THE INFLUENCE OF BODY MASS AND BODY COMPOSITION ON BONE FUNCTIONAL ADAPTATION

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by

ROB’YN JOHNSTON

Committee Members

Dr. Libby Cowgill, Advisor
Dr. Todd Vanpool
Dr. Gregory Blomquist
Dr. Kevin Middleton

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The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled:

THE INFLUENCE OF BODY MASS AND BODY COMPOSITION ON BONE FUNCTIONAL ADAPTATION

presented by Rob'yn Johnston

a candidate for the degree of doctor of philosophy,

and hereby certify that, in their opinion, it is worthy of acceptance.

Dr. Libby Cowgill

Dr. Todd Vanpool

Dr. Gregory Blomquist

Dr. Kevin Middleton

DEDICATION

It takes a village to raise a dissertation, and to this village I am eternally grateful. To the members of the Cowgill Lab, Stephanie Child, Colleen Young, and Elizabeth Cho; and other graduate students in the Anthropology and PAS Departments, and particularly Kate Trusler and Aaron Johnson. To my best friend and constant supporter, Rachel Garrett, who has provided hours of laughter and a shoulder to cry on. Every one of you has added to one of the best experiences of my career, and I am grateful to have known each of you and to continue to follow your accomplishments.

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ABSTRACT

The proposed dissertation follows a three article format. The articles are distinct, but each pertains to the same subject of research. The first article applies structural equation modeling to factors influencing bone functional morphology in modern humans. The second article continues to analyze the role of the two primary drivers of bone functional morphology in humans, body mass and lean mass, in a cadaveric sample. The third article applies bone functional morphology to a novel field of analysis, that of deer body mass estimation in zooarchaeology. All three pieces focus on the role of body mass, body mass estimation, and the role they play in bone functional adaptation.

CHAPTER 1

INTRODUCTION

This dissertation is focused on the influence of body mass on bone functional morphology in a variety of modern contexts, each with its own unique sample to better address the specific question under analysis. Its aim is to contribute to debates over the role of body mass versus that of lean mass on the cross-sectional geometry of the limbs. Furthermore, it extends the use of cross-sectional geometry to a new faunal analysis application in the archaeological record.

The first paper in this dissertation (chapter 2) uses structural equation modeling in a sample of 10,624 individuals (4,839 female, 5,785 male), 20-90 years old ($\bar{x}$ = 47.6) in order to evaluate potentially causal factors in the relationship between body mass and bone strength. The original data was drawn from the Third National Health and Nutrition Examination Survey (NHANES III), which collected dual x-ray absorptiometry scans (DXA), and therefore had available data on femoral subtrochantic cross-sectional geometry. We predicted that 1) body mass will be the primary determinant of bone cross-sectional geometry in the proximal femur, despite the modulating effects of body composition and exercise and 2) increased exercise frequency will produce greater cross-sectional geometric properties, either directly or via increased muscle mass. Structural equation modeling proved a valuable tool for undertaking this analysis, and results indicated that both body mass and lean muscle amount had a combined effect on cross-sectional properties, and that exercise did not confer a large direct effect on bone bending strength, but indirectly modified body mass and lean mass.

The second paper in this series (chapter 3) explores the relationship between mass and bone strength by evaluating cross-sectional properties in the upper and lower limb of human cadavers (n=45). We initially hypothesized that total body mass would explain more variation in the femur than the humerus, while lean mass would better explain the variation of the upper limb. Despite not being a weight-bearing bone, the humerus had a stronger relationship with body mass than the femur. Additionally, BMI had a strong relationship with all four locations analyzed for each bone, likely because of the relationship between torsional strength and beam length.

The final manuscript of my dissertation work (chapter 4) changes focus slightly and applies the patterns observed in humans to a non-human species, white-tailed deer (*Odocoileus virginianus*). For this project, the metapodia of 64 *O. virginianus* were obtained from a meat processing plant during the first weekends of the Missouri gun hunting season. Cross-sectional geometry has been used to estimate the body mass of humans, and this analysis produced similar equations to estimate the body mass of *O. virginianus* using the metapodial. Cortical area was the best predictor of body mass in deer, and estimations of body mass were comparable to previous research on deer body mass estimates. This research was previously published in the Journal of Archaeological Science: Reports, Volume 37, June 2021.

CHAPTER 2

THE PATH LESS TRAVELED: USING STRUCTURAL EQUATION MODELING TO INVESTIGATE FACTORS INFLUENCING BONE FUNCTIONAL MORPHOLOGY

Rob'yn A. Johnston, Libby W. Cowgill

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Introduction: The Many Influences on Bone Bending Strength

Over fifty years of experimental research using both humans and animal models have clearly demonstrated that bone responds to its mechanical environment, and that elevated physical activity leads to increased bone size, strength, and mineral content (Carter & Beaupre, 2001; Duncan & Turner, 1995; Frost 1987; Frost 2003; Robling, Burr, & Turner, 2000; Robling, Hinant, Burr, & Turner, 2002; Rubin & Lanyon, 1982; Ruff, 2000; Ruff, Holt, & Trinkaus, 2006; Turner, 1998; Umemura et al., 1997). In addition to physical activity, body mass appears to be a major determinant of bone mass. Body mass is the base load that the skeleton experiences during life (Moro et al. 1996; Ruff 2002; van der Meulen et al. 1996), and therefore has been suggested to be the primary predictor of bone strength and cross-sectional properties (Moro et al. 1996). During adolescent bone acquisition, body mass explains up to 88% of the variation in bone strength, more than any other factor (Ruff 2003a; Ruff 2003b; van der Meulen et al. 1996). Measurements of bone strength, particularly cortical area, correlate positively with body mass across all ages, even in experimental models that modify body mass through calorie restriction (Stein et al. 1998, Ionova-Martin et al. 2010). Both humans and animals who suddenly do not have to support their body mass tend to lose bone mass even if, as in the case of astronauts, they are actively using their muscles (Jaworski et al., 1980, Leblanc et al. 1990, Frost 1996).

Extremely low or high human body mass results in deviations from typical patterns of bone strength and density. Studies of young women with low body mass resulting from anorexia nervosa have generally noted low bone mineral density, often resulting in osteoporosis or osteopenia (Carmo et al., 2007; DiVasta et al., 2007; Hotta, Shibasaki, Sato, & Demura, 1998; Miller et al., 2006; Turner et al., 2001; Zipfel, Specht, & Herzog, 1998). In many cases, it appears that this reduction in bone quality and mass is caused not by inadequate nutrition, but by low body mass itself, as similar patterns of reduced bone mineral density are seen in thin women without eating disorders (Galusca et al., 2008). This is further observed in over-trained endurance runners, who tend to suffer from low bone mineral density with lowered body mass despite high activity (Pollock et al., 2010). This suggests that low body mass may result in insufficient mechanical stimulation to maintain healthy levels of bone mass.

In contrast, the literature on obesity, bone shape, and bone strength has yielded mixed and inconclusive results. Obesity has traditionally been seen as protective against bone loss in older adults (Mazess et al 1987, Reid et al. 1992, Felson et al 1993, Marcus et al 1994, Ravn et al 1999, Reid 2002, Zhao et al 2007, Migliaccio et al 2011). However, newer research has found that obese individuals have relatively weaker bone when the effects of high overall body mass are taken into account, though whether this is attributed to low amounts lean muscle mass, increased sedentism, or hormonal effects varies (Petit et al. 2005; Zhao et al 2007, Shultz et al. 2009; El Hage et al. 2013; Sornay-Rendu et al. 2013, Andersen et al. 2014, Ealey et al. 2017). For example, obese girls have a higher incidence of forearm fracture, but it is unclear if this is caused by their obesity or is related to the excess weight exposing an underlying lifelong skeletal strength deficiency (Skaggs et al. 2001). In contrast, some research has suggested that obesity does not lead to bone shape or strength changes at all and bending strength stays consistent even during weight loss (Uusi-Rasi et al. 2010; Agostini and Ross 2011; Mak et al 2019). Rarely, obesity is suggested to lead to increased bone strength and bone mineral density, which many believe it is a consequence of increased total mechanical load (Ma et al. 2011; El Hage et al. 2013, Vandewalle et al 2013, Reeves 2014). However, bone strength and mineral density may be a misleading measure; bone may increase in quantity but suffer from poor organization and lower bone quality, meaning the maximum fracture load remains unaffected (Ionova-Martin et al. 2010). Finally, it is unclear if certain cross-sectional parameters such as subperiosteal breadth and cortical area are adapted only to current body mass, or whether lifetime peak body mass may still influence parameters in any way.

Part of the difficulty in untangling the relationship between obesity and bone strength is that a variety of factors may be influencing bone bending strength in obese individuals. It remains unclear, for example, whether total mass or lean muscle mass is the primary driver of bone functional adaptation. On one hand, bone mass must be sufficient to support total organismal mass, and some research has detected relationships between cross-sectional areas and fat mass or total body mass that exist above and beyond larger muscular area (Kanehisa et al. 1998). In contrast, more recent attempts to estimate body composition from skeletal shape have found that lean mass is the primary force shaping cross sectional properties and that the use or addition of fat mass as a factor fails to improve explanatory models (Colletti et al. 1989, Petit et al., 2005, Pomeroy et al. 2018). Finally, muscle mass can impact cross sectional properties by changing the distribution of cortical area to combat higher levels of strain in specific directions (Hamrick et al. 2000; Schönau 1997).

Furthermore, there are suggestions that increases in body mass may change the way obese individuals move, and extensive animal and human evidence suggests that manner of loading (in addition to level of loading) can influence bone shape (Blob and Biewener 1999, 2000; Griffen and Kram 2000; Carlson 2005; Carlson and Judex 2007, Cowgill et al. 2010). Changes in the bone diaphyseal shape and strength in obese individuals may be due to these gait differences caused by increased body mass. Biomechanical analyses have noted that obese individuals alter their standing and sitting patterns to minimize load on the back and reduce hip torque, including widening the distance between the feet, shortening stride length, spending more time in the stance phase of walking, and increasing hip abduction angles and external rotation with increased foot eversion (Agostini and Ross 2011, Lai et al. 2008, Hills and Parker 1992). Some research has also noted lower levels ground reaction forces and shorter anteroposterior propulsive forces, whereas others found increased forces through the hip, knee, and ankle (Lai et al., 2008; Shultz et al., 2009). It is unclear if these differences are a function of walking at a speed for research purposes that is not self-selected, if it is a consequence of lower physical activity, or if it is a compensation for increased instability during gait (Hills and Parker 1992). These postural and locomotor changes may contribute to a variety of purported results ranging from decreased general bone strength (Petit et al. 2005) to increased diaphyseal mediolateral dimensions, even after controlling for physical activity, hormones, nutritional levels, and age (Agostini and Ross, 2011; Petit et al. 2005).

Lastly, a further complicating factor is potential interactions between body weight and activity. It is well documented that activity levels influence bone strength and quality in humans (Carter and Hinton 2013, Bridges et al. 2000, Frost 2004, Hamrick et al. 2006, Marchi and Shaw 2011, Ruff 1987, Ruff 1994, Ruff et al. 1984, Ruff et al. 2006, Ryan and Shaw 2015, Shaw and Stock 2009, Shaw and Stock 2013, Stock 2006, Trinkaus et al 1994, Trinkaus and Ruff 2012). However, it is unclear how that specifically interacts with obesity and elevated body mass. On one hand, obesity is often accompanied by lower overall levels of physical activity, which presumably results in lower bone mass due to lack of mechanical stimulation (Chau et al 2012, Chirchir et al 2016, Choi et al. 2010, Frost 2004, El Khoury et al. 2017, Roemling and Quin 2012). In contrast, it seems possible that obese individuals who are active may actually have elevated bone strength due to the high base load their skeleton experiences due to excess body weight (Agostini and Ross 2011, Beck et al. 2009, Ortinau et al 2017, Ruff et al 1991, Tsukahara et al. 1999). Studies comparing the activity levels of obese individuals have suggested that active obese individuals have larger cross-sectional properties and greater bone density than those of sedentary, equally obese individuals (El Khoury et al. 2017, Gutin 2008). In addition, it may be possible to distinguish between active obese individuals and inactive ones by the rugosity of their muscle attachments (Godde and Taylor 2013). Further complications arise in studies that increase physical activity as part of obesity treatment, as this often increases lean mass amount and decreases body fat as a side effect of changing activity levels (Gutin 2008, Gutin et al. 1999).

Given that the causes of variation in bone size and strength is complex and multifactorial, statistical methods designed for disentangling causal relationships between multiple factors are necessary. Structural equation modeling (SEM), an analytical tool used commonly in ecology among other fields, is well-designed to handle the complex relationship between these factors. Structural equation modeling tests how well a multivariate set of non-experimental data fits a predefined set of relationships. It acts similarly to sequential multiple regressions, but with the ability to test the expected relationships derived from theoretical models and can be created to assume causality between variables in the model. SEMs also are well-suited to data where multicollinearity and latent factors are a concern. Therefore, we suggest that SEMs are a useful tool to disentangle the factors connecting body mass, body composition, activity, and cross-sectional geometry of the femur, shedding light on the primary influences on bone strength in both the present and the past.

This analysis uses a complex set of factors, including sex, total body mass, lean body mass, exercise frequency, peak body mass, and age to explore their combined and individual effects on bone strength. We test two hypotheses: first, total body mass will be the primary determinant of bone cross-sectional geometry in the proximal femur, despite the modulating effects of body composition and exercise; second, increased exercise frequency will produce greater cross-sectional geometric properties, either through direct mechanical stimulation or by increasing muscle mass.

