

Morphometric panel regression equations for predicting body mass in immature humans

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Abstract

Objectives: Predicting body mass is a frequent objective of several anthropological subdisciplines, but there are few published methods for predicting body mass in immature humans. Because most reference samples are composed of adults, predicting body mass outside the range of adults requires extrapolation, which may reduce the accuracy of predictions. Prediction equations developed from a sample of immature humans would reduce extrapolation for application to small-bodied target individuals, and should have utility in multiple predictive contexts.

Materials and Methods: Here, we present two novel body mass prediction equations derived from 3468 observations of stature and bi-iliac breadth from a large sample of immature humans ($n = 173$) collected in the Harpenden Growth Study. Prediction equations were generated using raw and natural log-transformed data and modeled using panel regression, which accounts for serial autocorrelation of longitudinal observations. Predictive accuracy was gauged with a global sample of human juveniles ($n = 530$ age- and sex-specific annual means) and compared to the performance of the adult morphometric prediction equation previously identified as most accurate for human juveniles.

Results: While the raw data panel equation is only slightly more accurate than the adult equation, the logged data panel equation generates very accurate body mass predictions across both sexes and all age classes of the test sample (mean absolute percentage prediction error = 2.47).

Discussion: The logged data panel equation should prove useful in archaeological, forensic, and paleontological contexts when predictor variables can be measured with confidence and are outside the range of modern adult humans.

KEYWORDS

bi-iliac breadth, children, juveniles, stature

1 | INTRODUCTION

Because of its robust covariation with a wide variety of ecological and physiological characteristics, body mass is a highly informative variable for neontologists and paleontologists alike. Among the subfields of anthropology, prediction of body mass is a frequent objective in archeology (e.g., Holt, 2003; Kurki, Ginter, Stock, & Pfeiffer, 2010; Pomeroy and Stock, 2012; Rosenberg, Zuné, & Ruff, 2006; Ruff et al., 2006; Siegmund and Papageorgopoulou, 2011; Vercellotti, Alclati, Richards, & Formicola, 2008), forensics (e.g., Moore and Schaefer, 2011; Schaffer,

2016) and paleontology (e.g., Arsuaga, Lorenzo, Gracia, & Marti, 1999; Ruff and Walker, 1993; Ruff, Trinkaus, & Holliday, 1997; Trinkaus, Churchill, Ruff, & Vandermeersch, 1999). This objective has often been achieved through the development of body mass prediction equations (BMPEs): univariate or multivariate linear regressions of dental or skeletal dimensions on body mass. For application to hominin individuals in archeological or paleontological contexts, two primary classes of BMPEs have been developed: “mechanical” equations, which rely on dimensions of load-bearing skeletal elements as predictor variables (Elliott, Kurki, Weston, & Collard, 2016a,b; Grine, Jungers, Tobias, &

Pearson, 1995; McHenry, 1992; Ruff, Scott, & Liu, 1991; Ruff et al., 2012; Ruff, 1994, 2000a; Squyres and Ruff, 2015;), and “morphometric” equations, which rely on stature and living bi-iliac breadth to model¹ the overall size of the body (Ruff, 1991, 1994, 2000b; Ruff, Niskanen, Junno, & Jamison, 2005; Ruff et al., 1997). In their evaluation of the relative accuracy of these two approaches, Auerbach and Ruff (2004) recommended morphometric BMPEs whenever the relevant variables (stature and bi-iliac breadth) were available.

Regardless of the choice of predictor variables and applicative goals for BMPEs, all prediction equations are constrained by the availability of appropriate reference samples: paleontologists are limited to generating BMPEs from living taxa, while archeologists are limited to generating equations from living human populations. The limitations imposed by sample availability occasionally necessitate extrapolation beyond the bounds represented by the reference sample, including predicting body masses from predictor values that are smaller or larger than those of the reference sample, or predicting body mass in taxa outside the reference sample's phylogenetic bracket (*sensu* Witmer, 1995). In a narrow sense, any extrapolation violates a fundamental assumption of the statistical process of prediction: that members of the predicted sample belong to the same population as the reference sample (Smith, 2009). However, due to the limitations of sample availability, strict maintenance of this assumption would render prediction equations ineffectual. In practical application, the primary negative consequences of extrapolation are greater uncertainty around predicted values (Aiello, 1992; Hens, Konigsberg, & Jungers, 1998; Konigsberg, Hens, Jantz, & Jungers, 1998; Ruff, 2007) and a general decrease in predictive accuracy (Yapuncich, 2017a; Yapuncich, Gladman, & Boyer, 2015).

