to the field, but there are numerous limitations, including sample composition and appropriate modeling. The Denver Growth Study, which was undertaken between 1927 and 1967 (McCammon, 1970), was commonly used by studies in Table 3.1 as a source of longitudinal data. Longitudinal growth studies often have small sample sizes and restrict demographic variability, including population and socioeconomic status, to attempt to reduce variation (Bogin, 2005; Cameron, 1986; Eveleth & Tanner, 1990; Healy, 1986; Tanner, 1986). The specific inclusion criteria for a longitudinal study that leads to homogenous datasets are not ideal for forensic contexts, especially for places with high levels of variation in the population, like the United States (U.S. Census Bureau, Population Estimates Program (PEP), 2021). Current methods that included cross-sectional data to construct stature estimation models also restricted their samples to include only one population (Abrahamyan et al., 2008; Brits et al., 2017). Somewhat entwined with sample composition is sample size. A major limiting factor to subadult stature estimation is small sample size, especially of complete individuals with known demographic information (Chu, Stull, & Sylvester, 2022; Stull, L'Abbé, & Ousley, 2014). While two of the studies in Table 3.1 had large samples sizes ( $n > 450$ ), the remaining five methods have remarkably small samples. Because growth studies and

subadult stature estimation should cover the entire ontogenetic period, large sample sizes are required (Stull, Corron, & Price, 2021).

<b>Table 3.1</b> – Subadult stature estimation methods in the biological anthropology literature.				
<b>Citation</b>	<b>Type</b>	<b>Sample Size</b>	<b>Age Range (years)</b>	<b>Data Source</b>
Abrahamyan et al. (2008)	Mathematical	413	6-18	Cross-sectional
Brits et al. (2017)	Mathematical	59	10-17	Cross-sectional
Brits et al. (2018)	Anatomical	53	10-17	Cross-sectional
Feldesman (1992)	Mathematical	576	8-18	Mixed-longitudinal
Robbins Schug et al. (2013)	Mathematical	20	0.5-11.5	Longitudinal
Ruff (2007)	Mathematical	20	1-17	Longitudinal
Smith (2007)	Mathematical	67	3-10	Longitudinal

While most adult stature estimation equations are population specific (Ahmed, 2013; Dayal, Steyn, & Kuykendall, 2008; Menéndez Garmendia, Sánchez-Mejorada, & Gómez-Valdés, 2018; Nor et al., 2013; Sládek et al., 2015), a recent evaluation of forensic stature estimation in the United States demonstrated the benefit of global models – particularly for individuals whose population affinity cannot be reliably estimated (Albanese, Osley, & Tuck, 2016; Albanese, Tuck, et al., 2016). If biological profile methods are reliant on other aspects of the biological profile for accuracy, then the absence of one piece of the biological profile – be it sex, age, or population affinity – substantially reduces the chances for identification. A relevant limitation to current subadult stature estimation methods is that age must be estimated first because all methods have either selected age ranges for their reference sample (Abrahamyan et al.,

2008; Brits et al., 2018; Feldesman, 1992; Robbins Schug et al., 2013; Smith, 2007) or have generated individual equations by chronological age (Ruff, 2007). While subadult age estimation methods have increased in availability, accuracy, and precision (Corron et al., 2019; Langley, 2016; Lottering et al., 2017; Rissech, Márquez-Grant, & Turbón, 2013; Sgheiza, 2022; Stull & Armelli, 2021; Stull, Chu, Corron, & Price, 2022; Stull et al., 2014), estimating other aspects of the biological profile remains a source of compounding error when estimating stature. Subadult sex estimation methods are also becoming more prevalent and reliable (Cole, Chu, & Stull, 2021; Garvin et al., 2021; Klales & Burns, 2017; Stull, Cirillo, Cole, & Hulse, 2020; Stull, L'Abbé, & Ousley, 2017), but population affinity estimation methods for subadults are only beginning to be explored (*e.g.*, Reinman, 2019). These combined difficulties for estimating the subadult biological profile suggest that stature estimation methods should be inclusive for variation in age, sex, and population.

Stature is highly heritable (Arinami et al., 1999; Hirschhorn et al., 2001; Krishan et al., 2012), but has also been demonstrated to have plasticity, which increases human variation (Bogin & Loucky, 1997; Bogin, Smith, Orden, Varela Silva, & Loucky, 2002; Boldsen, 1995; Jantz, Jantz, & Devlin, 2016). Stature secular change has also been observed worldwide, which changes the patterns of stature with certain groups growing taller and others retaining mean height (Bertsatos & Chovalopoulou, 2018; Jantz et al., 2016; Larnkjaer, Attrup Schrøder, Maria Schmidt, Hørby Jørgensen, & Fleischer Michaelsen, 2007; Myburgh, Staub, Rühli, Smith, & Steyn, 2017; Shin, Oh, Kim, & Hwang, 2012). As such, it is important to use stature estimation methods created using appropriate reference samples, depending on the target population (Konigsberg &

Frankenberg, 2013; Menéndez Garmendia et al., 2018; Ross & Konigsberg, 2002). In addition to stature, secular change has also affected growth and maturation (Bogin, 2013; Klepinger, 2001; Roche, 1979; Ulijaszek, 2001) and the proportional (*i.e.*, allometric) relationship between long bones and stature (Jantz et al., 2016; Jantz & Jantz, 1999; Meadows & Jantz, 1995). Considerations for the effects of secular change and other plastic responses on stature necessitate the periodic updating of methods reflect the changing relationships between long bone measurements and stature and subsequently increase the applicability of a method, especially for subadult populations, where the added complexities of ontogeny may compound error in stature estimates.

While appropriateness of data is essential for developing a method, the choice of statistical model is equally important. The prevalence of linear regression models in stature estimation indicates a tacit assumption of a linear relationship between long bone lengths and stature (*e.g.*, Ahmed, 2013; Duyar, Pelin, & Zagyapan, 2006; Konigsberg et al., 1998; Menéndez Garmendia, Sánchez-Mejorada, & Gómez-Valdés, 2018; Nor et al., 2013; Sjøvold, 1990). In subadult stature estimation, linear models have also been widely used, although it is widely known that neither long bone growth (Ives & Humphrey, 2017; Stull et al., 2022, 2014), nor its relationship with stature is linear (Cameron, 1986; de Onis et al., 2012; Healy, 1986; Shohoji & Sasaki, 1984). While linear regression is easy to calculate, interpret, and distribute, stature estimation methods using linear regression to appreciate a nonlinear relationship are invalid (Konigsberg, Frankenberg, Sgheiza, & Liversidge, 2021; Sgheiza, 2022; Stull et al., 2022; Stull, Price, Corron, & Chu, 2020).

Accuracy, precision, and generalizability are important for determining the appropriateness of a method for forensic contexts (*Daubert v. Merrel Dow Pharmaceuticals, Inc.*, 1993; *Kumho Tire Company, Ltd. V. Carmichael*, 1999; Grivas & Komar, 2008; Lesciotto, 2015). For adult stature estimation, researchers found that stature estimation equations created using reference samples that are temporally distinct from the target population yield imprecise (mean square error between 12.5-58.5cm) estimates of stature (Wilson et al., 2010). Findings suggest that the effects of secular change on long bone length and stature necessitate updated mathematical stature estimation equations to increase accuracy and precision (Jantz & Jantz, 1999; Wilson et al., 2010). For generalizability, Wilson and colleagues (2010) also suggested using stature estimation equations that were created to estimate any type of stature (cadaveric, forensic, or living) rather than just forensic stature, which is the stature given in a missing person's report (Ousley, 1995). This critical evaluation of adult stature estimation for forensic application speaks to the importance of updating subadult stature estimation methods as well – as methods created for the U.S. population utilized samples that are also temporally distinct from the current target population (Wilson et al., 2010). It also demonstrates how accuracy cannot be the only metric by which stature estimation equations are compared – sometimes accurate models sacrifice generalizability when the data are too precise and lack variability.