Materials and Methods

Sample

The sample used here is a subset of the data obtained as part of the Third National Health and Nutrition Examination Survey (NHANES III) (CDC, 1994). NHANES III was conducted 1988 to 1994 as a multistage, stratified survey with the goal of assessing the health and nutritional status of the population of the United States. The NHANES III study examines a broad range of descriptive health and nutrition statistics across a cross-section of sex, race, ethnic, and age categories. A subsample of the study was also given dual x-ray absorptiometry scans (DXA), the gold standard for assessing bone density measurements at the hip. Criteria for selection for the original study were that participants be at least 20 years of age, of either sex, not currently pregnant, and have at least one hip that had never been previously fractured (CDC, 1994). Beck and colleagues (2006) later processed these DXA scans using the Hip Structure Analysis program (Martin & Burr, 1984) resulting in 13,615 individuals with available cross-sectional geometry of the femoral subtrochanteric region.

The current analysis was restricted to 10,624 individuals (4839 female, 5785 male), 20-90 years old ($\bar{x}$ = 47.6 [IQR=31-64]) from the original NHANES study pool. These individuals were drawn from the initial hip structure analysis study based on the completeness of their scans and other variables, detailed below. Age and sex were self-reported to the interviewer during the screening phase of the project, before the more detailed biometric and laboratory data were taken. In addition to age and sex, the specific variables included from the NHANES III dataset used in this analysis were current body mass, lifetime peak body mass, upper leg length as a proxy for height and beam length, and skinfold measurements (triceps, subscapular, suprailiac, thigh), and frequency of different forms of exercise. Cross-sectional geometric properties were derived from the initial hip structure analysis study and included cross-sectional area (CSA) and polar second moment of area (J).

Body mass was recorded using an electronic load-cell scale by the survey-taker at Mobile Examination Centers, temporary medical centers for specialized equipment that are moved to centralized locations for NHANES data collection. Mass was recorded in kilograms to two decimal places, with subjects wearing only underwear and paper sanitary gowns. 159 individuals were underweight (BMI <18), 1475 individuals were normal to overweight (BMI 18-29), and 8991 individuals were obese (BMI > 30). Individuals also self-reported their highest lifetime recorded weight and their weight ten years ago.

Survey-takers asked individuals to self-report their frequency of certain types of exercise. Individuals reported the number of times they had participated in a variety of physical activities (e.g., walking a mile without stopping, jogging, running, weightlifting, swimming, dancing, other) in the 30 days prior to the interview phase of the survey. These frequency measurements (NHANES Adult Questionnaire Section T, HAT1S-HAT26S) were summed to create a total exercise score for each individual that captured their overall estimated activity frequency in the past 30 days. While duration of each activity was not recorded in NHANES III, frequency of activity may still be a useful exercise measurement as short, frequent bouts of bending stimulate bone deposition equally or better than less frequent but prolonged bouts of bending (Robling et al 2000, Robling et al. 2002).

All individuals included in this project were also required to have valid anthropomorphic measurements for upper leg length, mass, and skinfold measurements (triceps, subscapular, suprailiac, thigh) to calculate lean mass amount via body fat percentage. Upper leg length was measured with the subject seated and knee bent; the distance was measured between the proximal border of the patella and the inguinal crease below the anterior superior iliac spine, following the center of the thigh. Measurements were recorded three seconds after the calipers were applied to the skin and the hand released. Skinfold thickness was recorded to the nearest tenth of a millimeter. Thigh skinfold was taken on the right thigh at the calculated thigh midpoint, with no weight on the measured leg. The triceps skinfold was taken on the right upper arm, at the calculated midpoint. The subscapular midpoint was taken on the right inferior angle of the scapula. The suprailiac skinfold was taken with the subject standing and the calipers anterior to the right superior iliac crest. These were used to calculate body fat percentage following the Siri (Siri, 1961) and Sloan (Sloan, Burt, & Blyth, 1962; Sloan, 1967) equations, which use skinfold measurements to calculate body density, and then to calculate body fat percentage. Body fat percentage was multiplied by the participant’s weight and then subtracted by the total to calculate the amount of combined lean mass and organ mass. Summary statistics are included in Table 1.

Table 1: Participant Summary Statistics.

	Parameter	$\bar{x}$ (σ)	Range
Females (n=4839)	Age (yr)	47.7 (19.16)	20.0-90.0 (IQR = 31-64)
	Mass (kg)	65.3 (12.26)	31.9-138.3
	Lean Mass (%)	74.5 (5.91)	56.3-87.6
	Total Exercise Amount (instances)	17.2 (23.18)	0-334
	Lifetime Peak Mass(kg)	70.1 (13.8)	39.0-176.4
	CSA (cm^2)	3.66 (0.65)	1.59-7.19
	J (cm^4)	3.37 (0.92)	1.29-8.62
Males (n=5785)	Age (yr)	47.7 (19.05)	20.0-90.0 (IQR = 31-64)
	Mass (kg)	78.4 (13.8)	40.5-148.5
	Lean Mass (%)	83.9 (7.09)	50.5-97.98
	Total Exercise Amount	22.93 (28.20)	0-355
	Upper Leg Length (cm)	42.0 (3.43)	27.6-56.1
	Lifetime Peak Mass (kg)	85.3 (15.1)	49.4-174.6
	CSA	4.86 (0.83)	2.29-9.27
	J	5.75 (1.63)	1.70-16.11

Cortical area and polar second moment of area were calculated from DXA scans, which were administered to individuals at the Mobile Examination Centers. This means that the individuals given home examinations, specifically very elderly individuals who were not mobile enough to travel to the Mobile Examination Centers, would be excluded from this selection. Cortical area and polar second moment of area were calculated from DXA scans using the Hip Structure Analysis Program; for the specific mathematics underlying the conversion to cross-sectional properties, see Martin and Burr (1984).

Structural Equation Modeling

Structural equation modeling (SEM), and its subset called path analysis, is a form of statistical analysis that evaluates the relationships between multiple independent and dependent variables. SEM acts similarly to a set of sequential multiple regressions, but with the added benefit of allowing expected causal relationships predicted from theoretical models to be defined and explicitly tested (Ullman and Bentler 2003). In essence, the model acts as a hypothesis test about the strength of causal relationships between the specified variables for a particular dataset. Models are evaluated on two factors: the fit of the model to the dataset and the strength of the predefined relationships between variables, which are expressed as standardized coefficients. As more variables are added, modification indices can be used to test if certain relationships between variables are necessary, or whether removing them improves the model's fit.

SEM was chosen for this research as it complements the complex relationships inherent in the data. SEM has a robust history of use in fields such as ecology and evolutionary biology (Malaeb et al. 2000, Pugesek et al. 2003, Eisenhauer et al 2015), psychology (Ullman and Bentler 2003), medical research (Hawellek et al. 2016), and educational research (Khine 2013). Comparatively few articles using this method have been published in biological anthropology, and the majority have focused on factors influencing primate social groups (Chapman, 2006; Bannar-Martin, 2013), fertility and gestation (Little 1989, Snopkowski & Kaplan 2014, Hackman and Hruschka 2020; Dinh et al. 2022, Kim et al. 2023), and anthropometric variation (Potter et al 1983, Bailey et al. 1985; Devor et al. 1986; Sciulli & Rao, 1975; Tambs et al., 1992; Holton and Franciscus 2008; Landi et al. 2021; Fiala et al. 2021). In general osteological research, SEM has been used to examine the factors influencing fracture risk across individuals (Jepsen et al. 2007, Stattin et al. 2021).

SEMs for this paper was performed using the Lavaan package for the R Program for Statistical Computing (Rosseel 2012). A basic model with body mass, lean mass, cross-sectional area (CSA), and polar second moment of area (J) was used as the starting point, and each additional factor (age, total exercise amount, lifetime peak body mass, upper leg length) was then added to the model and connected to the cross-sectional properties.

These connections between each new factor were defined using modification indices. Modification indices are used to create a model whose fit indices indicated a good representation of the data for potential regression or correlation relationships that were mathematically determined plausible by the model itself. This was done by choosing the largest theoretically-justifiable linkage. These linkages were required to be theoretically justified, as modification indices only indicate potential connections and not necessarily logical ones. For example, a linkage suggesting that lean muscle mass amount had a causative relationship determined by total number of exercise days would be included, but a linkage suggesting that total number of exercise days was caused by cortical diameter measurement was not. Model fit was tested using Chi-square, Root Mean Square Error of Approximation (RSMEA), and Comparative Fit Index (CFI). For SEMs, the Chi-square tests the null hypothesis that the model adequately represents the data; significant Chi-square values ($p<0.05$) indicate a poorly-fitting model (Gatignon, 2010). RSMEA analyzes the discrepancy between the sample covariance and the optimal parameter model; generally, it should be less than 0.06 (Hu & Bentler, 1999). Finally, CFI tests the hypothesized model versus the data for discrepancy size; it ranges from 0-1 and should be greater than 0.90-0.95 (Hu & Bentler, 1999).

One challenge in using structural equation models is reporting effect size for a single component in a complicated model, particularly in a model such as this one where the sample sizes are comparatively large and therefore, likely to attain significance even when actual effects are small. In this model, we have used semi-partial correlation coefficients (*r*) as a standardized method to report the strength and direction of the association between the independent and dependent variable. This relationship looks at the correlation of the residuals of the variables of interest once the impact of the other variables has been removed (Abdi 2007). In general, $r > 0.1$ is considered a small effect, and $r < 0.5$ is considered a large effect (Cohen 1988, 1992).

Results

In the following path model diagrams, relationships between the variables, marked in square boxes, are indicated by their connecting arrows. Variables can either be independent, having no arrows pointing to them; dependent, where arrows point at them; or intermediate dependent, where they serve as a modulating factor between the input variable and the outcome variable. Dark arrows indicate a positive relationship; pale arrows indicate a negative relationship. Single-headed arrows indicate a directional relationship, with the indicated variable being influenced by the variable at the base of the arrow; double-headed arrows indicate covariance between the variables.

Due to high multicollinearity between cross-sectional area (CSA) and polar second moment of area (J) as well as between sexes, four separate models were fit to the data. Models reached significance with the same parameters and connections between

CSA and J, but differed between males and females. The female model could not reach a good model fit using upper leg length, so it was dropped from the analysis for females. However, adding in history of intentional weight loss drastically improved model fit for females. Nearly all applicable parameters reached high levels of significance ($p<0.001$) simply due to large sample size. As such, the proportion of variation explained by the model components for each endogenous variable and the semipartial correlation coefficients (*r*) for each contributor are detailed in the tables below.

Male Model Results

The male models (Figure 1-2) reached significance with all parameters of interest (χ^2= 0.39, df=1, CFI = 1.0, RSMEA probability range 0.000-0.022). The male model determined that nearly all parameters had a statistically significant effect on the cross-sectional geometry of interest, as expected for this size of sample (Table 2).

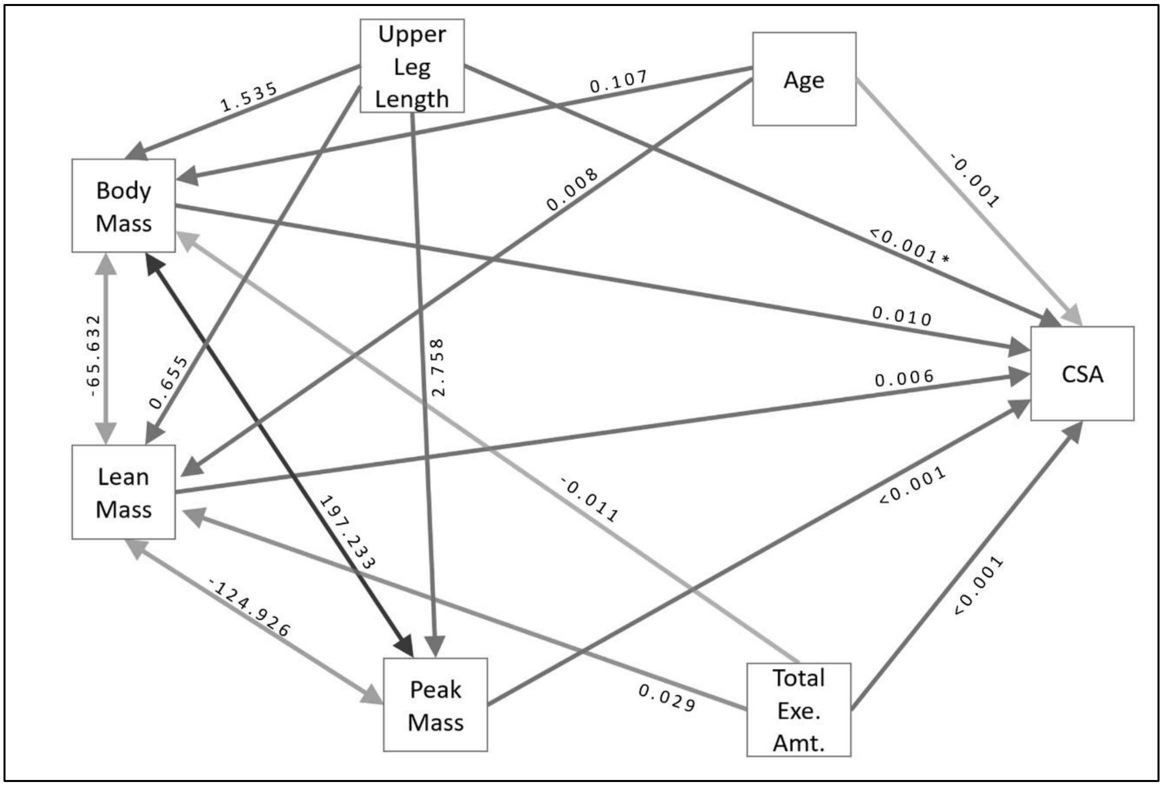

FIGURE 1: Male model created for analysis of CSA. Paler lines indicate a negative relationship, darker lines indicate positive relationship. Directional relationships are indicated with single arrow heads, while covariate relationships are indicated with two arrow heads. Values on the lines indicate the magnitude change in the dependent variable with a one unit increase in the independent variable.