Of direct relevance to this study, extrapolation decreases predictive accuracy when applying BMPEs derived from adult modern human populations to small-bodied humans, whether the samples of interest represent archeological (Kurki et al., 2010) or modern juvenile (Walker, Yapuncich, Sridhar, Cameron, & Churchill, 2017) populations. To mitigate this loss of predictive accuracy, several researchers have developed mechanical BMPEs to apply to juvenile or otherwise small-bodied hominins (Robbins, 2007; Robbins, Sciulli, & Blatt, 2010; Robbins Schug, Gupta, Cowgill, Sciulli, & Blatt, 2013; Ruff, 2007; Ruff, Trinkaus, & Holliday, 2002; see also Cowgill, 2017). However, prior to this study, no juvenile-specific morphometric BMPEs have been available. Given the recommendations of Auerbach and Ruff (2004), developing juvenile-specific morphometric equations will likely be beneficial for forensic, archeological, and paleontological applications.

Previously published studies of juvenile BMPEs have used two different regression approaches to generate the predictive equations. For their equations, both Ruff (2007) and Robbins et al. (2010) used a longitudinal sample tracking 20 individuals (10 females and 10 males) from the Denver Growth Study (McCammon, 1970) from 6 months of age through late adolescence. For the entire sample, Ruff (2007) and Robbins et al. (2010) had a total of 690 observations (i.e., standardized radiographs of limb bones). To generate equations, these studies pooled the individuals by age and calculated ordinary least squares regressions for each age category between 1 and 17 years. Unfortunately, age-structured prediction equations have a practical disadvantage, as the age of the target individual must be inferred in order to determine the most appropriate equation (Robbins Schug et al., 2013). When applied to archeological or paleontological groups, which may differ from recent humans in either or both developmental rate and maturation milestones, it can be difficult to infer a specimen's age with confidence (Dean and Lucas, 2009; Dean and Smith, 2009).

As an alternative to the age-structured equations of Ruff (2007) and Robbins et al. (2010), Robbins Schug et al. (2013) generated prediction equations using panel regression models. Panel regression, a statistical technique borrowed from econometrics, is specifically intended for application to data representing repeated measures of subjects over a series of regular intervals (Baltagi, 2013; Dougherty, 2011). Panel regression models have two substantial advantages relative to age-structured least squares regressions. First, they do not require inference about the age of the target individual. Second, even after accounting for serial autocorrelation, the estimated parameters of panel regression models are more robust, as including both cross-sectional and longitudinal dimensions of the data confers more degrees of freedom. Despite these advantages, panel regression methods have rarely been used to analyze anthropometric growth studies (such as the Denver Growth Study modeled by Robbins Schug et al., 2013).

In this study, we use panel regression models to generate two novel morphometric BMPEs specific to immature humans. Our sample consists of 3,468 longitudinal observations of juvenile individuals ($n = 74$ females, 99 males) included in the Harpenden Growth Study (Tanner, Whitehouse, & Takaishi, 1966a,b). This study differs from previous studies that focused on predicting juvenile body mass (Robbins et al., 2010; Robbins Schug et al., 2013; Ruff, 2007) by (1) generating morphometric, rather than mechanical, BMPEs; (2) greatly increasing the size of the reference sample (3,468 vs. 690 observations); and (3) using panel regression to account for the autocorrelation of longitudinal observations rather than generating a series of age-structured least squares equations. We then evaluate the accuracy of the novel equations relative to the morphometric BMPE (the female equation of Ruff et al., 1997) previously identified as being the most accurate for human juveniles (Walker et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Body mass prediction equations

Panel regression models were derived from measurements of stature and living bi-iliac breadth collected during the Harpenden Growth