Using a large, cross-sectional sample from the 21<sup>st</sup> century would alleviate some of the limiting factors with previously published subadult stature estimation methods and account for any effects of secular change that may affect the accuracy of past methods created using data from the 20<sup>th</sup> century. The current study uses the Subadult Virtual

Anthropology Database (“SVAD”), which is one of the largest collections of contemporary, cross-sectional subadult skeletal data currently available (Stull & Corron, 2022). One technique that can be learned from previous subadult stature estimation methods is their use of radiographs to obtain skeletal measurements. Indeed, the use of medical imaging for aiding in estimating aspects of the biological profile is not new, as radiographic images have been long been used to study dental development (*e.g.*, Demirjian, Goldstein, & Tanner, 1973; Moorrees, Fanning, & Hunt Jr., 1963) and long bone growth (Buschang, 1982; Maresh, 1943, 1955, 1970). As medical imaging (*e.g.*, radiographs, computed tomography scans, or magnetic resonance imaging) has become more prevalent, virtual anthropology has become more prevalent as a means of increasing sample sizes of marginalized skeletal populations (Abegg et al., 2020; Dedouit et al., 2014; Franklin & Blau, 2020; Ousley, Daly, Frazee, & Stull, 2008; Stull, Garvin, & Klales, 2020; Uldin, 2017; Weber, 2014, 2015; Weber et al., 2001).

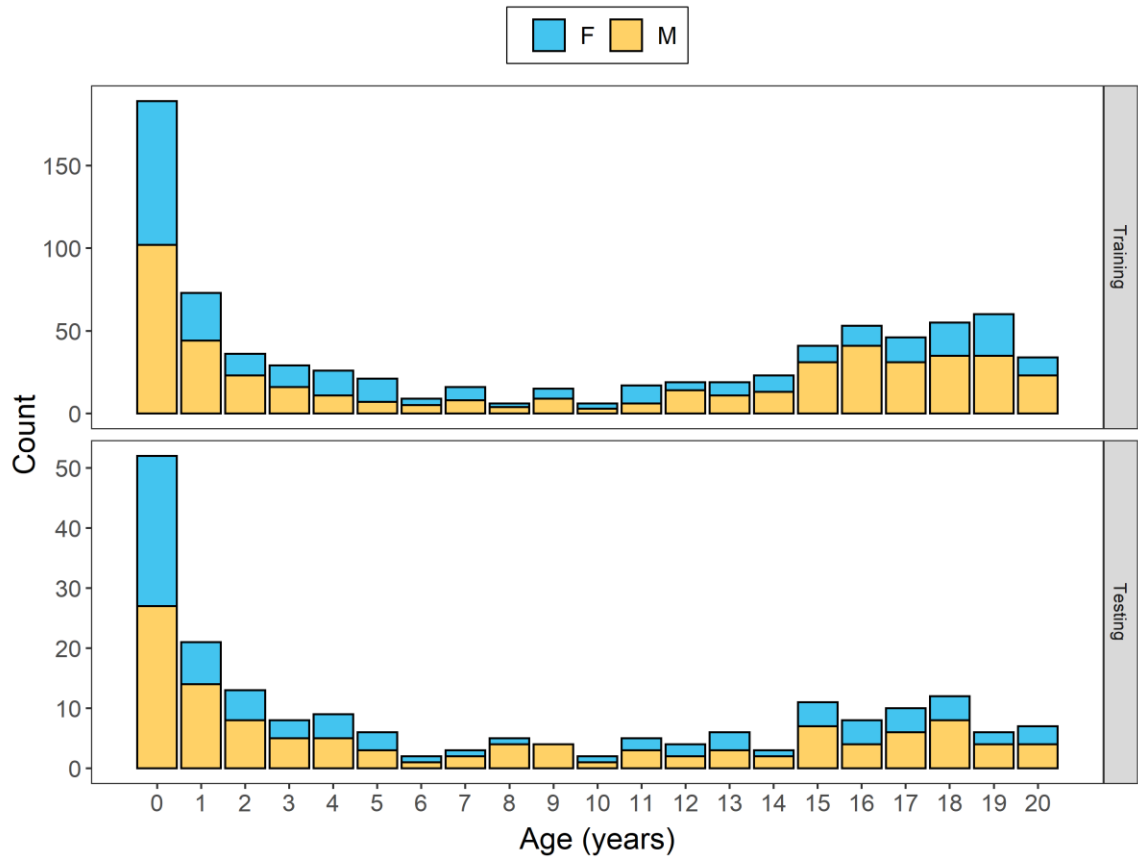
An increase of skeletal data also affords novel considerations for subadult stature estimation. As such, this study aims to address previous limitations of subadult stature estimation and update methods for contemporary U.S. forensic cases by 1) using a large, cross-sectional sample of subadults with known demographic information, 2) incorporating breadth measurements as well as lengths for greater applicability, and 3) using nonlinear models to quantify the relationship between long bone measurements and stature. With these three adjustments, subadult stature estimation methods that maintain accuracy and precision can be immediately implemented in forensic casework.

## Materials and Methods

A subset of individuals from the SVAD that are from the United States (U.S.) were used in this study. The sample included 990 individuals aged between birth and 20 years old. The sample was randomly separated into training (80%) and testing (20%) sets for model optimization and testing (Figure 3.1). Eighteen diaphyseal dimensions (see Table 3.2) were collected until the onset of epiphyseal fusion following an adapted protocol for CT images (Stull & Corron, 2021). Once fusion was estimated to be ‘active’, maximum length and breadth measurements adapted from Langley and colleagues (2016) were collected; these measurements include epiphyses. Recent research has confirmed it is appropriate to combine diaphyseal and maximum measurements so the entire ontogenetic period can be evaluated (see *Chapter 2: Expanding long bone ontogeny in biological anthropology*). Collected diaphyseal and maximum long bone dimensions include length, proximal breadth (excluding femur), transverse midshaft breadth, and distal breadth were all collected in anatomical position. Two additional measures were calculated by adding humerus and radius length and femur and tibia length, following previous studies (Brits et al., 2017; Ruff, 2007). Cadaveric stature and age were also retained for analysis. Because sex and population affinity estimation for subadults have not yet been reliably established (Austin & King, 2016; Shirley & Tersigni-Tarrant, 2017), pooled data were used to construct and test stature estimation models to maximize



applicability.



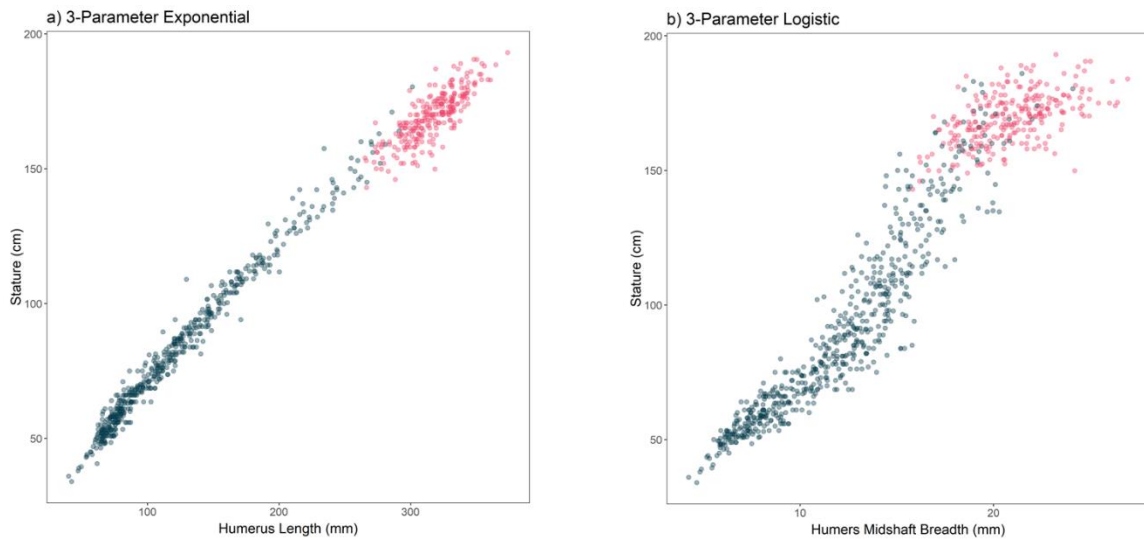
**Figure 3.1** – Sample distribution for training and testing sets filled by sex.