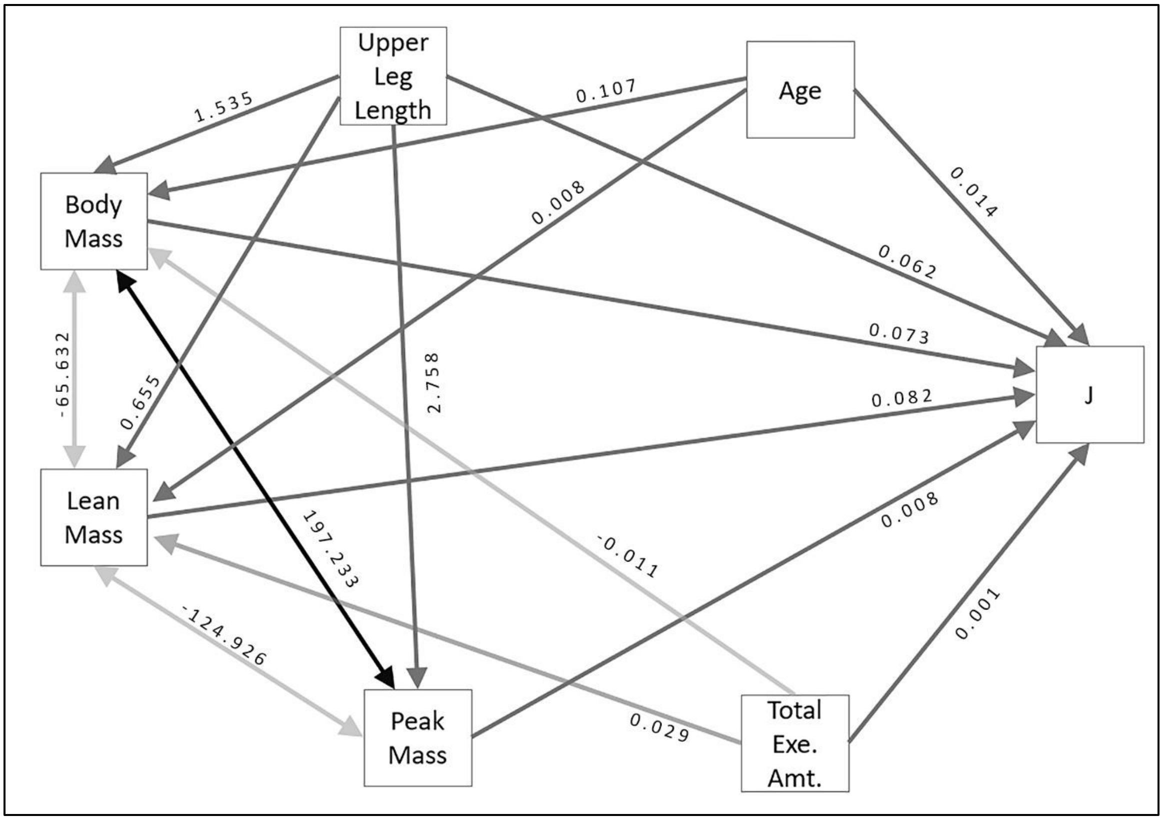

FIGURE 2: Male model created for analysis of J. Pale lines indicate a negative relationship, darker lines indicate positive relationship. Directional relationships are indicated with single arrow heads, while covariate relationships are indicated with two arrow heads. Values on the lines indicate the magnitude change in the dependent variable with a one unit increase in the independent variable.

Table 2: Male model parameter results.

Parameter	Affected by	Parameter Change	Standard Error	*r*
CSA	Lean Mass	0.006	< 0.001	0.225
	Body Mass	0.010	< 0.001	0.736
	Age	-0.001	< 0.001	-0.131
	Total Exercise Amount	<0.001	< 0.001	0.055
	Peak Body Mass	<0.001	< 0.001	0.07
	Upper Leg Length	<0.001*	0.001	0.018
J	Lean Mass	0.082	0.001	0.288
	Body Mass	0.073	0.002	0.594
	Age	0.014	0.001	0.232
	Total Exercise Amount	0.001	< 0.001	0. 020
	Peak Body Mass	0.008	0.001	0.202
	Upper Leg Length	0.062	0.003	0.148
Body Mass	Age	0.107	0.002	-0.024
	Total Exercise Amount	-0.011	0.02	0.093
	Upper Leg Length	1.535	0.035	0.278
Lean Mass	Age	0.008	0.004	-0.105
	Upper leg length	0.655	0.02	0.064
	Total Exercise Amount	0.029	0.003	-0.011
Peak Mass	Lean Mass	-2.525	0.049	0.219
	Upper leg length	2.758	0.105	0.288
Covariances				
Body Mass / Lean Mass		-65.632	1.504	-0.701
Body Mass / Peak Mass		197.233	4.179	0.86
Lean mass / Peak Mass		-124.926	0.082	-0.56

The model parameters explained approximately 47.8 percent of variation in cross sectional area (CSA). CSA was positively influenced by both lean muscle amount and total mass. Total mass had a slightly smaller direct impact, with a 0.010 cm^2 increase per kilogram increase total mass, and lean muscle mass causing a 0.006 cm^2 increase per kilogram increase in muscle mass. Total exercise amount and peak lifetime body mass were significant contributors but had minimal effects (<0.001 cm^2 increase in cortical area per unit increase). Age had a significant, but minimal (-0.001 cm^2 decrease per year) effect on cross-sectional area.

Model parameters explained 50.8% of variation in polar second moment of area (J). Like CSA, J was also primarily affected by the direct effects of lean mass amount and total body mass. Each kilogram increase in lean mass amount increased J by 0.082 cm^4, while each kilogram of total body mass increased J by 0.073 cm^4. Age had a more significant impact on J than CSA, increasing it by 0.014 cm^4 per year. Total days exercised in the past 30 days had a small but significant positive effect, increasing J by 0.001 cm^4 per day exercised. Interestingly, highest lifetime body weight also affected J, increasing J by 0.008 cm^4 per kg increase in highest lifetime body mass. Upper leg length, representing beam length and height, also had a significant positive effect on J, increasing it by 0.064 cm^4 per centimeter length increase.

The indirect complicating effects of exercise, beam length, and peak body mass had a surprising impact on lean mass amount and total body mass. Total body mass was impacted most strongly by upper leg length, representing height (1.535kg per cm increase), followed by age (0.107kg per year) and negatively affected by total exercise instances (0.011kg decrease per instance). Lean mass was strongly related to upper leg length and stature, increasing 0.655kg with every centimeter increase. Total days exercised had the next largest impact, increasing lean mass amount by 0.029lb per instance of exercise. Finally, lean mass amount increased with age (0.008lb per year), potentially representing a loss of body fat as age increases. The similar magnitude of impact between lean mass amount and total body mass on CSA or J would be highly modified by, say, the opposite impacts of total exercise amount on these two properties.

Female Model Results

In order to reach significance, a separate female model (Figure 3) was required to adequately fit the data to significance (χ^2= 0. 806, df = 2, CFI = 1.0, RSMEA probability range 0.00-0.018). Upper leg length could not be integrated in a way that produced a well-fitting model. When intentional weight loss (IWL) was used in place of upper leg length, the model reached significance and adequate representation of the data.

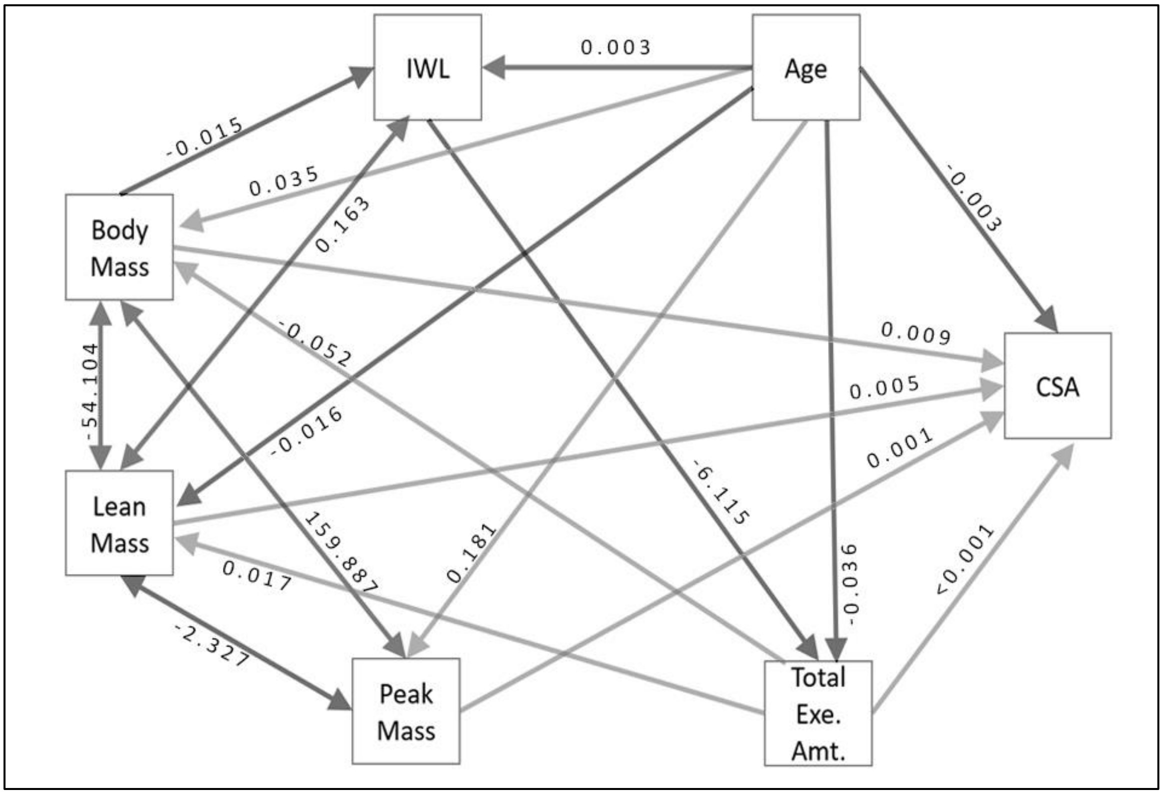

FIGURE 3: Female model created for analysis of CSA. Paler lines indicate a negative relationship, darker lines indicate positive relationship. Directional relationships are indicated with single arrow heads; covariant relationships are indicated with two arrow heads. Values on the lines indicate the magnitude change in the dependent variable with a one unit increase in the independent variable.

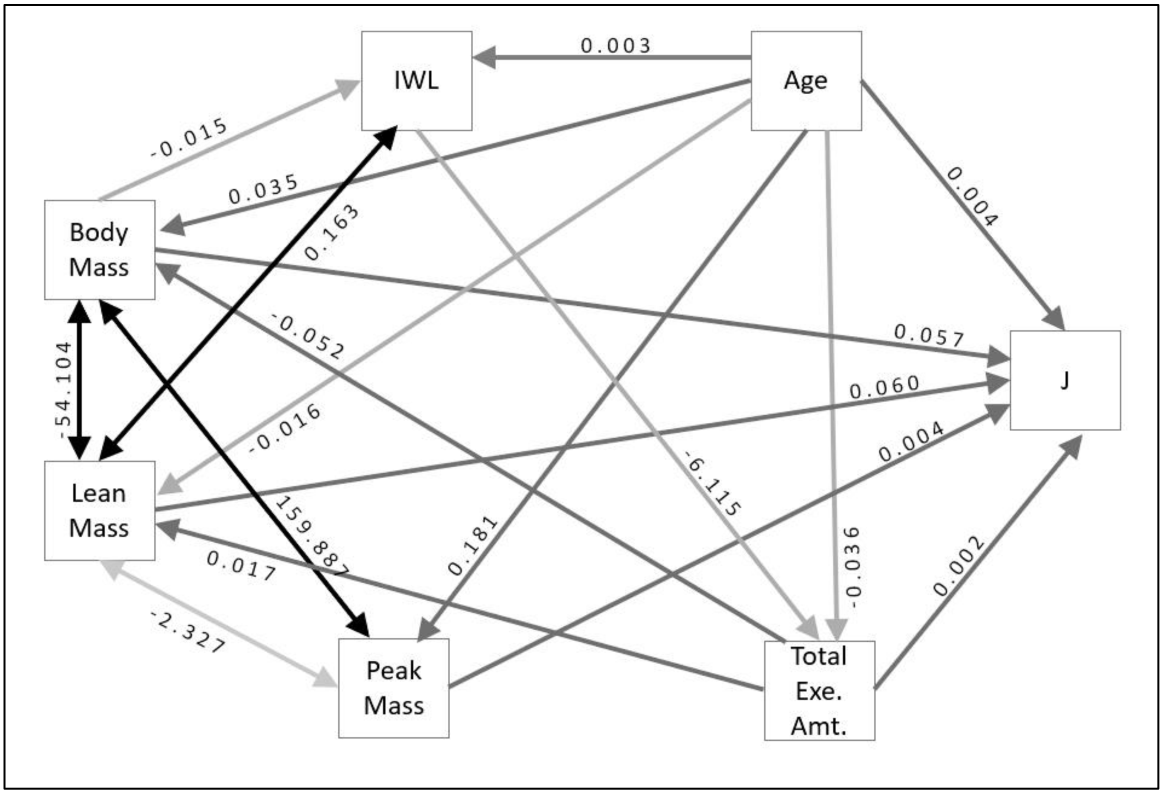

FIGURE 4: Female model created for analysis of J. Paler lines indicate a negative relationship, darker lines indicate positive relationship. Directional relationships are indicated with single arrow heads; covariant relationships are indicated with two arrow heads. Values on the lines indicate the magnitude change in the dependent variable with a one unit increase in the independent variable.