¹Although morphometric equations are frequently described as “modeling the body as a cylinder” (e.g., Cowgill, 2017; Nikita and Chovalopoulou, 2017; Pomeroy and Stock, 2012; Walker et al., 2017), this is technically inaccurate. If the body were modeled as a cylinder, the prediction equation would be $\text{Body Mass} = \pi \cdot (\text{BIB}/2)^2 \cdot \text{Stature}$ (in which BIB is bi-iliac breadth and represents the diameter of the cylinder, and stature represents its height). Morphometric equations can more accurately be described as multiple linear regressions with two independent variables (stature and bi-iliac breadth) that capture the globally maximum height and a locally maximum width of the body.

TABLE 1 Descriptive statistics (mean, standard deviation [SD], and range) for females in Harpenden growth study (HGS)

Age	Individuals	Stature (cm)			Bi-iliac breadth (cm)			Body mass (kg)		
		Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
4	10	101.4	3.4	97.4–106.0	16.8	0.8	15.5–18.2	16.8	1.4	14.9–19.1
4.5	14	105.7	3.8	99.9–112.3	17.4	0.8	16.1–18.8	18.0	1.7	15.7–21.0
5	19	109.1	3.3	103.5–115.3	17.8	1.0	15.6–19.3	18.9	1.8	16.1–21.9
5.5	27	112.8	5.1	100.2–122.0	18.3	1.0	15.8–19.9	20.0	2.3	15.0–24.6
6	27	116.0	5.2	102.4–126.0	18.6	1.0	16.4–20.1	20.7	2.4	15.4–26.1
6.5	34	118.7	5.4	104.6–128.5	19.0	1.0	16.7–20.5	21.7	2.5	15.9–27.3
7	37	121.5	5.5	107.0–132.3	19.4	1.0	17.1–21.1	22.9	2.8	16.6–29.9
7.5	42	123.2	6.5	108.9–135.3	19.6	1.2	16.9–21.6	23.5	3.4	16.1–32.2
8	47	126.4	6.5	110.2–138.3	20.1	1.2	17.1–21.9	25.0	3.6	16.8–32.8
8.5	49	128.6	6.7	113.0–141.5	20.4	1.3	17.4–22.6	26.2	3.8	17.9–34.7
9	53	130.8	6.9	115.2–144.5	20.8	1.2	17.6–22.9	27.5	4.2	17.9–37.2
9.25	21	133.9	5.2	126.7–145.7	21.2	1.3	18.7–23.1	29.3	4.2	23.5–38.3
9.5	62	133.5	6.8	119.0–148.0	21.2	1.3	18.4–24.3	29.1	4.3	20.9–40.5