<b>Table 3.2</b> – Long bone measurements per bone and their abbreviations used. Not all types of measurements were conducted on each bone, denoted by a (-).				
<b>Bone</b>	<b>Length</b>	<b>Proximal Breadth</b>	<b>Midshaft Breadth</b>	<b>Distal Breadth</b>
Humerus	HDL	HPB	HMSB	HDB
Radius	RDL	RPB	RMSB	RDB
Ulna	UDL	-	UMSB	-
Femur	FDL	-	FMSB	FDB
Tibia	TDL	TPB	TMSB	TDB
Fibula	FBDL	-	-	-

All analyses were conducted in R and RStudio (R Core Team, 2022; RStudio Team, 2022). Kendall's tau correlation coefficients were calculated to explore the

relationship between stature and diaphyseal dimensions. The bivariate relationships were also visualized to inform the type of models to be tested. Three modeling types were selected (Table 3.3): linear regression to compare with past stature estimation methods, 3-parameter exponential, which is like a power law and roughly resembles un-altered (not-logged) relationships between length and stature (Figure 3.2a), and a 3-parameter logistic, which has a sigmoidal shape that roughly resembles un-altered (not-logged) relationships between breadth and stature (Figure 3.2b).

<b>Table 3.3</b> – Three equations used to model the relationship between diaphyseal dimensions and stature	
Linear Regression	$y = ax + b$
3-Parameter Exponential	$y = a - be^{-cx}$
3-Parameter Logistic	$y = \frac{a}{(1 + be^{-cx})}$



**Figure 3.2** – Bivariate relationship between a) humerus length or b) humerus midshaft breadth and stature. Diaphyseal dimensions (blue filled circles) and maximum dimensions (pink filled circles) are both included.

Simple and multiple regression models were created using the training sample. Univariate linear models for each bivariate relationship were generated using the *stats* package (R Core Team, 2022). In addition, stepwise regression, using the *caret* package (Kuhn, 2020), was used to generate one multiple linear regression, as some evidence shows that multivariate models can provide more precise estimates (Stull & Armelli, 2021; Stull et al., 2022, 2014). In addition, univariate nonlinear models for each bivariate relationship were generated using the *nlstools* package (Baty et al., 2015), with the 3-parameter exponential model used to model lengths, and the 3-parameter logistic model used to model breadths. Point estimates and 95% prediction intervals (PI) were calculated for the testing sample. Model performance was evaluated using four metrics (Table 3.4): test accuracy, root-mean-square error (RMSE), standard error of estimate (SEE), and mean absolute deviation (MAD). Test accuracy evaluates the accuracy of the model, which is defined as the number of individuals whose known stature fell within the 95% PI. The remaining three metrics represent precision, or distance between estimated stature and known stature, and are all differentially used by other biological profile methods.

<b>Table 3.4</b> – Equations for each metric used to evaluate model performance.			
<b>Test Accuracy</b>	<b>Root-mean-square Error (RMSE)</b>	<b>Standard Error of Estimate (SEE)</b>	<b>Mean Absolute Deviation (MAD)</b>
$\frac{n_{correct}}{N}$	$\sqrt{\frac{\sum_{i=1}^N (x_i - \bar{x}_i)^2}{N}}$	$\sqrt{\frac{\sum_{i=1}^N (x_i - \bar{x}_i)^2}{N - 2}}$	$\frac{\sum_{i=1}^N ( x_i - \bar{x}_i )}{N}$

## Results

Kendall's tau correlations are for all long bone dimensions and stature ranged from 0.759-0.907 (Table 3.5). In general, lengths were more strongly correlated with

stature than breadths, although proximal and distal breadths were more strongly correlated with stature than midshaft breadths. Combining proximal and distal lengths did display a stronger correlation with stature.

<b>Table 3.5</b> – Kendall’s tau correlation coefficients ( $r$ ) for the upper and lower limb dimensions in relation to stature.			
<i>Upper Limb</i>		<i>Lower Limb</i>	
HDL	0.9054	FDL	0.9051
HPB	0.8304	-	-
HMSB	0.8195	FMSB	0.8388
HDB	0.8541	FDB	0.8706
RDL	0.8954	RDL	0.9050
RPB	0.8260	TPB	0.8686
RMSB	0.8085	TMSB	0.8190
RDB	0.8103	TDB	0.8577
UDL	0.8954	FBDL	0.9068
UMSB	0.7589	-	-
HDL + RDL	0.9043	FDL + TDL	0.9074

In total, 39 stature estimation models were created. Two variables had unsuccessful nonlinear fits and did not produce a model: radius and tibia distal breadth. Performance metrics for all models are summarized in Table 3.6 and are ordered by testing accuracy; each variable has the metrics for a linear and non-linear model.

### **Performance: Linear Models**

Testing accuracy ranged from 92.67-99.38% for univariate and multivariate linear models (Table 3.6). Models using long bone length, except for the multiple linear regression model, all achieved over 95% testing accuracy, with a mean accuracy of 97.43%. Breadth models achieved a mean accuracy of 94.92% accuracy, with five out of 12 models (HMSB, HPB, TDB, TMSB, and FMSB) achieving accuracy greater than

95%. The multiple linear regression model (consisting of FDL, FBDL, HDL, RMSB, UMSB) had a testing accuracy of 94.77%.

Model performance patterns are the same for RMSE and SEE, as their equations are near-identical, except for the value by which the sum of squared error is divided ( $n$  vs.  $n-2$ , respectively). RMSE ranged from 4.40-17.36cm. The SEE values ranged from 4.43-17.43cm. Length models are more precise than breadth models. The multiple linear regression model had the lowest RMSE and SEE of all linear models. A small RMSE paired with lower testing accuracy suggests that the combination of variables used (FDL, FBDL, HDL, RMSB, UMSB) made the model too precise, resulting in a 95% PI too narrow to include known stature. The highest RMSE and SEE values – and therefore the least precise models – were from the smallest measurements (i.e., midshaft breadths).

Model precision based on MAD values reveal slightly different patterns, as the metric uses absolute error instead of squared error (Table 3.3). MAD values ranged from 4.08-15.37cm. The multiple linear regression model maintained its position as the most precise, followed by all lower limb length models, except for TDL. Surprisingly, FBDL is the second-most precise model based on MAD but has higher RMSE and SEE.

### **Performance: Nonlinear Models**

Nonlinear testing accuracy ranged from 91.43-97.04%. There were no discernible patterns in measurement type or variable type (*i.e.*, upper or lower limb) regarding testing accuracy. Of note, nonlinear femur breadth models (FMSB, FDB) were more accurate than the nonlinear FDL model. Like linear model results, length models achieved a mean testing accuracy of 96.20%, whereas the breadth models had a slightly lower mean

testing accuracy of 94.45%. Surprisingly, the model combining FDL and TDL did not achieve accuracy greater than 95%, though only by a thin margin as it presented with a testing accuracy of 94.92%. In this case, the stronger relationship of FDL+TDL with stature and the flexibility of the nonlinear model resulted in predictions that were over-fit to the training data and did not account for variation in the test data. RMSE values range from 4.04-16.94cm and SEE values range from 4.05-17.04cm. Again, patterns gleaned using RMSE reflect those using SEE. From the perspective of precision, the combined proximal and distal length models (HDL+RDL and FDL+TDL) were the most precise, followed by all length models. There was a minimum of 3cm difference in precision between length and breadth models. Again, the smallest measurements (typically midshaft breadths) were the least precise.

The nonlinear MAD values range from 3.65-15.91cm. Lower limb length models were the most precise, except for FDL. Interestingly, the most precise length models for the upper and lower limb were UDL and FBDL, albeit by a narrow margin (~0.1cm). Again, the models with the least precision (highest MAD) are midshaft breadths.