The female model continued to emphasize the impact of lean mass amount and total body mass (Table 3). Weight was the primary driving of CSA factor with by far the highest semipartial correlation of any factor, increasing 0.009 cm^2 per kg of weight. Lean mass amount increased CSA by 0.005 cm^2 increase per kg increase of weight. Age decreased CSA by 0.003 cm^2 increase per year, and lifetime peak weight increased CSA minimally by 0.001 cm^2 increase per kg. Total exercise had a significant but minimal impact, less than 0.001 cm^2 increase per instance of exercise.

Table 3: Female Model Results

Parameter	Affected by	Parameter Change	Standard Error	*r*
CSA	Lean Mass	0.005	<0.001	0.163
	Body Mass	0.009	<0.001	0.647
	Age	-0.003	<0.001	-0.375
	Total Exercise Amount	<0.001	<0.001	0.053
	Peak Body Mass	0.001	<0.001	0.095
J	Lean Mass	0.060	0.003	0.388
	Body Mass	0.057	0.002	0.758
	Age	0.004	0.001	0.075
	Total Exercise Amount	0.002	<0.001	0.041
	Peak Body Mass	0.004	0.001	0.143
Peak Mass	Age	0.181	0.02	0.114
	Lean Mass	-2.844	0.408	-0.551
Total exercise amount	IWL	-6.115	0.712	-0.133
	Age	-0.036	0.017	-0.029
Body Mass	Age	0.035	0.009	0.055
	Total Exercise Amount	-0.052	0.008	-0.097
Lean Mass	Age	-0.016	0.004	-0.051
	Total Exercise Amount	0.017	0.002	0.142
IWL	Body Mass	-0.015	0.001	-0.355
	Age	0.003	0.001	-0.029
Covariances				
Lean mass amount /total mass		-54.104	1.298	-0.751
Lean mass amount / IWL		0.163	0.021	0.059
Total mass/peak mass		159.887	22.357	0.525
Lean mass amount / peak mass		-2.327	14.097	-0.016

Approximately 43.7% of variation in polar second moment of area (J) explained by the model effects. J was more significantly affected by the factors in the female model, with nearly equal contributions from both weight and lean muscle amount. However, the semipartial correlation suggests that body mass is a much stronger contributor to J when all other factors are taken into account despite the similar increases. Increases in weight raised J by 0.057 cm^4 per lb increase, and lean mass amount raised J by 0.060 cm^4 per lb increase. J was altered to a less dramatic degree by age (0.004 cm^4 per year), exercise amount (0.002 cm^4 per instance), and peak lifetime weight (0.004 cm^4 per lb increase).

Confounding factors also contribute to the primary drivers of CSA and J changes in females. Total body mass was positively influenced by age in females (0.035 lb increase per year) and negatively influenced by total exercise instances (0.052 lb decrease for each instance). Lean mass amount increased with exercise amount (0.036 lb increase per exercise instance) and decreased with age (0.016 lb decline per year of age). The inclusion of intentional weight loss, however, was particularly interesting. Intentional weight loss attempts increased with age (0.003 chance per year) and decreased with higher current mass (0.015 chance decrease per lb of mass). Most interestingly, intentional weight loss strongly decreased total exercise amount, reducing it by 6.115 instances, the largest effect of any parameter.

Discussion

As has been noted in anatomy, medicine, and ecology (e.g. Nelson et al. 2008, Marsh et al. 2013, Eisenhauser et al 2015), SEM is underused considering the value it can provide in the analysis of more complex systems. The human skeleton is constantly responding to a wide range of stimuli, and SEM is uniquely situated to examine the effects of these factors simultaneously. The ability to specifically test models with causal relationships is particularly attractive in complex biological relationships, where some correlations are intuitively causal and changes in one cannot alter the other, such as age and weight: aging may bring about weight changes, but weight changes cannot alter age. Other relationships may have reciprocal influence on each other, such as changes in exercise amount and body mass. SEM can handle a variety of such relationships within a single model.

SEM is particularly helpful in deconstructing the levels at which changes in activity, body mass, and lean muscle mass affect skeletal properties. It was determined that, contrary to our first hypothesis, body mass and lean muscle amount often have a combined impact on cross-sectional properties, and body mass is not always the primary driver of cross-sectional properties. Body mass is typically the driver of cross-sectional area, but body mass and lean mass have similar effects on the polar second moment of area, J. Peak body mass, while it correlated with current mass, had minimal direct effects on CSA but surprisingly had a strong direct effect on J, despite decreasing strongly with increases in lean mass. Unsurprisingly in males, weight covaried strongly with height. Interestingly, though, J also covaried strongly with height independently of effects of overall body size, suggesting that continued standardization of J to beam length in path analysis is important.

The influence of exercise also did not confer a large direct effect on CSA or J. However, exercise modified body mass and lean mass, indirectly modifying the bending strength of bone and supporting our second hypothesis. Exercise frequency correlated with decreased body mass and increased muscle mass in males; these two effects would have opposite effects on bone bending strength. Mass would have the stronger impact, but as its influence declines, this would exaggerate the impact of muscle mass. In females, exercise seems to only affect lean mass and have a non-significant effect on body mass, magnifying what is typically a minimal direct effect on bone bending strength. In females, intentional weight loss was associated with decreased exercise frequency. It is unclear why this relationship was significant; perhaps women who are decreasing their calorie intake as part of intentional weight loss have less energy to expend on exercise, were closer to their desired weight and did not see a need to exercise more, or that women who choose intentional weight loss are in situations that force them to be sedentary, such as desk jobs, instead of being able to be active. Intentional weight loss attempts also decreased with increased body mass, and covaried positively with lean mass amount. This relationship is supported by previous studies suggesting that maintaining muscle mass during intentional weight loss resulted the maintenance of bone strength (Sirola et al. 2006), as well as the varied documented relationships between intentional weight loss, bone strength, and muscle mass (Villareal et al. 2006, Uusi-Rasi et al. 2010, Shapses and Sukumar 2012).

The benefit of using NHANES III is that the dataset contains a significant sample size and detailed data. Additional useful data, however, was not consistently collected on the NHANES III participants and would be helpful in exploring the impact of other factors which have been suggested to influence on cross-sectional properties. For example, the sex-specific models showed that males and females, despite having similar overall patterns, had different magnitudes of effects. This may be due to estrogen levels (Devlin and Lieberman 2007, Devlin 2011), but NHANES III lacks data on overall hormone levels. Sex can be used as a proxy for hormone levels in this study, but more detailed data, especially coupled with the age data to explore the effects of menopause in women, would be valuable in future models. Another major drawback was the use of

DXA data for estimating cross-sectional properties, which confines the region studied to approximately 80% of femoral shaft length. While it has been suggested that the proximal femur may be a valuable place for examining the effects of body mass and muscle mass (Niimimaki et al 2018, Moore 2008, Pomeroy et al. 2019), it is also possible that the proximal femur may also respond to pelvic shape and resulting muscle force changes (Iglic et al 1993, Ruff 2000, Shaw and Stock 2009, Slemenda et al 1996). Many studies prefer the femoral midshaft for calculating cross-sectional properties, and this path model cannot be directly applied to those results. Finally, the set of skinfold measurements selected for NHANES III was surprisingly difficult to use for calculating body fat percentage. The only set of equations that could be used were the Siri (1961) and Sloan (Sloan, Burt, & Blyth, 1962; Sloan, 1967) equations, while more modern body fat percentage equations were missing at least one necessary measurement. Future work should focus on validating these results with a more precise set of circumference or skinfold measurements.

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CHAPTER 3

CRITICAL MASS: THE EFFECT OF BODY MASS AND LEAN MASS ON LOAD-BEARING AND NON-LOAD-BEARING SKELETAL ELEMENTS.

Rob’yn A. Johnston, Libby W. Cowgill

Introduction

The complex question of how body composition and mass affect the bending strength of long bones has been a frequent puzzle in studies of bone functional adaptation. Body mass, the base load bone is exposed to during life, has been shown to be an important predictor of limb bone strength, particularly in the lower limbs (Ruff et al. 1993, Ruff 2000, Ruff 2002, Ruff 2005). However, several important questions remain. It is unclear whether body mass has systemic or regional effects, specifically if it also affects non-weight bearing elements like the humerus. Further, it is not known whether total body mass influences limb bone strength or if the primary predictive factor is lean muscle mass. Using a sample of cadaveric individuals to estimate body composition, this study compares the cross-sectional properties of the upper, non-weight-bearing limb to the lower, weight-bearing limb. Based on the hypothesis that body mass does not generally affect the upper limb, we expect that total body mass should explain more of the variation in lower limb strength and rigidity, particularly in total cross-sectional area, but lean mass percentage should explain more of the variation in the cross-sectional measurements of the non-weight-bearing upper limb.

The Challenges of Body Mass

Analysis of cross-sectional geometry, which models long bones as beams in order to reconstruct activity in past populations, requires that bone parameters are standardized by a biomechanically relevant measure of body size. This is typically done by using some form of body mass and/or body mass multiplied by beam length, as mass is the base load to which the lower limb is regularly exposed (Ruff 2000). The cross-sectional geometry of the lower limb has been shown to have a strong relationship with overall mass and standardizing by body mass is usually the first step in analyzing bone bending properties (Ruff et al 1991, Ruff 2000a, Ruff 2000b, Holliday 2002, Holt 2003, Ruff 2003, Janz et al. 2004, Devlin and Lieberman 2007, Marchi et al. 2006, Marchi 2008, Cowgill et al. 2010). This relationship is theoretically well-supported due to the lower limb's obvious role in supporting 100% of body weight during human bipedalism.

Previous research has suggested that humeral cross-sectional properties also scale well with body mass in adults despite not being weight bearing (Trinkaus et al. 1994, Ruff 2000b, Ruff 2003, Sparacello and Marchi 2008). Therefore, many researchers choose to standardize by body mass as it has been proposed that the humerus follows the same body size scaling as the lower limbs (Ruff, 2000b, Marchi et al. 2006, Shaw and Stock 2009). Conversely, it has been proposed that the upper limb may have a different relationship to body mass as it is not typically load-bearing in adult humans. The human upper limb has frequently been described as freed from the constraints of a locomotor and load bearing role and relegated primarily to manipulative tasks (Bridges 1989, Haapasalo et al 2000). These studies often rely on standardization by measurements of maximum length or maximum length raised to a power (Ruff et al 1993, Weiss 2003, Marchi et al. 2006).

The question of appropriate scaling for limb robusticity is related to on-going debates over whether bone functional adaptation is local or systemic. Lieberman (1996) suggested that even non-weight-bearing bones like the cranium can be influenced by higher overall activity because of systemic hormonal effects. This systemic adaptation hypothesis has some limited support (Baab et al 2018, Goto et al 2023), but more extensive studies have found no overall change in cranial bones with increased activity or biomechanical load (Reeves 2014, Copes et al 2018). On the other hand, many studies have found that bending strength patterns in long bones are consistent with specific and localized habitual activities (e.g., Trinkaus et al. 1994, Stock and Pfeiffer 2001, Auerbach and Ruff 2004, Shaw and Stock 2009b).

In addition to debates over whether bone functional adaptation is local or systemic, it is not clear if bone responds more strongly to base load experienced, which is total mass including fat mass, or just lean body mass. The effect of lean mass and muscle strength on bone is well established. For example, lean mass is the strongest predictor of bone strength in overweight adolescent girls (El Hage et al 2010). In addition, muscular forces appear to be a major driver of cross-sectional geometry in children and adults throughout the femur (Janz et al 2004, Godde and Taylor 2013). The humerus is strongly affected by high-strain behavioral activity even in the absence of high impact loading via gravity; for example, the humerus of athletes has been shown to have increased torsional rigidity based on the demands of their sport (Shaw and Stock 2009). Research on athletes has shown that weightlifters tend to have increased cortical area, which could be attributed to larger muscle areas (Kaneshisa et al. 1998). An analysis of older Afro-Caribbean men found that leg lean mass best explained cross-sectional area and BMD, as well as partially explaining subperiosteal width (Semanick et al 2005). Finally, the proximal femur is suggested to respond to changes in lean muscle mass more dramatically than the midshaft femur because of its position within the hip musculature (Travison et al 2008, Moore 2008).