9.75	24	137.4	5.4	129.1–149.8	21.8	1.3	19.5–24.6	31.1	4.4	24.8–41.4
10	70	136.5	6.7	121.0–151.0	21.6	1.3	18.4–24.8	30.5	4.4	22.2–44.3
10.25	31	140.2	5.4	132.0–153.2	22.3	1.3	19.5–25.2	32.6	4.5	25.3–47.0
10.5	68	139.3	7.0	123.1–155.5	22.1	1.4	19.2–25.4	32.3	4.8	22.8–46.8
10.75	37	143.1	5.9	132.8–158.0	22.7	1.4	19.2–25.6	34.1	4.3	27.0–45.6
11	67	142.1	7.3	125.3–159.9	22.6	1.4	19.3–26.3	34.1	5.0	23.4–48.3
11.25	40	144.7	6.2	130.8–158.4	23.1	1.3	20.5–26.7	36.3	4.3	27.9–45.4
11.5	63	145.1	7.6	127.8–163.3	23.2	1.5	20.4–27.2	36.3	5.6	23.8–53.8
11.75	48	147.6	6.8	134.0–164.4	23.7	1.5	20.5–27.6	38.2	4.9	29.4–49.1
12	58	148.7	8.0	129.6–165.5	23.9	1.6	20.4–28.0	38.9	6.5	25.2–60.8
12.25	46	151.2	6.5	137.1–166.6	24.3	1.5	21.2–28.3	40.7	5.4	31.5–51.2
12.5	51	151.5	7.8	132.9–165.5	24.3	1.6	21.3–27.8	41.2	6.9	26.4–62.5
12.75	43	153.3	6.9	134.4–167.5	24.7	1.5	21.6–27.9	42.6	5.8	27.9–54.4
13	48	154.9	7.2	137.7–168.5	25.0	1.5	21.9–28.0	44.4	7.0	30.5–64.0
13.25	37	155.2	6.6	141.0–166.1	25.1	1.5	21.2–27.9	44.7	6.6	30.9–57.7
13.5	43	157.1	7.1	140.2–168.7	25.6	1.5	22.7–28.6	47.4	7.4	31.9–66.5
13.75	33	157.3	7.2	141.7–169.1	25.6	1.5	23.0–29.0	46.9	6.1	32.8–56.9
14	37	159.6	6.8	143.0–169.9	26.0	1.6	22.9–29.2	49.8	7.5	34.3–68.2
14.25	24	159.4	7.7	143.8–170.5	26.0	1.6	22.8–28.2	49.5	7.9	35.6–62.0
14.5	35	160.5	6.4	144.3–172.1	26.3	1.7	22.7–29.2	51.7	8.1	36.5–68.6
14.75	20	160.0	7.1	144.9–172.3	26.5	1.5	23.1–29.0	50.3	7.9	36.6–64.1
15	34	161.1	6.2	145.9–173.0	26.8	1.7	23.4–30.1	53.0	8.4	36.6–71.3
15.5	20	161.3	6.4	146.7–172.2	27.6	1.9	23.7–30.4	53.6	9.6	38.9–75.7
16	32	161.7	6.1	147.2–172.4	27.4	1.8	24.2–30.5	54.5	7.8	38.3–72.7
17	30	161.3	6.4	147.4–173.1	27.4	1.7	24.2–30.4	55.2	8.4	39.3–75.6
18	21	161.8	6.9	147.8–173.8	27.7	1.6	24.2–30.3	56.2	7.8	39.2–73.4