<b>Table 3.6</b> – Equations and performance metrics for all linear and nonlinear stature estimation models, ranked by test accuracy. Two nonlinear models had unsuccessful fits (RDB and TDB) and are therefore not included in the table.					
<b>Variable</b>	<b>Equation</b>	<b>Test Accuracy (%)</b>	<b>RMSE (cm)</b>	<b>SEE (cm)</b>	<b>MAD (cm)</b>
HDL+RDL	$24.80 + 0.26x$	99.38	5.10	5.13	5.52
RDL	$24.45 + 0.65x$	98.82	5.75	5.78	6.14

TDL	$232.1 + 0.37x$	89.95	5.33	3.30	5.56
UDL	$20.97 + 0.58x$	97.66	5.28	5.31	5.71
FBDL	$33.00 + 0.38x$	97.27	5.03	5.05	4.85
HMSB	$-6.71 + 8.22x$	97.16	11.56	11.62	10.21
RDL	$296.55 - 295.32e^{-0.0035x}$	97.04	4.43	4.46	4.39
HDL+RDL	$324.73 - 318.54e^{-0.0013x}$	96.91	4.05	4.08	3.93
FBDL	$339.27 - 319.61e^{-0.0017x}$	96.72	4.31	4.33	3.65
FMSB	$\frac{208.76}{1 + 10.84e^{-0.0530x}}$	96.67	8.25	8.30	8.10
FDL+TDL	$32.13 + 0.17x$	96.61	4.85	4.88	5.22
HPB	$-3.93 + 3.97x$	95.60	7.95	8.01	8.31
UDL	$337.84 - 336.41e^{-0.0027x}$	96.49	4.39	4.42	3.88
TDL	$328.25 - 310.78e^{-0.0018x}$	96.13	4.36	4.40	3.82
FDL	$32.2 + 0.31x$	96.61	4.97	5.00	5.10
HPB	$\frac{231.41}{1 + 9.01e^{-0.0758x}}$	95.92	7.62	7.67	7.75
HDL	$337. - 328.85e^{-0.0021x}$	95.83	4.36	4.39	3.99

HDL	$25.33 + 0.46x$	95.83	5.32	5.35	5.54
TDB	$18.43 + 3.07x$	95.81	9.92	9.98	8.34
FDB	$\frac{217.13}{1 + 9.35e^{-0.0047x}}$	95.81	8.22	8.27	6.96
TMSB	$0.41 + 7.42x$	95.60	9.59	9.64	7.92
FDL	$365.51 - 345.22e^{-0.0013x}$	95.56	4.29	4.32	4.06
FMSB	$-3.28 + 6.84x$	95.56	9.03	9.08	7.31
UMSB	$\frac{208.87}{1 + 15.75e^{-0.2950x}}$	95.27	16.94	17.04	15.91
HDB	$\frac{197.82}{1 + 10.56e^{-0.0716x}}$	94.97	7.39	7.43	7.03
FDL+TDL	$351.12 - 331.75e^{-0.0007x}$	94.92	4.04	4.06	3.76
RPB	$1.01 + 8.16x$	94.86	9.92	9.97	7.57
Multiple <sup>1</sup>	$18.92 + 0.53 \times \text{FDL} + 0.11 \times \text{FBDL} + 0.19 \times \text{HDL} + 0.89 \times \text{RMSB} - 0.15 \times \text{UMSB}$	94.77	4.40	4.43	4.08
FDB	$2.04 + 2.12x$	94.76	9.03	9.08	7.61
UMSB	$-18.26 + 13.10x$	94.67	17.33	17.43	15.37
HMSB	$\frac{211.24}{1 + 12.18e^{-0.1837x}}$	94.32	10.85	10.91	9.98



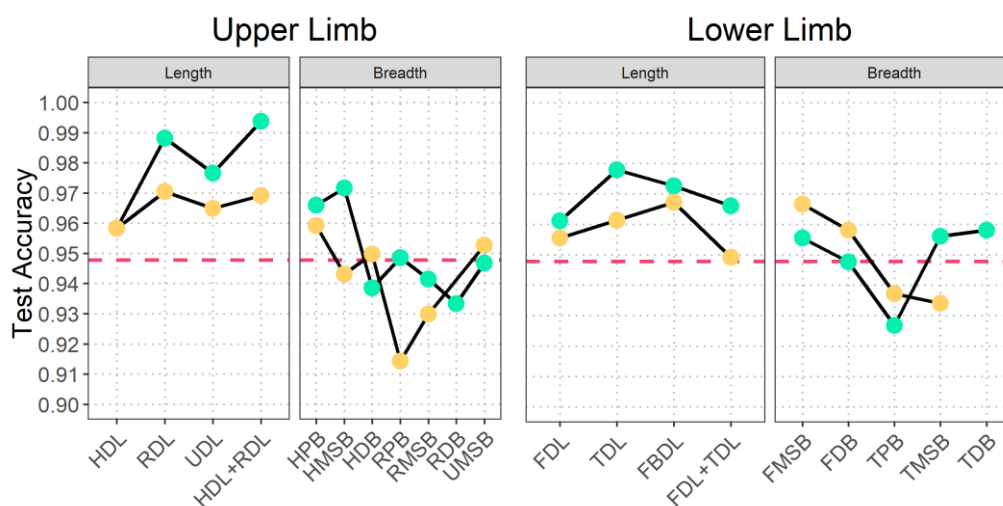
RMSB	$-13.28 + 12.08x$	94.15	13.69	13.78	12.33
HDB	$2.21 + 2.88x$	93.85	9.02	9.07	8.22
TPB	$\frac{197.62}{1 + 7.47e^{-0.0545x}}$	93.71	8.11	8.15	7.75
TMSB	$\frac{206.07}{1 + 10.13e^{-0.1696x}}$	93.41	9.52	9.57	8.09
RDB	$1.36 + 5.41x$	93.33	11.50	11.56	9.04
RMSB	$\frac{207.70}{1 + 13.94e^{-0.2730x}}$	92.98	12.86	12.94	11.93
TPB	$16.95 + 2.17x$	92.67	9.63	9.68	7.51
RPB	$\frac{195.94}{1 + 11.56e^{-0.2100x}}$	91.43	8.55	8.60	7.84
<sup>1</sup> Variables in the multiple linear regression: FDL + FBDL + HDL + RMSB + UMSB * Two nonlinear models had unsuccessful fits: TDB and RDB					