In contrast, however, previous research on cross-sectional properties of the femoral midshaft strongly suggests that lower limb bone strength is affected by total body mass, not just lean body mass alone (Moore 2008. Moro et al. 1996; Ruff 2003; Schoenau et al. 2000; Schönau 1997; Schönau et al. 1996; van der Meulen et al. 1996; van der Meulen et al. 1993). Additional studies have found support for the influence of total body mass on bone strength at the sub-trochanteric level (Petit et al., 2008; Pomeroy et al 2018, Johnston and Cowgill in prep). Other research has detected a positiveeffect of BMI on the mediolateral and anteroposterior dimensions of the femur (Agostini and Ross, 2011). This extended to overweight girls, who tended to have increased cross-sectional area, though similar cortical thickness to their normal-weight peers. Finally, in addition to studies of humans, additional support for the relationship between bone strength and total body mass can be found in experimental animal research. In particular, cortical area correlates positively with total mass in experimentally manipulated mice (Judex and Carlson 2009). Murine models fed a high-fat diet, who had nearly double the typical amount of body fat, increased all their cross-sectional properties to match this higher weight, which supports the idea that the relationship between bone strength and total body mass, regardless of body composition, is important (Ionova-Martin et al 2010).

It remains difficult to disentangle the influence of muscle mass and lean tissue from that of total mass which includes bone lean tissue and fat. Several studies have found minimal interaction between lean muscle amount and cross-sectional geometry. Murine models with increased muscle size and similar body masses have detected minimal impact of muscle size on cross-sectional properties (Hamrick et al 2000). Studies looking at a diverse sample of ethnicities found that bone mineral density correlated more strongly total mass rather than fat mass, though there was a weak correlation with lean muscle mass (Moro et al 1996). It has been further suggested that in situations of inverse mass-lean mass relationships like obesity, non-weight bearing bones should show more influence of lean mass amount (Godde and Taylor 2013).

Given these issues, this research will explore the differential effects of total and lean body mass on both the load bearing and manipulative regions of the skeleton. The humerus is predicted to be equally affected by overall body composition, but as it is not affected by ground reaction forces and the daily impact of body mass (Bridges 1989, Larsen 1997, Bridges et al. 2000, Auerbach and Ruff 2006). This study will compare the bending strength of the lower and upper limb in a cadaveric sample with measurements of body composition in order to provide insight into the best methods of standardizing cross-sectional measurements as a whole. Based on the hypothesis that body mass does not affect the upper limb, we expect that total body mass should explain more of the variation in lower limb cross sectional properties, particularly cross-sectional area. Lean mass percentage, in contrast, should explain more of the variation in the cross-sectional measurements of the non-weight-bearing upper limb.

Materials And Methods

Sample: Soft tissue data and osteological data was collected from 45 individuals donated to the University of Missouri Medical School through its Gift of Body Program. Research permissions were granted through the University of Missouri Donor Research and Education policies and in compliance with the Institutional Review Board policies for the University of Missouri-Columbia. Individuals were comprised of 20 females and 25 males and were primarily white when ethnicity was provided (76%). As is common with donated cadavers, sample age skewed older (mean age 76, range 42-103), and individuals in the sample can be reasonably assumed to have been less active leading up to their deaths.

Methods**:** This study uses cross-sectional geometric properties, predicted body mass, and two measurements of body composition: body mass index (BMI) and lean mass, calculated using body fat percentage (BF%).

Cross-sectional properties: The primary biomechanical variables for this analysis were cross-sectional properties of the upper and lower limbs. In order to calculate humeral and femoral cross-sectional geometry, the humerus and femur were removed, measured, sectioned, and photographed for analysis after cadaver dissection. Sections were taken at 80% and 50% of femoral biomechanical length, equivalent to the midsection and subtrochanteric regions, and 50% and 35% of humeral biomechanical length (Ruff et al. 1993, Trinkaus et al 1994).

Osteological data were preferentially taken from the right side when available, and the left when knee or hip replacements precluded accurate measurement and typical bending patterns. Length measurements of both the humerus and femur were taken with digital calipers or an osteometric board to the nearest millimeter. For the humerus, properties were standardized by biomechanical length. Individuals with bilateral joint replacements were dropped from analysis of lower limbs but used for analyses of upper limbs when appropriate.

Cross-sectional geometry was calculated using MomentMacro (Ruff 2006) to analyze transverse photographs of bone sections. This analysis examined cross sectional area (CSA), total area (TA), polar second moment of area (J), and measurements of bending rigidity through the mediolateral and anteroposterior planes (I_x and I_y). Measurements of CSA and TA have been previously associated with changes in body mass, J is typically associated with activity and therefore muscle force, and Ix and Iy may pick up on gait or muscular force directional differences during activity.

Body Composition: BMI is calculated as weight (kg) divided by height squared (m) and is one of the earliest and most commonly applied measurements of body fatness (Suchanek et al. 2012). This makes it appealing for studies using skeletal remains to examine body composition, as height and weight are easily estimated from dry bone. BMI is not commonly used in the biomechanical literature, though several studies have used it as a marker for obesity when looking at bone strength and density (e.g., Petit et al 2004, Reeves 2014, Iwaniec and Turner 2016). The difficulties with BMI is that it tends to misclassify individuals as normal weight or obese regardless of their body fatness, does not correspond well to actual body fatness, can misclassify particularly muscular individuals, may misclassify individuals of non-white ethnicity, and does not have separate measurements for males versus females (Bergman et al. 2011).

To calculate lean muscle mass, it was first necessary to calculate BF% using measurements of limb and body circumference. Circumference measurements were taken following definitions used by the Third National Health and Nutrition Examination Survey (NHANES III). The circumferences were defined as seen in Table 1. Circumference measurements were taken using a flexible tape measure and recorded to the nearest millimeter.

Table 1: Measurement definitions as defined by NHANES III

Measurement	**Definition**
Forearm circumference	Forearm circumference at widest part.
Abdominal Circumference	Waist at narrowest part
Hip circumference	Hip at widest part of buttocks
Thigh circumference	Thigh by 1cm below buttock crease
Calf circumference	Calf by widest part

Body fat percentages were then calculated from circumference measurements of the cadavers following Katch and McArdle (1983)'s sex-specific formulae for less-active older (26+) adults. Katch and McArdle (1983)'s formula was preferred for this project as individual body masses prior to the addition of embalming fluid were not reported, and this body fat formula does not require a base mass to calculate BF%. The circumference measurements were determined to be within 2.5-4% of body composition determined by more precise hydrostatic weighing (Katch and McArdle 1983). For males, this formula relies on hip, abdominal, and forearm circumference in inches to calculate body fat percentage:

$$\text{BF\%} = (\text{hip}*1.05) + (\text{abdominal}*0.90) - (\text{forearm}*3.00) - 15.0$$

For females, the formula relies on abdominal, thigh, and calf circumferences in inches to calculate body fat percentage:

$$\text{BF\%} = (\text{abdominal}*1.19) + (\text{thigh}*1.24) - (\text{calf}*1.45) - 18.4$$

This percentage was then multiplied by total mass and the result deducted from the total mass to provide a measurement of lean mass, which includes bone and organ weights as well.

Body Mass: Estimated body mass was calculated following Squyres and Ruff (2015) from femoral bicondylar breadth, which was taken with calipers to the nearest millimeter. Many studies of body mass estimation are available in the literature, which many investigators preferring methods that utilize femoral head size (Auerbach and Ruff, 2004, Chevalier et al., 2017, Lacoste Jeanson et al., 2017, Pomeroy et al., 2019). This method used here was selected as many cadavers had two hip replacements, meaning accurate femoral head measurements were not available on either side. Mass estimation from the knee has been shown to have similar error rates compared to femoral head estimation (7 to 9%) (Squyres and Ruff 2015).

Statistical Analysis: Humeral and femoral cross-sectional properties were regressed using ordinary least square regressions on lean mass, overall predicted mass, and BMI. The fit of these regressions were compared using adjusted R-square and Akaike Information Criterion, adjusted for smaller sample sizes, to compare their predictive power. Best-fitting model using AICc determined by comparing all equations and selecting the regression with the lowest AICc score. If another regression had an AICc within 4 AICc units of the best-performing model, it was included as an equally well-fitting model.

Results

Mean BMI in the sample was 28.6 (range 25.0-32.7) and was also biased towards obese individuals: no individuals were within normal BMI ranges (BMI 18.5-24.9), 32 individuals classified as overweight (BMI 25.0-29.9), and the remaining 13 classified as obese (BMI 30.0+). Similar to the results with BF%, at approximately 29% obesity rates, this sample is actually much lower in obesity than the United States as a whole (41.9% in 2017) and in United States adults above the age of 60 (41.5% in 2017) (CDC 2022). No adults in this sample have severe obesity (BMI>40.0+), probably because embalming cadavers of this size leads to a prohibitively heavy weight for transport and storage. 71.1% of the sample classifies as overweight, however, which is strongly overrepresented versus the United States population.

Predicted mass, lean mass, and BMI had significant relationships to all cross-sectional properties in both the humerus and the femur. Adjusted r-squared, used as a measure of predictive power, found that predicted body mass explained the most variation in all cross-sectional properties, though BMI was not dramatically worse as a predictive measure (Table 2).

Akaike Information Criterion scores comparing predictors for each cross-sectional property suggest that overall, total body mass is the strongest model. Lean mass amount was always the worst-fitting model, regardless of bone and location. Surprisingly, mass predicted cross-sectional properties best in the humerus at both locations for all properties, explaining between 57-74% of all variation despite the humerus not directly bearing weight.

Table 2: Adjusted r-squared by limb location.

	80% Femoral Length			50% Femoral Length		
Cross sectional property	Lean mass (kg)	Mass	BMI	Lean mass (kg)	Mass	BMI
TA	0.502	0.509	0.477	0.361	0.423	0.354
CA	0.510	0.450	0.439	0.464	0.447	0.398
J	0.482	0.466	0.446	0.387	0.441	0.369
I_x	0.459	0.487	0.383	0.375	0.438	0.337
I_y	0.430	0.385	0.430	0.337	0.371	0.344

	50% Humeral Length			35% Humeral Length		
	Lean mass (kg)	Mass	BMI	Lean mass (kg)	Mass	BMI
TA	0.674	0.735	0.665	0.646	0.692	0.631
CA	0.665	0.639	0.612	0.555	0.570	0.541
J	0.645	0.705	0.656	0.591	0.650	0.598
I_x	0.683	0.623	0.666	0.587	0.644	0.598
I_y	0.523	0.644	0.549	0.581	0.639	0.583

Discussion

Body mass, lean mass, and BMI were all good predictors for both upper and lower limb elements at all levels. Equations with total body mass had the lowest AIC score, though in several cases, equations relying on BMI had AIC scores that were within 8 AIC units of the best-performing model, suggesting equivalent strength of explanation.

The strong relationship between bone rigidity and BMI is interesting, as BMI is typically a poor predictor of body composition (Bergman et al 2011). However, the core components of BMI, body mass and height, are two of the more common standardization factors used in correcting for body size in cross sectional geometry. Areas are typically standardized to body mass, torsional measurements to body mass x bone length, and bending rigidity measurements like I_x and I_y to body mass x bone length^2 (Ruff 2018). As this closely mirrors the inputs to the formula of BMI, it is not surprising that a strong relationship exists between cross-sectional properties and BMI regardless of body fatness. What is unexpected is the strength of the relationship between BMI and TA or CA, which are typically not standardized by beam length, only mass. The results for the lower limb match previous results using DXA of the proximal femur in modern non-industrial populations (Pomeroy et al 2019), who found minimal explanatory power to predict body fat, but strong predictive relationships between cross-sectional area, lean mass, and total mass. Against expectations, this study found no major differences in the patterns of significance between the upper and lower limbs.

Additionally, body mass explained more of the variation in the upper limb than the lower, contrary to the hypothesis that weight-bearing limbs would show a stronger effect of body mass. Instead, body mass explained up to 25% more variation in the upper limb than the lower. This suggests that the impact of body mass on the limbs is systemic. Since these individuals were likely not performing intense labor in the period leading up to their deaths, their upper limb loads may have been more predictable. As cadaver donors are typically older and often choose to donate near their time of death (Dluzen et al. 1996), it is likely that they are in poor health or perhaps bedridden leading up to their donation, suggesting that they are likely extremely sedentary. This may drastically alter the impact of lean muscle mass if the limbs are simply not loaded in the time leading to death. Furthermore, aging typically leads to a loss of muscle mass and an increase in total fat mass (He et al 2003, Zamboni et al. 2003, Hughes et al 2004), which may further weaken the influence of muscle mass on bone bending strength through inactivity.

Limitations of Analysis

One unique feature and potential drawback to this study is that it focused on donated cadavers, who tend to be much older than the typical samples. Many studies comparing cross-sectional geometry of limbs have focused on younger individuals and/or prime-age adults (e.g. DiVasta et al. 2007, Shaw and Stock 2009, Cowgill et al 2010, Devlin et al 2010, Shaw and Stock 2013). Older adults, particularly postmenopausal women, may be suffering from osteoporosis (Nelson et al 2000, Sirola et al 2006, Uusi-Rasi et al. 2010, Sornay-Rendu et al 2017, Hallkivst et al 2018). In addition, elderly women have larger cross-sectional area (CSA) values than younger women despite lower estrogen levels post-menopause, but this does not compensate for reduced bending strength (Meta et al 2006). Furthermore, the relationship between body mass and bone strength and rigidity may differ over the life cycle; in elderly populations, the influence of body mass and muscle mass seem to be independent of activity and distance walked (Semantick et al 2005). The results of this study help illuminate the forces that may shape bone bending strength in older individuals but may not extrapolate as well to prime-age individuals.