TABLE 2 Descriptive statistics (mean, standard deviation [SD], and range) for males in Harpenden growth study (HGS)

Age	Individuals	Stature (cm)			Bi-iliac breadth (cm)			Body mass (kg)		
		Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
4	18	103.0	4.1	96.8–111.4	16.8	0.8	15.3–18.7	16.9	1.4	14.1–19.2
4.5	20	107.1	4.5	100.2–115.4	17.4	0.8	15.8–19.3	18.3	2.0	14.9–22.2
5	28	109.7	4.0	104.2–118.6	17.8	0.9	16.0–20.5	18.9	2.1	15.6–23.3
5.5	35	112.0	4.4	105.7–122.5	18.0	1.0	15.4–21.0	19.6	2.2	16.8–24.1
6	42	114.9	4.4	107.3–125.8	18.4	1.0	15.5–21.4	20.3	2.1	17.0–25.6
6.5	44	117.9	4.6	109.1–128.5	18.8	1.1	15.9–21.7	21.3	2.3	17.9–27.2
7	47	120.7	4.7	112.2–132.7	19.2	1.1	16.3–22.2	22.4	2.5	18.4–29.5
7.5	56	123.4	4.7	114.8–136.0	19.6	1.2	16.5–22.5	23.7	2.7	19.5–31.3
8	62	125.9	4.9	115.9–138.5	20.0	1.2	17.0–22.7	24.9	2.8	20.2–33.1
8.5	70	128.5	5.1	117.9–141.5	20.4	1.2	17.1–23.4	26.4	3.2	20.5–36.1
9	82	131.0	5.1	120.4–144.8	20.7	1.2	17.3–23.9	27.6	3.5	21.4–38.5
9.5	85	133.5	5.1	122.2–147.4	21.1	1.3	17.7–24.3	29.1	3.8	21.9–40.5
9.75	1	134.2	-	-	20.7	-	-	28.5	-	-
10	90	136.1	5.3	124.1–150.0	21.5	1.3	18.0–24.5	30.4	3.9	23.5–40.7
10.5	94	138.6	5.3	126.4–152.1	21.8	1.3	18.1–24.9	32.1	4.2	24.2–46.0
10.75	2	139.6	2.0	138.2–141.0	22.8	1.3	21.9–23.7	37.5	1.5	36.4–38.5
11	92	141.1	5.5	128.9–155.7	22.1	1.3	18.6–25.6	33.6	4.7	25.6–50.2
11.25	44	142.8	5.4	129.5–155.5	22.2	1.5	18.7–25.1	34.8	5.0	27.6–53.3
11.5	82	143.5	5.8	130.7–157.9	22.5	1.3	18.5–25.9	35.2	4.9	28.0–53.3
11.75	53	145.2	5.9	131.5–159.7	22.6	1.4	18.6–25.9	36.3	5.2	29.5–52.1
12	70	146.5	5.5	136.1–158.9	22.9	1.3	18.8–26.1	37.0	5.3	27.8–55.0
12.25	59	148.0	6.0	137.1–160.8	23.1	1.4	18.9–26.6	38.0	5.7	28.6–55.9
12.5	69	149.2	6.0	138.4–163.0	23.3	1.3	19.2–26.7	39.2	5.8	29.7–57.9
12.75	64	151.2	6.2	139.0–165.8	23.6	1.3	19.9–27.1	40.6	6.5	29.6–61.0
13	67	152.4	6.6	139.9–168.4	23.8	1.4	19.3–27.4	41.5	6.7	31.0–64.0
13.25	62	154.1	6.5	140.8–168.9	24.1	1.5	19.6–27.8	42.8	6.9	30.4–63.6
13.5	62	155.7	6.9	142.1–171.9	24.2	1.6	19.8–28.3	44.2	7.1	31.7–65.5
13.75	58	157.7	7.1	142.7–173.9	24.5	1.7	19.8–28.7	45.8	7.4	31.5–67.7
14	55	159.7	7.5	143.9–175.2	24.8	1.6	20.4–29.1	47.1	7.3	31.6–62.3
14.25	48	161.3	7.2	147.7–176.7	25.1	1.8	20.5–29.5	48.9	7.7	38.6–68.6
14.5	50	163.7	7.5	147.6–178.1	25.5	1.8	21.0–29.8	50.9	7.4	39.7–71.1
14.75	43	165.6	7.1	150.3–180.3	25.9	1.8	21.0–30.2	52.5	7.5	41.3–70.0
15	50	166.2	7.6	148.4–182.0	26.1	1.8	21.2–30.4	53.3	7.7	35.6–70.8
15.5	28	168.1	8.6	151.2–184.5	26.4	1.9	22.0–29.8	54.4	6.8	37.1–71.6
16	51	171.0	6.9	154.6–186.3	27.0	1.6	22.3–31.3	58.3	6.4	40.9–72.7
17	45	173.1	6.2	161.3–188.0	27.3	1.8	22.9–31.9	61.6	7.6	47.3–83.5
18	38	175.3	6.4	162.1–194.3	27.9	1.8	23.5–32.6	64.3	8.2	48.0–84.6