### Model Comparisons

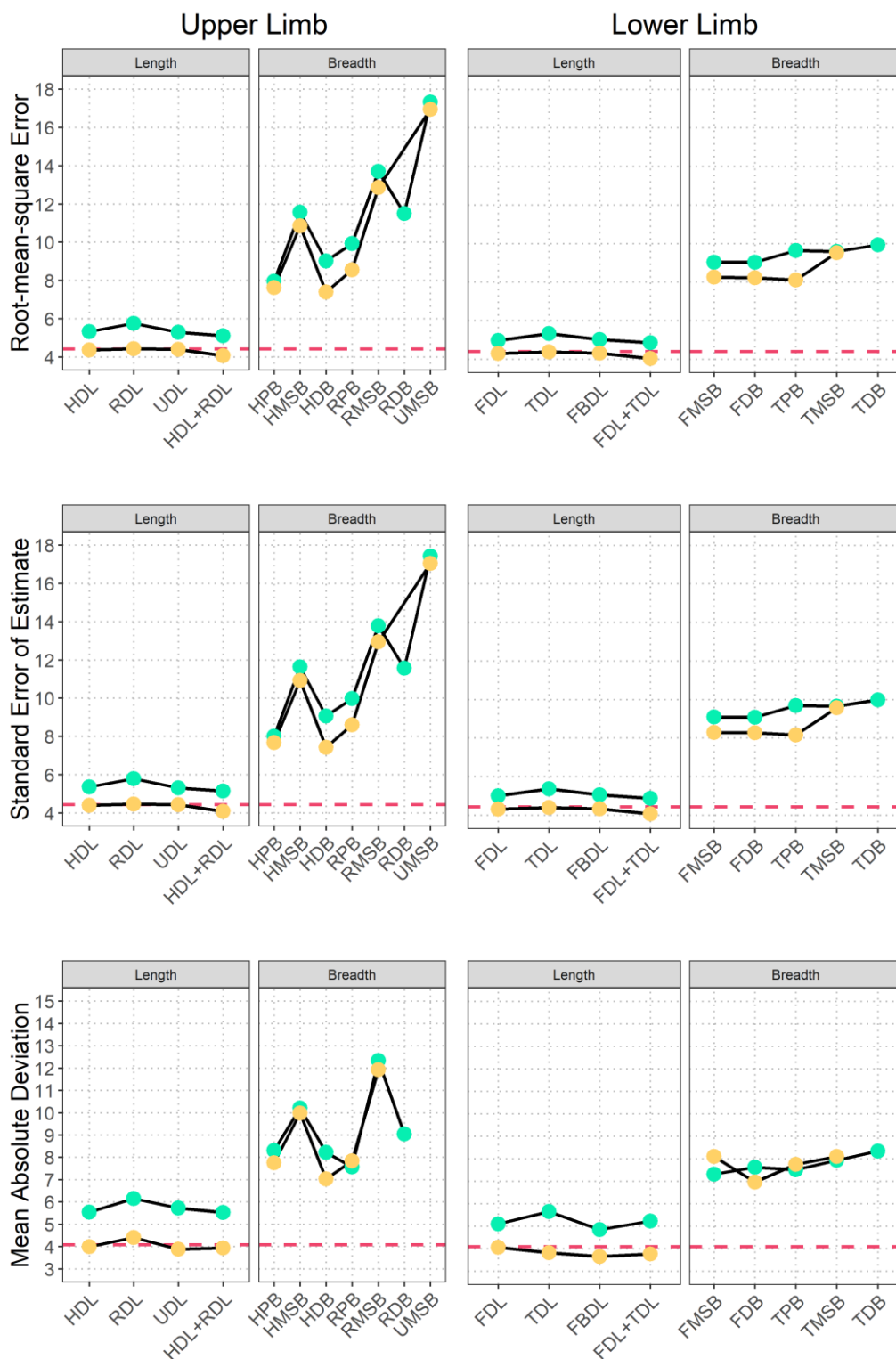
All model performance metrics were visualized to facilitate direct comparisons between linear and nonlinear models. Univariate linear and nonlinear models are more accurate than the multiple linear regression model (Figure 3.3). When considering precision, nonlinear length models are as precise, or more precise, than the multiple linear regression model (Figure 3.4). All precision metrics demonstrate all nonlinear breadth models are more precise than linear breadth models, except for RPB using MAD.

Residual plots with loess lines were generated using linear models (HDL+RDL, RDL, TDL, UDL, FBDL) and nonlinear models (RDL, HDL+RDL, FBDL, FMSB,

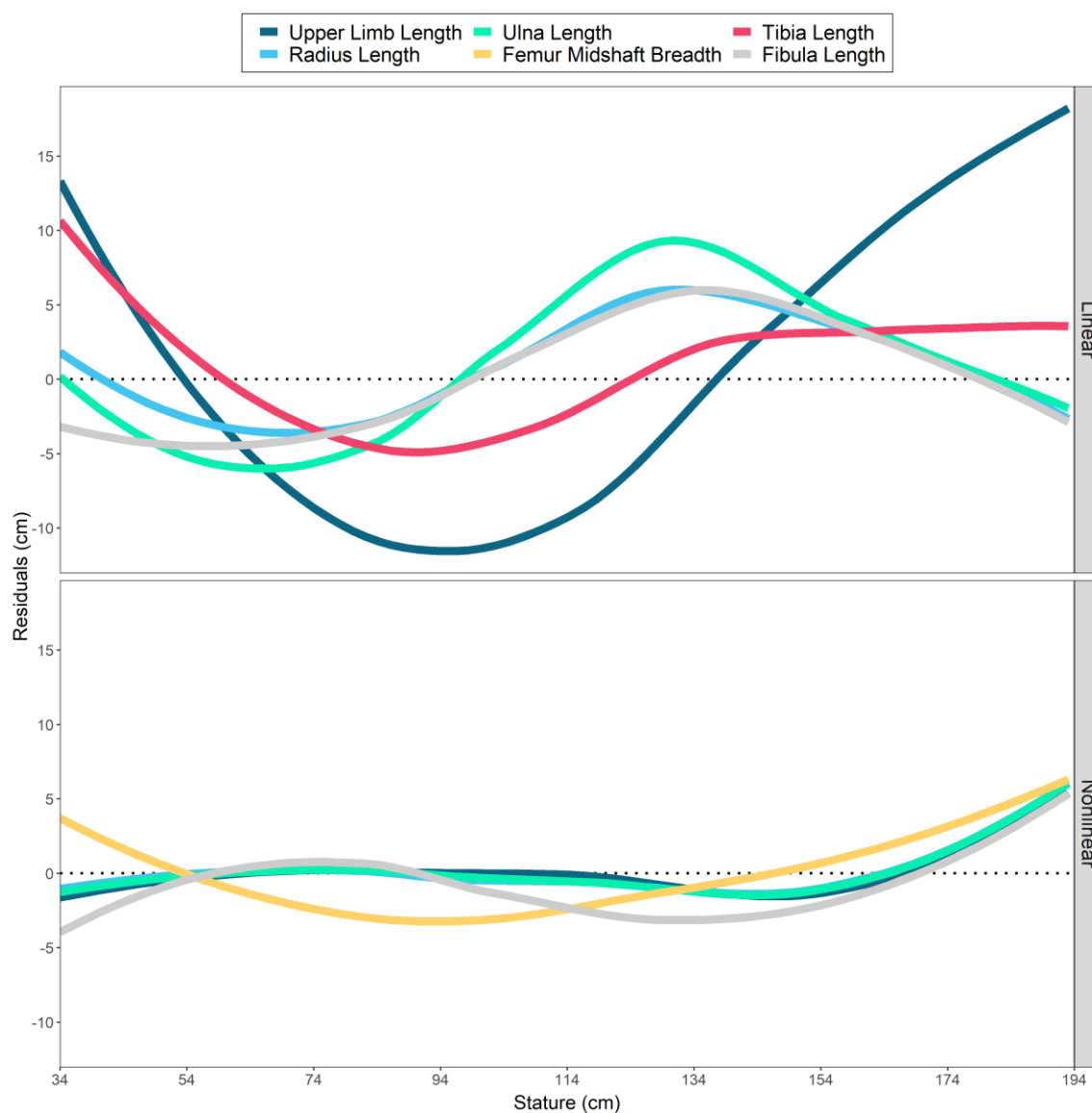
UDL) with the highest testing accuracy to support a discussion about accuracy and precision (Figure 3.5). Linear models present with greater error (deviance from  $y=0$ ), which is in line with the precision metric results (Table 3.6). In comparison, the five most accurate nonlinear models all have residual trends within 5cm of known stature. Of note, nonlinear length models of the upper limb all display near-identical residual trends. The nonlinear FMSB residual trend is distinct from the rest of the nonlinear residual trends, demonstrating the difference in relationship to stature information contained within length and breadth measurements. The clustering of residual trends by upper and lower limb are not as distinct in the linear models. Interestingly, radius (RDL), ulna (UDL), and fibula length (FBDL) models follow relatively similar residual trends, and the residuals of the upper limb length and tibia length models are more distinct.



**Figure 3.3** – Test accuracy for all univariate stature estimation models. Linear models are in green, nonlinear models are in yellow. The red dashed line represents the test accuracy for the multiple linear regression model.



**Figure 3.4** – Precision metrics for all univariate stature estimation models. Linear models are in green, nonlinear models are in yellow. The red dashed line represents the performance metrics for the multiple linear regression model.



**Figure 3.5** – Mean residuals of stature predictions (in cm) for the top five (5) most accurate linear (top) and nonlinear models (bottom).