Another potential drawback to this study is that due to the nature of the sample, multiple important factors, including total body mass and lean body mass, had to be estimated. Unfortunately, it was not possible to obtain pre-embalming body masses from these individuals and embalming adds an amount of fluid weight that is not consistent across individuals, so estimating body mass at time of death was problematic. Similar to estimates of body mass from the femoral head, measurements estimated from knee breadth may more strongly represent body mass at the cessation of growth instead of at the time of death. This error should be evenly distributed throughout all individuals, but access to cadavers with known body masses at the time of death would be an additional improvement to similar samples in the future.

Conclusions

The impact of body mass on humerus was of particular note in this study. The goal of this analysis was to clarify the influence of body mass on humeral strength. While not weight-bearing and typically manipulative in bipedal humans, the humerus is still strongly impacted by body mass. This suggests that standardization by body mass is crucial for understanding humeral cross-sectional geometry even in the absence of direct loading. This also may suggest that the impact of mass is likely systemic on the skeletal system, perhaps triggered by hormonal signaling. The combined influence of muscle and body mass on the humerus should be explored in a larger sample of active adults to further understand this relationship. The results of this study also suggest that other bones than those of the lower limb have potential use for estimating body mass in archaeological samples.

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CHAPTER 4

ESTIMATION OF BODY MASS IN WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) USING CROSS-SECTIONAL GEOMETRY OF THE METAPODIAL

Rob'yn A. Johnston, Libby W. Cowgill, R. Lee Lyman

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Introduction

Live body weight of a particular species has a variety of analytical uses to explore past and present environments, as well as the role of humans within those spaces. For example, paleontologists estimate biomass to study paleoecology (e.g., Guthrie, 1968; Staff et al., 1985), and body mass informs aspects of intra- and inter-specific comparisons (Batchelor and Mead, 2007; Klein, 1964; Wolverton et al., 2007). Increases in body mass have been suggested to be caused by reduced intra- and inter-specific competition, as there are more resources available for each individual (Blackburn et al., 1993; Blackburn and Gaston, 1997; Densmore, 2009; Hefley et al., 2013; Klein, 1964; Purdue, 1987; Wolverton et al., 2007, 2009). Body mass has also been found to correlate with ecological variables such as soil fertility (Strickland and Demarais, 2006) and intensity of predation (Broughton, 1999, 2002; Edwards, 1967; Stiner et al., 2000; Wolverton et al., 2007, 2008).

Beyond general environment, body mass specifically helps inform models in zooarchaeology. The ability to calculate the live weight of prey carcasses was initially considered useful to analyses of human diet and in the assessment of the economic importance of prey species (Emerson, 1978; Lyman, 1979; White, 1953). Measurements of live weight can also be used to provide estimates of meat amounts for skeletal element transport models (Binford, 1978; Madrigal and Holt, 2002; Purdue, 1987; White, 1953). Body size decreases have also been related to questions of human intervention in wild animal populations and particularly the start of domestication (Boessneck and von den Driesch, 1978; Tchernov and Horwitz, 1991). Given body mass's analytical versatility, it is no surprise that equations to predict body mass from skeletal remains are a common focus of zooarchaeological research.

White-tailed deer (*Odocoileus virginianus*) are an important prey animal across nearly all of prehistoric North and Central America (McCabe and McCabe, 1984), making the body mass of this species a useful variable in zooarchaeological analyses. There is also an open question as to whether white-tailed deer were the subject of human management (Noble and Crerar 1993, Stewart and Finlayson, 2000, Needs-Howarth and Hawkins 2016). Furthermore, white-tailed deer have as many as 30 recognized subspecies and vary in size from the dwarfed Key Deer (*O. virginanus clavium),* which typically weight less than 39 kilograms (Boughton et al. 2019), to northernmost species like the Dakota white-tailed deer (*O. virginanus dacotum*), which typically weight approximately 100kg (Innes 2013). Anecdotally, the largest white-tailed deer reported have had estimated live weights in excess of 220 kilograms! Body weight is extremely sensitive to food availability, can vary even over very short geographic distances, and may not stabilize until well after the cessation of skeletal growth (Innes 2013). This range of variation makes the estimation of white-tailed deer weight a valuable tool for zooarchaeologists. In this paper, we summarize extant methods of estimating body mass and introduce a new technique for estimating the live weight of white-tailed deer based on skeletal dimensions.

Previous Research

Several methods have been employed to estimate amounts of meat represented by skeletal remains of white-tailed deer. The earliest was proposed by White (1953), and involved multiplying the minimum number of individuals (MNI) in a zooarchaeological collection by the average live weight of an adult individual, and then by a fixed edible meat percentage of a single adult animal. The percentage is assumed to be universally applicable to all individual animals within a species and thus to each individual represented in the MNI. However, as this method relies on MNI, it is heavily dependent on sample size and how MNI is derived (Lyman, 1979, 2008). More importantly, both the fixed percentage and the mean adult live weight ignore the particular mass of individuals represented in the assemblage (Lyman, 1979); an assemblage of 10 small-bodied white-tailed deer gives the same result as an assemblage of 10 large-bodied white-tailed deer. This fact has prompted efforts to improve the accuracy of body mass estimates based on MNI and the percentage conversion factor (e.g., Smith, 1975; Stewart and Stahl, 1977).

Bone weight has also been used to estimate total living body mass represented by a collection using two distinct techniques. What we refer to as quantification assumes a collection’s total bone weight represents 7% of live weight and estimates the total biomass accordingly (Casteel, 1978; Reed, 1963; Uerpmann, 1973). Problems with this technique include taphonomic processes such as mineralization, leaching, skeletal element composition of the sample, and weathering altering bone weight differentially across skeletal elements and taxa (Lyman, 1979; Uerpmann, 1973). In addition, similar to the problems associated with the fixed universal percentage factor proposed by White (1953), the 7% conversion figure makes for a blunt instrument at best. The second technique, bone mass allometry, establishes statistical relationships between total body weight and total skeletal weight of modern animals, and those relationships are then used to convert zooarchaeological skeletal weights to total biomass (Reitz and Cordier, 1983; Reitz et al., 1987). Along with all the taphonomic processes that influence the weight of the remains, skeletal composition of the bone sample matters greatly but is not accounted for in this technique. Thus, a pound of femora suggests the same total biomass as a pound of phalanges in spite of those weights likely corresponding to very different biomasses (Jackson, 1989; Lyman, 2008).

Most recently, commonly used methods quantify prehistoric meat diet using known relationships between the live weight of modern individuals and linear measurements of skeletal dimensions to predict body weights (e.g., Beisaw, 2007; Davenport, 1999; Densmore, 2009; Emerson, 1978, 1983; Garniewicz, 2005; Madrigal, 2014; Madrigal and Holt, 2002; Morris and Mead, 2016; Purdue, 1983a, 1983b, 1986, 1987; Wolverton et al., 2007). Measurements of these linear dimensions of bones are correlated to body mass with moderate-high strength (e.g., Casteel, 1974; Emerson, 1978). For example, linear measurements of white-tailed deer astragali correlate with body size and explain 87.2% of the variation in body mass (Emerson, 1978). Metapodial length and width also have a significant and strong correlation with dressed body mass

(Densmore, 2009); however, the dimensions measured may be subject to weathering and distortion that can affect estimates of individual body mass (Breslawski and Byers, 2015).

The main difficulty with using skeletal dimensions to calculate body mass is that adult deer body mass is particularly affected by habitat variables. Wolverton and colleagues (2009) have suggested that the clinal size variation observed in white-tailed deer may be a product of food availability as much as Bergmann's Rule. On a local level, weight of adult individuals can be affected by plant availability in different seasons (primary productivity), plant availability in different habitats, inter- and intra-specific competition, and annual seasonal variation in plant growth (Purdue, 1980; Wolverton et al., 2009). For instance, seasonal changes in the amount of food available on the landscape can have a major influence on individual body mass, and yearly variation in summer forage quality may limit final body size as well (Brown, 1961; Purdue, 1989; see Lyman, 2008:88). Droughts and particularly harsh years can affect body mass by decreasing the total amount of available food (Brown, 1961; Densmore, 2009), although older deer are less effected by environmental variation than fawns (Brown, 1961; Kirkpatrick, 1976).

Female deer experience even further variation in body size than males. The uterus and associated tissues and fluids of a pregnant deer can weigh 20-30 lbs (Kirkpatrick, 1976). Giving birth removes this weight, but even after accounting for fetal weight there is a 4% decline in body mass due to resource scarcity (Kirkpatrick, 1976). Yearlings can lose even more body mass during their first pregnancy due to stress (Kirkpatrick, 1976). When food availability and pregnancy are factored in, yearly variation in the body mass of white-tailed deer can approach 30% (Batchelor and Mead, 2007).

The constant fluctuation in body mass is difficult to capture using available estimation techniques dependent on skeletal measures. As indicated above, one technique commonly used today relies on bone size to predict body mass. Although it is generally true that big bones correlate with big bodies and vice versa, this relationship cannot capture many of the above seasonal shifts in body mass, nor are articular end dimensions directly modified by body mass after growth. In what follows, we propose a new technique of measuring skeletal elements that partially overcomes this problem.

A Warrant For, and Introduction of a New Technique

Skeletal tissue is a functional tissue that adapts to stresses encountered during life (Frost, 1987, 2003, 2004). The primary model for interpreting differences in long bone diaphysis shape focuses on bone's reaction to mechanical deformation. Long bone diaphyses respond to loading (or lack thereof) during life by depositing and resorbing bone in order to limit strain to a particular threshold (Frost, 2003). This ”thermostat” system minimizes the risk of fracture while also minimizing the amount of skeletal material present (Frost, 2003). A number of variables, including genetic background, environment, and behavior, modify this relationship; this larger phenomenon has been referred to as bone functional adaptation (Ruff et al., 2006).

One technique used to interpret changes in bone functional adaptation is cross-sectional geometry, which models long bone diaphyses using beam theory. The amount and distribution of bone around the neutral axis of a particular skeletal element is used to create estimates of bending strength in several directions (Ruff, 2000). Since the early 1980's, the relationship between diaphyseal morphology and loading has provided a theoretical model allowing the interpretation of behavior in the archaeological and paleontological record via cross-sectional geometry (Ruff, 2000). Studies of long bone cross-sectional changes due to exercise have used both murine models (Devlin, 2011; Hamrick et al., 2000; Judex and Carlson, 2009) and human athletes (e.g., Nikander et al., 2010; Shaw and Stock, 2013), but also occasionally other animal models, such as domestic sheep (*Ovis aries*) (Lieberman, 1996; Lieberman et al., 2004).

The primary predictor of bone cross-sectional properties is body mass, as body weight is the base load to which bone is exposed (Moro et al., 1996). During human adolescent bone acquisition, body mass explains up to 88% of the variation in cross-sectional properties, more than any other variable (Ruff, 2003a, 2003b; van der Meulen et al., 1996). Bone strength measurements of the femur correlate with weight across all ages (Robbins et al., 2010; Stein et al., 1998). This suggests that cross-sectional geometry has strong potential to predict body mass in a wide variety of animals.

Importantly, long bone diaphyses remodel to match changes in body mass (Ionova-Martin et al., 2010). Calorically-restricted animals lose bone mass along with body mass despite otherwise consistent mineral and nutritional intake (Lee et al., 1986, 1993; Talbott et al., 1998), and this affects the cross-sectional geometry of long bone diaphyses. In a sample of mice that had reduced weight due to calorie restriction after adulthood, for example, cortical area was a much better predictor of body mass than femoral head diameter (Hamrick et al., 2000). Reduced cortical area was also observed in human women with lower-than-average body mass, whether due to healthy weight variation or excessive weight loss from anorexia nervosa (Galusca et al., 2008). On one hand, the bone dimensions typically used to estimate mass of white-tailed deer reach maximum size before maximum body mass is reached (Batchelor and Mead, 2007; Emerson 1978; Purdue 1987; Wolverton et al. 2007), thus dimension size may not reflect adult body mass, and certainly not weight changes throughout life. Variability in cross-sectional geometry of long bone diaphyses, on the other hand, does not suffer these issues and therefore is particularly applicable to estimating white-tailed deer body mass.

Metapodials are an ideal element to use due to their weight-bearing role and their tendency to preserve well in zooarchaeological assemblages (Lyman 1984, 1994). Linear measurements of metapodal bones have strong relationships with body mass (Densmore, 2009; Morris, 2003; Purdue, 1989). Bone diameter is also significantly correlated with body mass in cervids, even more strongly than bone length (Scott, 1987). This mirrors patterns in humans, where diaphysis measurements respond more plastically to changes in body mass than do articular ends and better reflect current body weight (Ruff et al., 1991). This suggests the cross-sectional changes that impact bone diameter may be robust predictors of body mass at death, more so than other, more typically used measurements. In this paper, we first develop new equations using the cross-sectional geometric properties of white-tailed deer metapodials to predict body mass. Second, we compare equations using long bone diaphyseal properties to those using articular surface measurements to evaluate the accuracy—closeness of the estimate to the true value—of two methods of body mass prediction.

Materials and Methods

Metapodia from 64 white-tailed deer were obtained from wild-shot individuals during the first weekend of the central Missouri firearm hunting seasons, November 2014 and 2016 (Johnston, 2021). Individuals were sorted into three ontogenetic categories as described by Purdue (1983a): unfused epiphyses (<20 months for females, <17-23 months for males), fused epiphyses with visible growth plate (20-29 months for females, and 23-29 months for males), and fused epiphyses with no remaining growth plate (29+ months for males and females). Sample sizes varied slightly between metacarpals (MC) and metatarsals (MT) because some epiphyses were damaged during disarticulation and processing, and fewer forelimbs than hindlimbs were available due to trophy skinning techniques (Table 1).

