



## Estimation of body mass in white-tailed deer (*Odocoileus virginianus*) using cross-sectional geometry of the metapodial

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### ABSTRACT

Zooarchaeologists have developed and used several techniques for estimating the body mass of individual prey animals. Many of these are based on skeletal variables such as minimum number of individuals, weight of remains, or linear dimensions of long bone articular ends. All of these techniques fail to account for individual variability in body mass across the lifespan driven by the primary productivity of the landscape, sex, ontogeny, and season of individual death. Because skeletons are weight-bearing, they constantly remodel in response to changes in body mass, making long bone cross-sectional properties an ideal metric for predicting body mass. Cross-sectional geometric properties of distal limb bones and body mass of white-tailed deer (*Odocoileus virginianus*) were measured in a sample of 64 recently harvested individuals. Best-fit regressions between cross-sectional skeletal dimensions and dressed body weight produce higher R-squared values and lower standard errors of the estimate than regressions between dressed body weight and linear dimensions of long bone articular ends. Cross-sectional geometry can provide new useful line of evidence for estimating body mass of prey animals, when available.

### 1. 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, 2017). Furthermore, white-tailed deer have as many as 30 recognized subspecies and vary in size from the dwarfed Key Deer (*O. virginianus clavium*), which typically weight < 39 kg (Boughton et al., 2019), to northernmost species like the Dakota white-tailed deer (*O. virginianus dacotum*), which typically weight approximately 100 kg (Innes, 2013). Anecdotally, the largest white-tailed deer reported have had estimated live weights in excess of 220 kg! Body weight is extremely

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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.

### 1.1. 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 affected 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.

### 1.2. 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 1980s, 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 metapodial 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.

## 2. 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

**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.

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.

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 D). All measurements were taken using digital calipers to the nearest 0.1 mm.

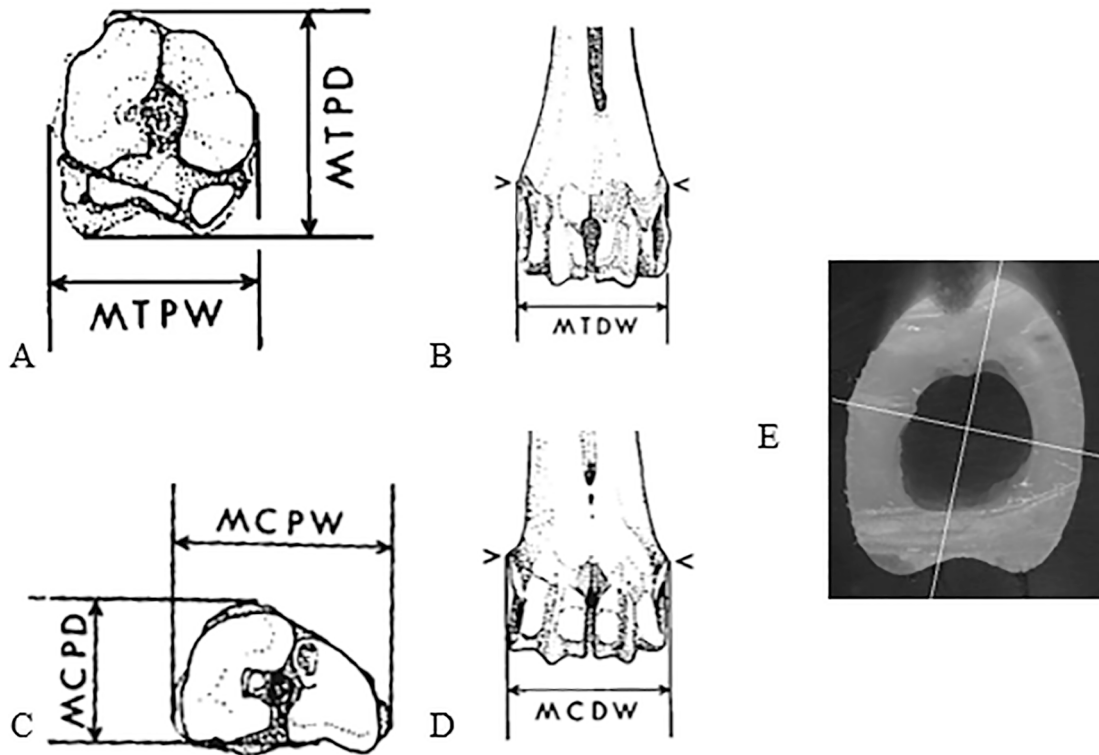
To calculate cross-sectional geometry, metapodial shafts were bisected at 50% of total length and the cross-section of the shaft was scanned into a JPEG file (Fig. 1E), oriented using the proximal articular facets and bone shape to determine orientation. Total cross-sectional area (TA) and cortical area (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).

## 3. 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.

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.



**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 (MCDW). E: example cross-section of shaft used to estimate cross-sectional geometric properties. Images A–D from [Purdue \(1987\)](#) with permission.

**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  $p < 0.05$ .

**4. 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

**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  $p < 0.05$ .

**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

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 1 m:2.54 f; Johnston 2.17 m:1 f) is having an influence on each sample's predictive accuracy. Second, Purdue's sample of males and females only includes individuals  $\geq 42$  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  $< 5\%$  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 maintains mean accuracy from between 40 and 78% of overall length in the human tibia, while J is much more restrictive (Sládek 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.

## 5. 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.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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