## Discussion

Stature estimation of immature skeletal remains is one aspect of the biological profile that has been under-represented in the forensic anthropology literature (AAFS Standards Board, 2019; Langley, 2017). This study addresses some of the past limitations

of subadult stature estimation research by using a large sample of known demographic information, breadth measurements, and nonlinear modeling techniques. Thirty-nine linear and nonlinear stature estimation equations are immediately available for use (Table 3.6). More than half (24 out of 39) of the stature estimation equations presented here achieved test accuracy greater than 95%. Of those 24 models, nine models - seven nonlinear and two linear - have RMSE and SEE values under 5cm. Accuracy and precision are important factors for choosing an appropriate model for estimating aspects of the biological profile (*Daubert v. Merrel Dow Pharmaceuticals, Inc.*, 1993; Grivas & Komar, 2008; *Kumho Tire Company, Ltd. V. Carmichael*, 1999; Lesciotto, 2015).

<b>Table 3.7</b> – Ten recommended stature estimation models for lengths (n=5) and breadths (n=5) based on high testing accuracy (>95%) and precision (<10cm). Models are ordered from lowest to highest SEE.				
Variable	Model Type	Equation	SEE (cm)	Test Accuracy (%)
<i>Lengths</i>				
Humerus + Radius Length	Nonlinear	$324.73 - 318.54e^{-0.0013x}$	4.08	96.91
Femur Length	Nonlinear	$365.51 - 345.22e^{-0.0013x}$	4.32	95.56
Fibula Length	Nonlinear	$339.27 - 319.61e^{-0.0017x}$	4.33	96.72
Humerus Length	Nonlinear	$337. - 328.85e^{-0.0021x}$	4.39	95.83
Tibia Length	Nonlinear	$328.25 - 310.78e^{-0.0018x}$	4.40	96.13
<i>Breadths</i>				
Humerus Proximal Breadth	Nonlinear	$\frac{231.41}{1 + 9.01e^{-0.0758x}}$	7.67	95.92
Humerus Proximal Breadth	Linear	$-3.93 + 3.97x$	8.00	96.60

Femur Distal Breadth	Nonlinear	$\frac{217.13}{1 + 9.35e^{-0.0047x}}$	8.27	95.81
Femur Midshaft Breadth	Nonlinear	$\frac{208.76}{1 + 10.84e^{-0.0530x}}$	8.30	96.67
Femur Midshaft Breadth	Linear	$-3.28 + 6.84x$	9.08	95.56

Table 3.7 contains ten recommended equations, five models for lengths and five models for breadths, for estimating subadult stature based on high test accuracy (>95%) and high precision (SEE < 10cm). It is recommended that the stature estimate of only one method be used in forensic reports, as combining stature estimates is considered inappropriate (AAFS Standards Board, 2019). Each aspect of the research design has a different influence on the performance and applicability of stature estimation models presented in the current study and are discussed below.

### **Sample Variation and Model Precision**

Equations for estimating subadult stature from long bones presented in this study were trained and tested on one of the largest sources of contemporary subadult skeletal data currently available. Data are cross-sectional, demographically variable, and are obtained from deceased individuals from a medicolegal context (Stull & Corron, 2022). All other methods of subadult stature estimation for forensic use were trained on longitudinal data from the Denver Growth Study (McCammon, 1970; Robbins Schug et al., 2013; Ruff, 2007; Smith, 2007) or other longitudinal studies (Feldesman, 1992), within one exception from South Africa using magnetic resonance imaging scans from a living population (Brits et al., 2017) and another in France using whole-body dual-energy x-ray absorptiometry scans of living children (Abrahamyan et al., 2008). Cross-sectional

data are more representative of the variability of a population (Hauspie & Roelants, 2012; Stull et al., 2014), as longitudinal studies are often highly controlled for specific demographic variables (Eveleth & Tanner, 1990; Healy, 1986; McCammon, 1970).

SEE values from the current study are larger than any of the reported SEE for other subadult stature estimation methods (Table 3.8). This finding is not surprising, as the data used to train and test the present models have far greater demographic variation and larger sample sizes compared to any other study sample (Garamszegi & Møller, 2010). Restricting the amount of variation in a longitudinal sample inherently makes any inferences from that data extremely specialized to the population under study. Methods created using longitudinal data, such as stature estimation equations, are therefore *over-fit* to the homogenous data and generally perform poorly when tested on demographically distinct groups (Cardoso, 2009; Garvin & Pulsipher, 2022; Smith, 2007).

<b>Table 3.8</b> – Standard error of estimate (SEE) values reported for the current study compared to other common subadult stature estimation methods using pooled sex. All values are in centimeters.					
	<b>Current Study</b>		<b>Smith (2007)</b>	<b>Ruff (2007)</b>	<b>Brits et al. (2017)</b>
Sample size	990		67	20	59
Age range (years)	Birth to 20		3 to 10	1 to 17	10 to 17
	<i>Linear</i>	<i>Nonlinear</i>			
Humerus	5.00	4.39	3.00	1.80 – 2.90	-
Radius	5.78	4.46	3.16	1.90 – 3.70	-
Ulna	5.31	4.42	2.91	-	-
HDL+RDL	5.13	4.08	-	1.70 – 3.90	-
Femur	5.00	4.32	2.46	1.70 – 3.40	3.30 – 3.69
Tibia	5.36	4.40	2.24	1.50 – 3.80	3.54 – 3.77
Fibula	5.05	4.33	2.24	-	-
FDL+TDL	4.88	4.06	1.97	1.60 – 3.20	3.16 – 3.23

Linear models from the present study had less precision compared to nonlinear models (Table 3.6 and Figure 3.4), but higher testing accuracy – especially when using length variables (Figure 3.3). Findings highlight the ongoing conversation about the importance of accuracy versus precision in biological profile estimation methods for forensic application, particularly in subadult age estimation (Corron et al., 2019; Schmeling, Geserick, Reisinger, & Olze, 2007; Stull & Armelli, 2021; Stull et al., 2022, 2014). Figure 3.5 demonstrates how linear models that have high accuracy can still produce stature estimates that are biased as much as 10 – 15cm. In comparison, nonlinear models with high accuracy produced less biased estimates, within 5cm; the differential performance could be potentially linked to the flexibility of nonlinear models that can detect - and account for - nuanced changes in the relationship between long bone measurements and stature (Figure 3.2).

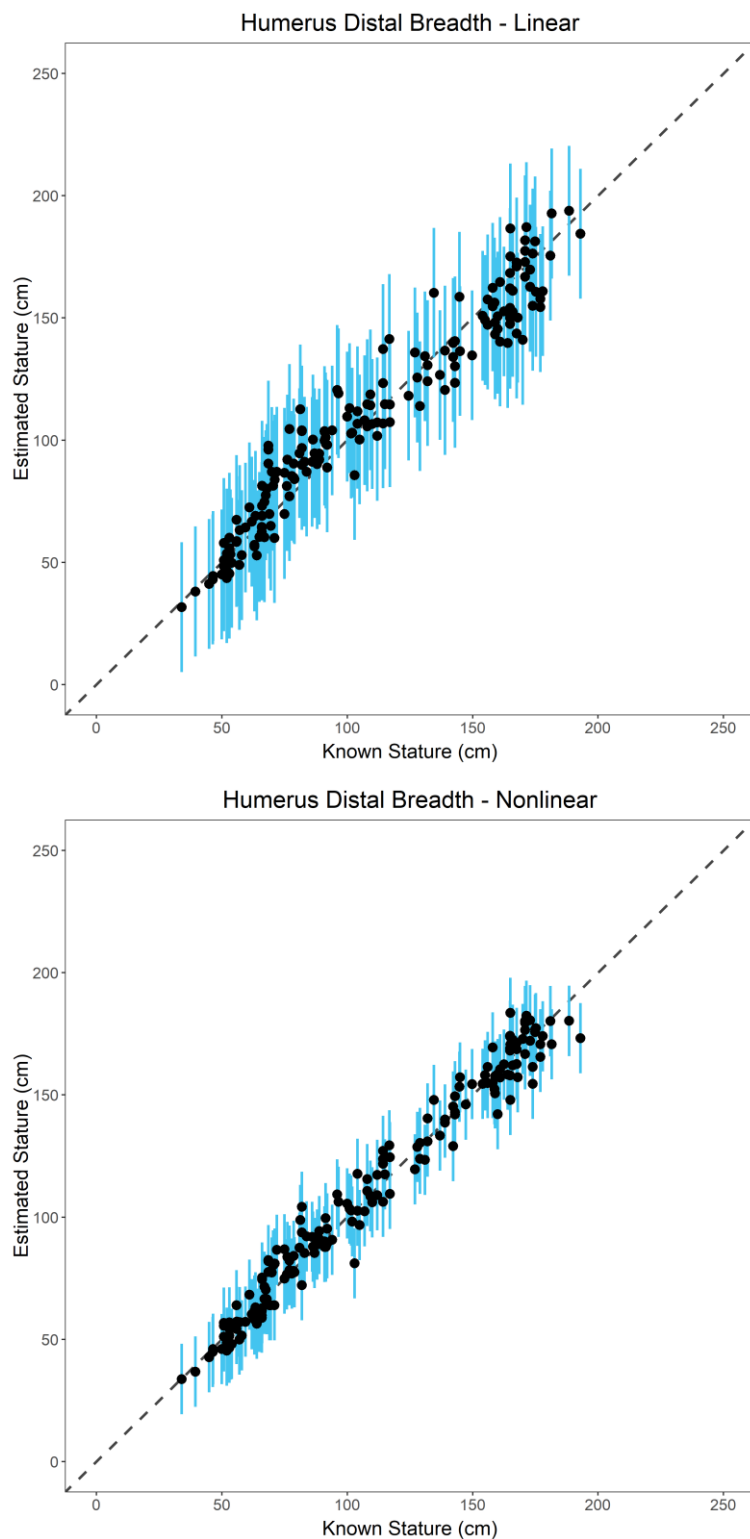
### **Model Considerations: Breadths and Nonlinear Modeling**