Carcass weight to the nearest pound was obtained from each deer carcass minus distal limb elements, viscera, hide, and head. The resulting ‘dressed carcass weight’ reflects the necessities of collecting data at a processing plant, and it is this weight rather than total live weight that we estimate. Distal limb elements were retained during skinning, and subsequently macerated to remove flesh and extract the metapodial.

Table 1: Sample sizes for each metapodial, based on fusion as a proxy for age.

	L MT	**R MT**	**L MC**	**R MC**
Unfused	9	9	8	11
Partially Fused	9	12	12	12
Completely Fused	42	43	37	38

NOTE: L, left; R, right; MT, metatarsal; MC, metacarpal

In order to directly compare predictions from articular ends to those from diaphyses without confounding effects from different researchers and samples, we duplicated the measurements taken by Purdue (1987) using our sample. Measurements of metapodial articular surface size were taken (Fig. 1), and two articular areas were calculated (Purdue, 1987). While Purdue referred to them as “cross sectional areas,” we refer to them as “articular areas” here to avoid confusion with the cross-sectional geometry terms. What we term the metapodial “proximal articular area” (PAA) was called metatarsal/metacarpal proximal cross-sectional area by Purdue (1987). Metapodial proximal articular area (MTPAA and MCPAA) was calculated following Purdue (1987): he assumed a roughly elliptical shape for the proximal metatarsal and used $\frac{MTPW}{2} \times \frac{MTPD}{2} \times \pi$ to estimate area, where MTPW is the maximum mediolateral width of the proximal end and MTPD is the maximum anteroposterior depth of the proximal end (Fig. 1A). A similar procedure was followed for MCPAA (Fig. 1C). The maximum metapodial distal articular width (MTDW and MCDW) is simply the latero-medial breadth of the distal metapodial (Fig. 1B and 1D). All measurements were taken using digital calipers to the nearest 0.1mm.

To calculate cross-sectional geometry, metapodial shafts were bisected at 50% of total length and the cross-section of the shaft was scanned into a JPEG file (Fig. 1E), oriented using the proximal articular facets and bone shape to determine orientation. Total cross-sectional area (TA) and cortical area (CA), which are proportional to long bone rigidity under compression, and polar second moment of area (J), which approximates bone rigidity under torsion, were calculated from the JPEG files using MomentMacro (Ruff 2006).

Least squares regression was used to predict dressed carcass weight from bone measurements. Mass was transformed using a cube root and areas with the square root to linearize the regressions. The analysis was conducted using multiple regression, with fusion status used as an interaction variable. Separate regressions for males and females would be ideal, but sex cannot be determined from isolated metapodia. Therefore, sexes were combined in our analysis. Regressions were calculated using Program R (R Core Team, 2016).

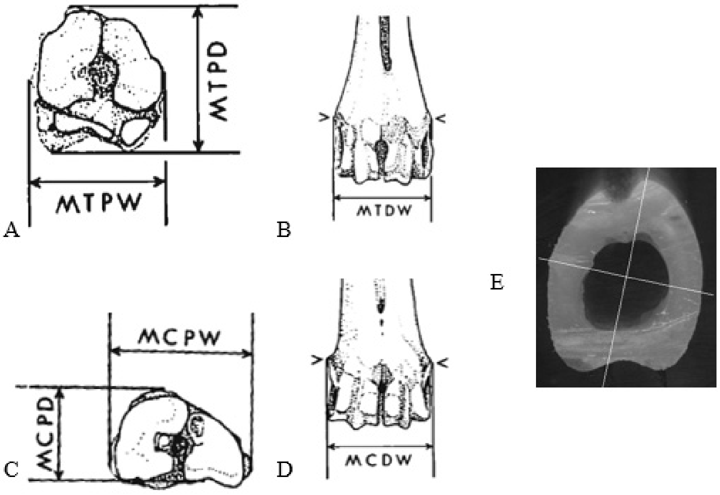


Fig. 1. Dimensions measured for each metatarsal. A: metatarsal proximal articular area (MTPAA). B: metatarsal distal width (MTDW). C: metacarpal proximal articular area (MCPAA). D: Metacarpal distal width. E: example cross-section of shaft used to estimate cross-sectional geometric properties. Images A–D from Purdue (1987) with permission.

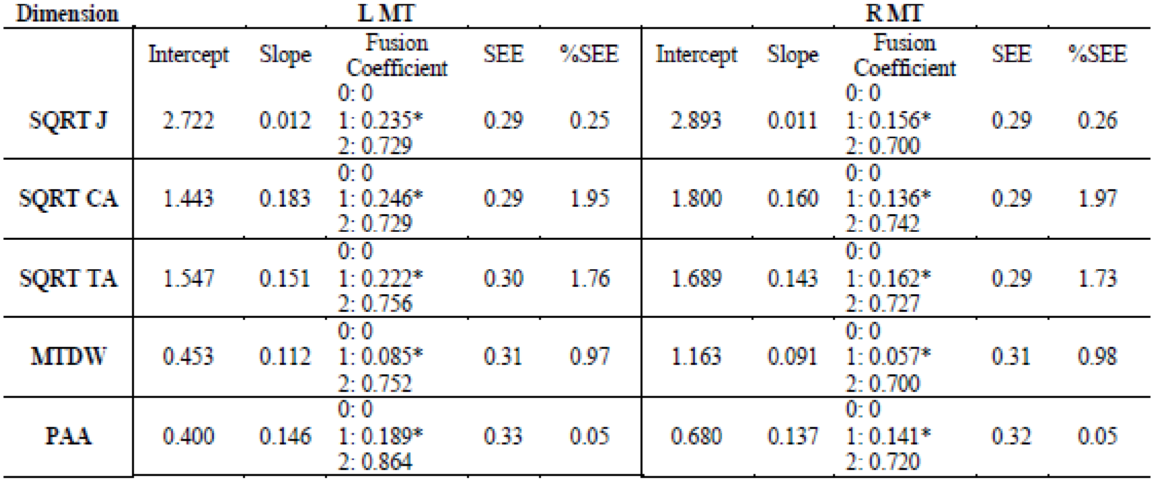
Results

Means and standard deviations for the linear and cross-sectional dimensions of each category of metapodial are given in Table 2. Right and left metatarsals were separated to avoid double-counting individuals and to determine if there was any difference by side. Wilcoxon rank sum tests suggest there is no significant difference between any left and right metapodial measurements outside of metacarpal proximal articular area ($p<0.001$). Preferring to err on the side of caution, both anatomical sides are retained in the tables. Regression equations predicting dressed body weight from the pooled age metapodials are found in Tables 3 and 4. Regression equations were run both with and without fusion as an interaction variable; fusion as a proxy for age is a significant predictor versus the pooled sample without the interaction, increasing R-squared values for regressions by at least 0.2. Therefore, the equations with fusion as an included variable are presented here. Significant equations for metapodials with individual age as a covariate are presented in Table 5.

Table 2: Means calculated for each metapodial, with standard deviations in parentheses.

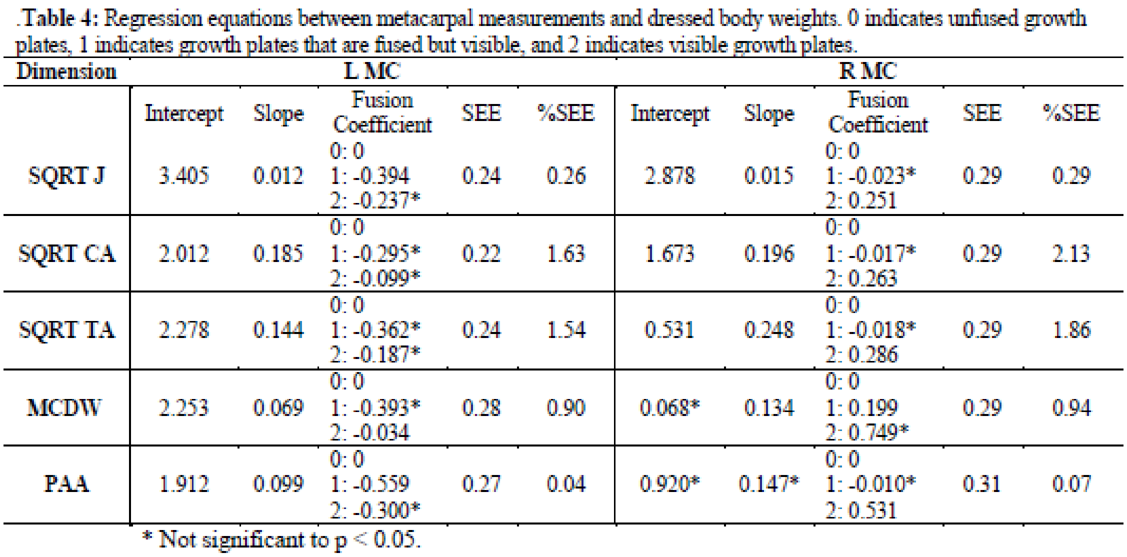
Dimension	**L MT (n=60)**	**R MT (n=64)**	**L MC (n=57)**	**R MC (n=61)**
J (torsional rigidity)	14003.90 (4963.98)	13248.5 (5226.76)	9630.23 (3453.43)	9766.41 (3637.07)
CA (cortical area)	224.34 (45.41)	218.06 (47.85)	183.10 (34.98)	184.52 (37.28)
TA (total area)	296.57 (54.56)	288.73 (57.58)	241.84 (45.38)	243.40 (47.74)
MTDW & MCDW	32.19 (1.80)	32.09 (2.04)	30.10 (2.25)	30.13 (2.01)
PAA (proximal articular area)	617.53 (66.68)	601.87 (64.06)	591.69 (126.75)	478.68 (61.35)

Table 3: Regression equations between metatarsal measurements and dressed body weights. 0 indicates unfused growth plates, 1 indicates growth plates that are fused but visible, and 2 indicates no visible growth plates.



Dimension	L MT					R MT				
	Intercept	Slope	Fusion Coefficient	SEE	%SEE	Intercept	Slope	Fusion Coefficient	SEE	%SEE
SQRT J	2.722	0.012	0: 0 1: 0.235* 2: 0.729	0.29	0.25	2.893	0.011	0: 0 1: 0.156* 2: 0.700	0.29	0.26
SQRT CA	1.443	0.183	0: 0 1: 0.246* 2: 0.729	0.29	1.95	1.800	0.160	0: 0 1: 0.136* 2: 0.742	0.29	1.97
SQRT TA	1.547	0.151	0: 0 1: 0.222* 2: 0.756	0.30	1.76	1.689	0.143	0: 0 1: 0.162* 2: 0.727	0.29	1.73
MTDW	0.453	0.112	0: 0 1: 0.085* 2: 0.752	0.31	0.97	1.163	0.091	0: 0 1: 0.057* 2: 0.700	0.31	0.98
PAA	0.400	0.146	0: 0 1: 0.189* 2: 0.864	0.33	0.05	0.680	0.137	0: 0 1: 0.141* 2: 0.720	0.32	0.05

* Not significant to $p < 0.05$.



.**Table 4:** Regression equations between metacarpal measurements and dressed body weights. 0 indicates unfused growth plates, 1 indicates growth plates that are fused but visible, and 2 indicates visible growth plates.

Dimension	L MC					R MC				
	Intercept	Slope	Fusion Coefficient	SEE	%SEE	Intercept	Slope	Fusion Coefficient	SEE	%SEE
SQRT J	3.405	0.012	0: 0 1: -0.394 2: -0.237*	0.24	0.26	2.878	0.015	0: 0 1: -0.023* 2: 0.251	0.29	0.29
SQRT CA	2.012	0.185	0: 0 1: -0.295* 2: -0.099*	0.22	1.63	1.673	0.196	0: 0 1: -0.017* 2: 0.263	0.29	2.13
SQRT TA	2.278	0.144	0: 0 1: -0.362* 2: -0.187*	0.24	1.54	0.531	0.248	0: 0 1: -0.018* 2: 0.286	0.29	1.86
MCDW	2.253	0.069	0: 0 1: -0.393* 2: -0.034	0.28	0.90	0.068*	0.134	0: 0 1: 0.199 2: 0.749*	0.29	0.94
PAA	1.912	0.099	0: 0 1: -0.559 2: -0.300*	0.27	0.04	0.920*	0.147*	0: 0 1: -0.010* 2: 0.531	0.31	0.07

* Not significant to $p < 0.05$.

In our sample, cross-sectional properties performed at least as well as our replication of Purdue's articular dimensions when judged by standard error of the estimate and R-squared values (Table 5). However, our sample performed less well than Purdue's, and this discrepancy is explored below.