Recommended models for immediate use (Table 3.7) include both linear and nonlinear length and breadth models. The selected models do not have the greatest precision, nor the highest test accuracy, but represent a balance between the two types of performance metrics. Models using breadth measurements were included to maximize applicability and prevent the estimation of diaphyseal lengths from fragmentary remains (Hoppa & Gruspier, 1996), which could potentially compound error for the stature estimate (Chu et al., 2022). Of the 25 breadth models generated, 11 achieved testing accuracy greater than 95%. While some breadth models retained high precision in addition to high accuracy (Table 3.6), all models had RMSE and SEE values 3-4cm larger than length models. Breadth measurements maintain strong correlations with

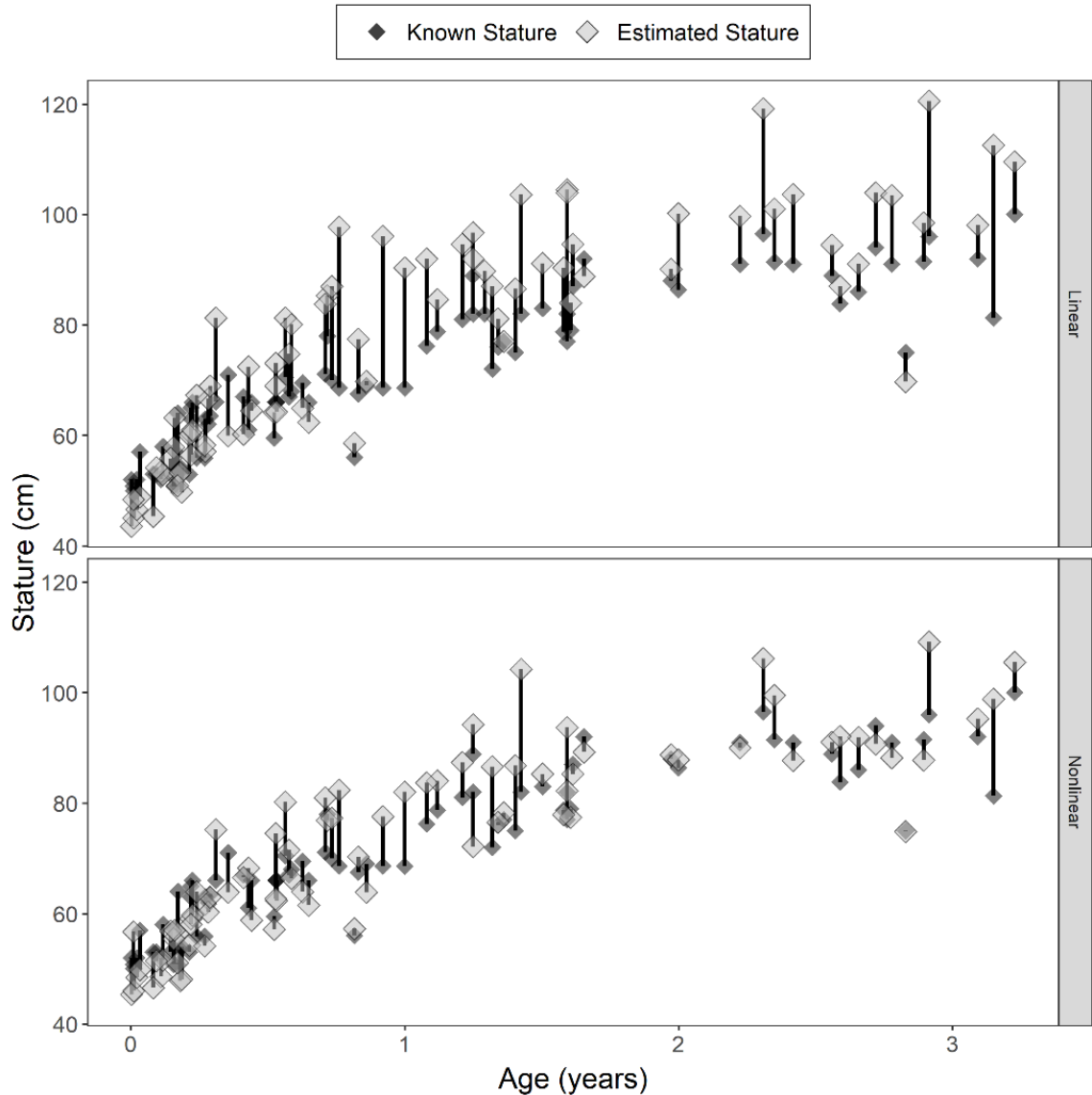


stature (Table 3.5), although weaker than the relationship between lengths and stature. The smallest measurements (midshaft breadths) were consistently less precise (Table 3.6), as was previously described for univariate age estimation models (Stull et al., 2014).

In addition to linear models, which are in line with previous subadult stature estimation methods (Brits et al., 2017; Robbins Schug et al., 2013; Ruff, 2007; Smith, 2007), two nonlinear were also used to generate stature estimation equations. The sigmoidal relationship between breadths and stature (Figure 3.2) was better appreciated using the 3-parameter logistic regression equation than using a linear equation, as is demonstrated through greater precision of the nonlinear models compared to linear model counterparts (Table 3.6). Figure 3.6 is a clear example of how the high variability of breadth measurements is better captured by the logistic model compared to the linear model, resulting in much narrower 95% PIs for the same test individuals. Note that there is also less bias in the estimated stature using the nonlinear models for when known stature is between 50-100cm, which covers the first three years after birth (Figure 3.7). This first life history stage is known for rapid growth in size prior to a deceleration in growth velocity during childhood through adolescence (Bogin, 2005; Cameron & Bogin, 2012).



**Figure 3.6** – Point and 95% prediction intervals (PI) for humerus distal breadth using the linear (top) and nonlinear (bottom) models to estimate stature.



**Figure 3.7** – Residuals of known stature (black diamonds) to estimated stature (grey diamonds) for individuals whose stature ranged from 50-100cm.