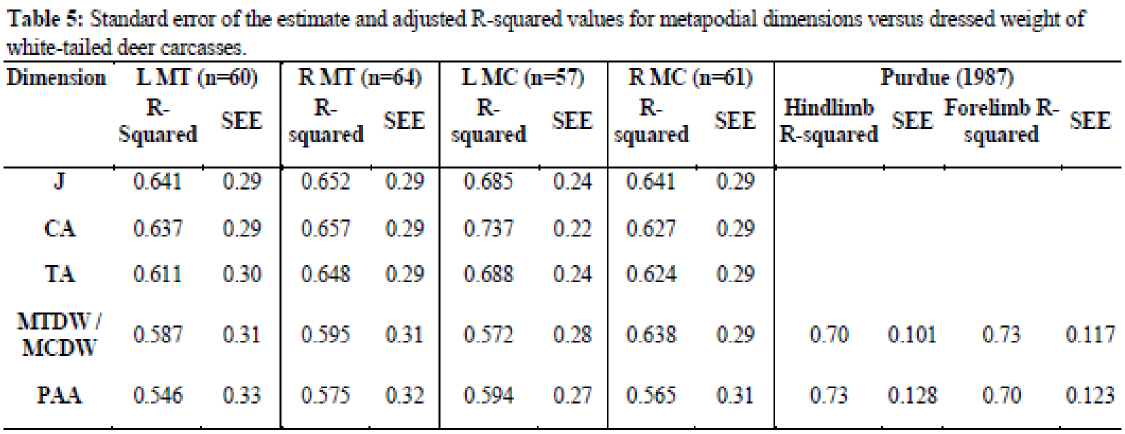


Table 5: Standard error of the estimate and adjusted R-squared values for metapodial dimensions versus dressed weight of white-tailed deer carcasses.

Dimension	L MT (n=60)		R MT (n=64)		L MC (n=57)		R MC (n=61)		Purdue (1987)			
	R-Squared	SEE	R-squared	SEE	R-squared	SEE	R-squared	SEE	Hindlimb R-squared	SEE	Forelimb R-squared	SEE
J	0.641	0.29	0.652	0.29	0.685	0.24	0.641	0.29				
CA	0.637	0.29	0.657	0.29	0.737	0.22	0.627	0.29				
TA	0.611	0.30	0.648	0.29	0.688	0.24	0.624	0.29				
MTDW / MCDW	0.587	0.31	0.595	0.31	0.572	0.28	0.638	0.29	0.70	0.101	0.73	0.117
PAA	0.546	0.33	0.575	0.32	0.594	0.27	0.565	0.31	0.73	0.128	0.70	0.123

Discussion

The most recent set of equations for predicting the dressed body mass of white-tailed deer based on bone dimensions comes from Purdue (1987). Importantly, he notes that:

> Differential growth of body parts, particularly the rapid development of lower leg bones relative to the slow accumulation of body weight, makes the estimation of weight for young deer inaccurate…estimates based on elements with fused epiphyseal plates are more trustworthy, but even here, body weight often continues to increase after the time of fusion. (Purdue 1987:8)

We applied a more plastic (from the perspective of the individual deer) set of bone measurements—cross-sectional geometry—that should adapt to current body mass and address the issues Purdue raised. Cross-sectional properties should change and adapt to current mass, whether the individual is a juvenile or a completely fused adult. R-squared values and SEE were calculated in order to compare our results both with Purdue's (1987) previously published formulae for estimating white-tailed deer dressed body mass from measurements of proximal articular surface (PAA) and with equations generated from articular surface measurements in our sample. The cross-sectional variables we measured had higher R-squared values than our replications of Purdue's (1987) articular end measurements (Table 5). This was expected as cross-sectional properties and particularly total cross-sectional area should be responsive to compressive forces—the main force placed upon the bones by body mass.

We compared our mixed-sex regressions to Purdue's (1987) mixed-sex regressions for metapodial articular surfaces. Our replications of Purdue's (1987) metapodial measurements (MTDW, MCDW, PAA) typically explain less variation in body mass (have lower R-squares) than do his measurements, and our replications also frequently have greater standard errors of the estimate than do his measurements (Table 5). There are two likely reasons for these differences. First, Purdue's sample was made up of 13 males and 33–36 females (depending on the dimension under scrutiny); our sample included 37–46 males and 17–21 females. Given the species is sexually dimorphic (e.g., Wolverton et al. 2009), it is likely the difference in sex ratios (Purdue 1m:2.54f; Johnson 2.17m:1f) is having an influence on each sample's predictive accuracy. Second, Purdue's sample of males and females only includes individuals ≥42 months of age, resulting in a relatively ontogenetically homogeneous set of animals that have most likely reached their maximum body growth. In contrast, our sample includes individuals from across the growth spectrum. Major differences in the ontogeny of individuals included in each sample are also likely having a major influence on the amount of variability in dressed carcass weight. Because of the likely influences of sexual and ontogenetic differences between our sample and Purdue's, we believe any indication of whether cross-sectional geometry is a better predictor of body mass than articular end dimensions must be derived from comparisons of those measurements from our sample alone.

Purdue (1987) converted the weight of the dressed deer carcasses in his sample to live weights. We employed a similar tactic and estimated live weights using Hamerstrom and Camburn's (1950) equation for converting dressed weight to live weight. Using estimated live weights slightly increased the standard error and R-squared values for equations predicting body mass from linear and cross-sectional measurements. This is expected, since adding an estimated parameter for live weight would introduce more error into the final result. Therefore, these equations are not presented here. Our equations based on directly measured dressed carcass weights do not preclude estimating whole body mass based on Hamerstrom and Camburn’s (1950) equation, Roseberry and Klimstra’s (1975) equation, or any other such equations.

Our analysis bears some similarities to human body mass estimations based on cross-sectional geometry. The standard error of the estimate (SEE) and %SEE for our deer sample were, however, much lower than the SEE and %SEE reported for similar regressions in other organisms, including humans, never reaching greater than 2% SEE (Tables 3 and 4). In comparison, when body mass equations were generated for juvenile human remains, the %SEE were never less than 5% SEE (Robbins, Schug and Goldman, 2014). This may be because of differences in quadrupedal versus bipedal locomotion, which would confine movement to particular planes, or differences in body composition between humans and white-tailed deer. Deer also have less variation in lower limb activity than do humans, which could influence the error rates.

Based on comparable SEE values and the highest R-squared value, cortical area (CA) was the best predictor of dressed body mass for our sample. This is theoretically plausible as cortical area is proportional to overall axial loading of the limb. Second, polar moment of the area (J) and total area (TA) of the metapodials were typically high-performing measurements, confirming Robbins and colleagues (2010) conclusion that cross-sectional measurements of the diaphyses were generally better predictors of body mass than linear measurements of articular ends.

There is an additional reason why cross-sectional measurements resulted in higher R-squared values and lower SEE than articular ends in our sample. Linear measurements of articular ends estimate body size (e.g., height, length), not body mass. As noted by Purdue (1987), size is a static property that will not be altered after the secession of growth, but weight is a dynamic property that will regularly vary across an individual's life. For example, two individuals of the same height may have drastically different weights at any point across their lifespans. Therefore, cross-sectional properties are likely to correlate well with body weight at the time of death, as opposed to adult linear measurements, which correspond to body size at the time of maturity.

Cross-sectional measurements may then have less broad utility than articular end measurements, but still may serve a role when available for analysis. One potential difficulty with cross-sectional geometry is that it is derived from shaft dimensions. Many long-bone articular ends are quite dense and tend to survive well in the archaeological record but are frequently damaged by predator gnawing and other taphonomic processes (e.g., Lyman, 1984, 1994, 2014; Marean and Frey, 1997; Marean and Spencer, 1991). Long bone diaphyses or shafts, in contrast, are often broken to facilitate marrow extraction (e.g., Noe-Nygaard, 1977) or simply through taphonomic processes. But a diverse array of evidence suggests that long bone shafts may often preserve sufficiently well relative to articular ends that the former provide larger minimum numbers of elements (MNE) than the latter (Marean et al., 2004). Even if metapodial shafts have been split, refitting fragments can produce sufficiently anatomically complete specimens that their cross-sectional geometry can be measured. Cross-sectional measurements can provide a supplemental line of evidence that can aid in zooarchaeological analyses.

One concern is that it may be difficult to locate the midshaft in an incomplete metapodial. Similar questions have been asked about human specimens, and it has been suggested that CA maintain mean accuracy from between 40-78% of overall length in the human tibia, while J is much more restrictive (Sladek et al, 2010). As the deer metapodial is more consistent in shape and has fewer muscle attachments than the human tibia, it may be feasible to use CA over a similar range to estimate mass even when the exact midshaft is unclear.

One benefit to diaphyseal cross-sections is that they do not rely on anatomical landmarks that may be destroyed or deformed by predator gnawing, weathering, or abrasion. A disadvantage of using diaphyses is they are typically diagnostic only to taxonomic Family, and sometimes only to taxonomic Order. For instance, there are several North American artiodactyls with adult body size very similar to white-tailed deer and thus far taxonomically diagnostic morphological features of the long-bone diaphyses are unknown (e.g., Hildebrand, 1955; Jacobson, 2003; Lawrence, 1951). Therefore, applying our regression formulae for white-tailed deer to bone assemblages that include remains of white-tailed deer, mule deer (*O. hemionus*), pronghorn (*Antilocapra americana*), and bighorn sheep (*Ovis canadensis*) will not doubt provide inaccurate estimates of meat amounts.

Our project suggests that cross-sectional measurements are good predictors of body mass, but we emphasize that the inclusion of other variables may increase their accuracy. We were not able to record the exact ontogenetic ages of specimens such as might be accomplished by noting aspects of tooth eruption and wear (e.g., Severinghaus, 1949; Taber, 1963). The ordinal-scale categories we used show the occasional impact of age on body mass estimates, typically between fully grown individuals and younger individuals, something previously noted by others (Emerson, 1978; Purdue, 1987). Importantly, it suggests caution when applying our method to mixed-age samples. Samples of known-age and sexed individuals would allow age–sex-specific regression lines that would be very useful for predicting body mass.

Conclusion

We present a new set of regression equations to predict the body mass of white-tailed deer. These equations are based on a biometric property previously unexplored in this species. Cross-sectional geometry of long bone diaphyses has been shown to be a useful tool for estimating human body mass, and we here expand its use to zooarchaeological applications. Cross-sectional properties explain more of the variation in body mass in white-tailed deer than dimensions of articular ends. These estimates compare favorably to previous research on deer body mass estimates. This suggests that our equations could be useful in refining estimates of total deer body mass by allowing calculations based on non-typically measured skeletal parts (long-bone diaphyses). Such would provide an assessment of diet that is more-or-less independent of more traditional measurement techniques. Despite the preservation challenges in measuring bone shafts, when available, our method should have wide-ranging applicability to the zooarchaeological record.

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CHAPTER 5

CONCLUSIONS

My research focuses on how body mass and body composition influence the cross-sectional geometry of bone. I use samples from modern contexts to better understand how fat mass, lean body mass, and total body mass may play a role in bone bending strength and take into account lifestyle details that may make this relationship more complex. My findings suggest that body mass is a critical component of the bending strength of the upper limb as well as the lower limb in humans, but that body mass and lean muscle mass work together to explain the strength of the femur. Lifestyle factors like exercise, often viewed as strong determinates of bone bending strength, operate more indirectly on bone by modifying total mass and body composition. While the majority of this research focuses on humans, it also suggests that using cross-sectional geometry to estimate body mass has applications in zooarchaeology and other fields. The central conclusions of this research are as follows.

1. Structural equation modeling (SEM) is an under-utilized approach to understanding complex systems in biological anthropology. Here, it was particularly useful in the analysis of purported causal relationships among activity, body mass, and lean muscle mass and their effect on skeletal properties. Body mass and lean muscle amount often have a combined influence on cross-sectional properties, and body mass is not always the primary driver of cross-sectional properties. Exercise did not have a large direct effect on bone strength; however, exercise modified body mass and lean mass, indirectly modifying the bending strength of bone. Exercise frequency affected males and females

differently: in males, it decreased body mass and increased muscle mass, but only affected lean mass in females. This also result also confirms the need to analyze males and females separately when evaluating bone and body mass relationships.

2. Body mass exerts at least as strong an influence on the humerus as it does on the femur. This suggests that standardization by body mass of robusticity in the upper limb is critical for understanding humeral cross-sectional geometry even in the absence of direct loading. This also may suggest that the effect of mass is likely systemic on the skeletal system, perhaps triggered by hormonal signaling. The combined influence of muscle and body mass on the humerus should be explored in a larger sample of active adults to further understand this relationship. The results of this study also suggest that other bones than those of the lower limb have potential use for estimating body mass in archaeological samples.
3. It is possible to predict the body mass of white-tailed deer using the diaphyseal measurements of the metapodial. Cross-sectional properties explain more of the variation in body mass in white-tailed deer than dimensions of articular ends, which have been a previous method of estimating mass. This suggests that our equations could be useful in refining estimates of total deer body mass by allowing calculations based on non-typically measured skeletal parts (long-bone diaphyses). Such estimates would provide an assessment of deer body mass that is more-or-less independent of more traditional measurement techniques. Our method should have wide-ranging applicability to the zooarchaeological record when the metapodial is available for analysis.

VITA

Rob’yn Johnston has been a doctoral student at the University of Missouri-Columbia after completing her Masters in Biological Anthropology in 2014. In her time at U. Missouri, she worked with a wide range of data samples, including cadaveric, field, and large-scale data. She has been a teaching assistant in the Department of Pathology and Anatomical Sciences for their Anatomy program, taught in the Department of Anthropology, and worked as a curatorial photographer at the University of Missouri Museum of Anthropology. She has also assisted with archaeological field work in Uzbekistan.

Rob’yn’s research focuses on body mass, body composition, and their interaction in shaping the functional morphology of bone, particularly in modern human populations.

Rob’yn is excited to step into her full-time role as a Culture Resources Specialist at AECOM following her graduation, and to continue spreading her love of anthropology to a new generation of students as an adjunct professor at Palomar College.