Nonlinear length models were more precise than linear length models, but not more accurate (Table 3.6). This may be because of the flexibility of nonlinear models quantifying the changes in growth velocity captured through fluctuating variability and differences in shape of ontogenetic trajectories depending on age ranges, as demonstrated in Figure 3.6 and in Chapter 2 (see Figure 2.9). Because the relationship between length

and stature is so strong (Table 3.2) and has relatively low variation (Figure 3.2), the nonlinear models may have overfit the data and resulted in 95% PIs that were too precise and therefore performed poorly on the test sample (Figure 3.6). The strong correlation (*i.e.*, linear relationship) between length measurements and stature, and the marginal difference in precision between linear and nonlinear length models, suggests that perhaps linear models are more appropriate for estimating stature when using long bone lengths. In this case, larger 95% PIs does a better job of capturing atypical relationships between long bone measurements and stature, and accounts for greater variability based on other intrinsic and extrinsic factors that may affect stature, such as sex or socioeconomic status (Bogin & Loucky, 1997; Bogin & Rios, 2003; Brits et al., 2017; Cameron, 2007).

The models generated in this study have an added benefit of not requiring age estimation prior to stature estimation. All prior subadult stature estimation models required either explicit knowledge (Ruff, 2007) or general knowledge of age for use (Abrahamyan et al., 2008; Brits et al., 2017; Robbins Schug et al., 2013; Smith, 2007). Long bone lengths are strongly correlated with age, enough so for use in subadult age estimation (Cardoso, Abrantes, & Humphrey, 2014; Facchini & Veschi, 2004; López-Costas, Rissech, Tranco, & Turbón, 2012; Primeau, Friis, Sejrsen, & Lynnerup, 2016; Rissech, Schaefer, & Malgosa, 2008; Scheuer, Musgrave, & Evans, 1980; Stull et al., 2022, 2014). Long bone lengths are also strongly correlated with stature, which is also what makes them appropriate to estimate stature (Abrahamyan et al., 2008; Brits et al., 2017; Feldesman, 1992; Robbins Schug et al., 2013; Ruff, 2007; Smith, 2007). Finally, stature is strongly correlated with age ( $r=0.958$  for the present sample) and is often used to assess typical growth in growth standards (Cameron, 1986; de Onis et al., 2012;

Duggan, 2010; Schillaci, Sachdev, & Bhargava, 2012). While subadult age estimation is one of the most studied aspects of the biological profile (e.g., Cardoso, Abrantes, & Humphrey, 2014; Corron et al., 2019; Langley, 2016; López-Costas, Rissech, Tranco, & Turbón, 2012; Lottering et al., 2017; Rissech, Márquez-Grant, & Turbón, 2013), it may still introduce additional sources of error or bias to the stature estimate, especially for individuals who fall on the ends of the age range. With strong relationships among age, long bone lengths, and stature, the estimation of age should not be necessary prior to stature estimation.

## **Conclusion**

Subadult stature estimation has been hindered by small sample sizes, limited use of long bone measurements, and linear modeling. The present study aimed to address several of these challenges by 1) using a large, contemporary, cross-sectional sample of subadult skeletal remains, 2) generating regression models using both lengths and breadths, and 3) utilizing both linear and nonlinear regression models to accommodate the nonlinear shape of long bone growth. The resulting models encapsulate the ontogenetic variation between skeletal measurements and stature and provide more options for subadult stature estimation that does not rely on the recovery of complete long bones or estimating age prior to stature estimation. These modifications better align with the underlying structure of the relationship between long bone measurements and stature, resulting in valid models with less error resulting from poor modeling assumptions.

Two types of long bone measurements were combined for the present stature estimation equations: diaphyseal and maximum (Langley et al., 2016; Stull & Corron,

2021). Both diaphyseal and maximum lengths have been used to estimate subadult stature, either using only diaphyseal measurements (Robbins Schug et al., 2013; Smith, 2007) or providing separate models for each measurement type (Brits et al., 2017; Ruff, 2007). There has been recent research suggesting that the two types of long bone measurements, specifically lengths, may be combined for analyses when standardized for size (see *Chapter 2: Expanding long bone ontogeny in biological anthropology*). No such tests were conducted for this study, although there does not appear to be measurement-specific bias in the precision or accuracy of the present models. The advantage of being able to pool these measurements is that practitioners with an unknown individual presenting with early stages of active fusion, where diaphyseal or maximum measurements can be taken, do not need to choose between two stature estimation models.

All 35 linear and nonlinear models generated in this study achieve test accuracy greater than 90%, with 24 out of 39 models achieving test accuracies above 95%. Models that follow a delicate balance of accuracy and precision should be used for forensic application (*Daubert v. Merrel Dow Pharmaceuticals, Inc.*, 1993; *Kumho Tire Company, Ltd. V. Carmichael*, 1999; Grivas & Komar, 2008; Lesciotto, 2015), and provided model recommendations include a mixture of linear and nonlinear models featuring lengths and breadth measurements. Length models should be prioritized over breadth models, although breadth models may be used in cases of fragmentary remains, when required, with high accuracy and decent precision. While the equations provided are immediately available for use, calculating 95% PIs adds complexity. Therefore, a graphical user interface, containing all 39 linear and nonlinear models, is in development to provide

point and 95% PIs for future forensic casework. The study is the first to use nonlinear models to estimate stature using immature skeletal remains. The large, diverse reference sample, integration of breadth measurements, and nonlinear modeling expands the applicability and appropriateness of subadult stature estimation in forensic anthropology. Implications for this study include future research to expand reference samples for global and population-specific methods and to generate subadult stature estimation methods for bioarchaeological remains.

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## Conclusion

Subadults and adults are treated as discrete groups in biological anthropology. In long bone research, the cutoff is typically based on the active fusion of the epiphyses, which initializes a change in definition from diaphyseal measurements to maximum measurements. The assumption that diaphyseal and maximum measurements cannot be combined into a single analysis inherently truncates subadult and adult samples and affects modeling options and interpretations. Furthermore, by sequestering appendicular ontogeny studies to only diaphyseal measurements, biological anthropologists draw conclusions on growth, development, and diversity based on a small subset of all available long bone data.

Subadult skeletal reference samples are already limited in availability. By incorporating exclusion criteria such as active epiphyseal fusion, the number of individuals in a study is further reduced. Instead, by combining diaphyseal and maximum long bone measurement definitions and utilizing new sources of subadult skeletal information – through a large CT database of subadults with known demographic information – we can begin to appreciate the continuum of all growth and variation through the stabilization of long bone ontogeny. This suite of (non)dissertation manuscripts is the first to explore appendicular ontogeny through three distinct perspectives: relative, index, and absolute.

**Specific Aim #1:** Relative diaphyseal and maximum long bone measurements can be combined into a single analysis. The combination exposed the stabilization of adult long bone length variation occurring much later than common definitions for adult

skeletons. Research using long bone measurements may consider adjusting the concept of what constitutes “adult” and “subadult” classifications – or remove such arbitrary designations altogether.

**Specific Aim #2:** The ontogenetic trajectory of the brachial and crural index does fluctuate until final adult ratios are stabilized between 15 and 20 years. In comparison to previous studies based on bioarchaeological samples, the shape of fluctuations of the brachial and crural index in a contemporary U.S. sample are different. Adult indices of the contemporary U.S. sample were also unexpectedly low for the brachial index and high for the crural index compared to comparative bioarchaeology samples, while the indices of the contemporary sample at other age categories were not as distinct. Findings from this study suggest that the stabilization of adult brachial and crural index may be different in contemporary populations compared to bioarchaeological samples and further inquiry into the sources of these differences should be pursued.

**Specific Aim #3:** The relationships between long bone length and stature in previous studies may be invalid or unreliable because of violating modeling assumptions for linear regression or have a narrow applicability because of sample composition, sample size, or specific age ranges. Stature estimation for subadult skeletal remains may find greater applicability and generalizability by using large, cross-sectional reference data, nonlinear models, and breadth measurements. Models that do not require other aspects of the biological profile (sex, age) were provided for immediate use in forensic anthropology.

Collectively, these three different investigations into appendicular ontogeny and variation have demonstrated how large sample sizes and alternative modeling approaches reveal different aspects of the relationship that subadult long bones hold with age, ecogeography, and stature. In doing so, future research can explore the consistency of patterned variation identified in the large U.S. sample used here. This research is a call for more contemporary subadult samples, a re-evaluation of bioarchaeological subadult samples, and more creative approaches to exploring appendicular ontogeny and variation in biological anthropology.