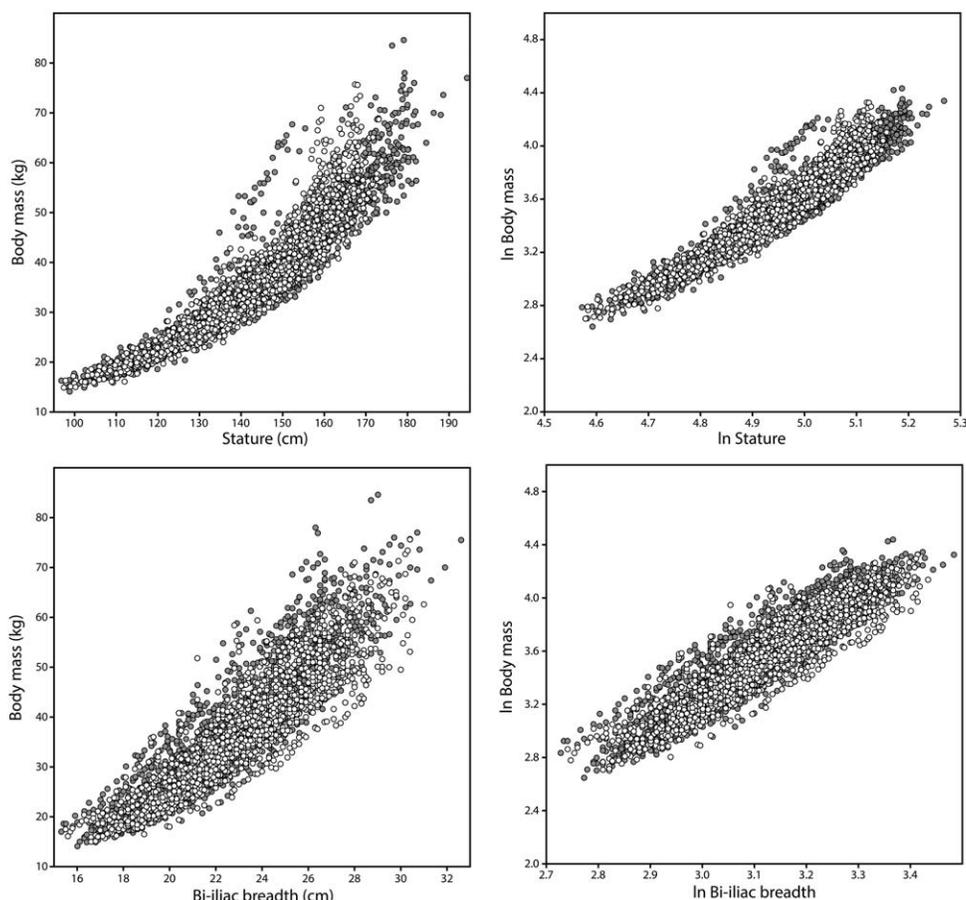


FIGURE 1 Scatterplots of bi-iliac breadth and stature against body mass with raw and natural log-transformed data. The most substantial impact of log-transforming data is to stabilize the variance of bi-iliac breadth. White circles indicate females; gray circles indicate males

Study (HGS) of London children started in 1948 (Tanner, 1981). The HGS provides a longitudinal sample consisting of 1,502 observations of 74 juvenile females (average observations per individual: 20.3, minimum: 6; maximum: 38) and 1966 observations of 99 juvenile males (average: 19.9; minimum: 4; maximum: 35). Summary statistics of the HGS sample are given for each time interval in Tables 1 and 2.

During the HGS, individuals were generally measured quarterly or semiannually on dates as closely centered on their birthdates as possible (e.g., an individual born on January 15th would ideally be measured on the 15th of April, July, and October). Over the course of the study, sampling frequency sometimes changed for some individuals (from quarterly to semiannually or annually). Due to heterogeneity of the sampling techniques over the course of the study, we conditioned the raw HGS data in two ways. First, because measurements were not always taken on the target date, we recentered all measurements to the nearest quarterly target dates (e.g., in the example above, a measurement taken on May 1st was recognized as the April 15th measurement). Second, because fewer measurements were recorded at younger and older ages, we restricted our sample to the more densely sampled ages (with a minimum of 20 observations) of 4 to 18 years old. Randomly missing observations result in an unbalanced panel comprised of 3,468 observations of 173 individuals across 39 time intervals. Boxplots of stature, bi-iliac breadth, and body mass for

these time intervals are shown in SOM Figure 1. Alternative resampling protocols (such as including all available data or only semi-annual observations) did not substantially impact the estimated parameters of the panel regressions (SOM Tables 1 and 2).

Morphometric BMPEs have not traditionally used log-transformed data (Ruff, 1994; Ruff et al., 1997, 2005; but see Ruff, 2007), but log-transformation has the beneficial properties of normalizing data and stabilizing variance. With a large reference sample such as the HGS data, normality of data is less of a concern. However, because the variance of both living bi-iliac breadth (BIB: cm) and stature (ST: cm) increases as body mass (BM: kg) increases (Figure 1), we generated equations using both raw and natural log-transformed data, with the raw data equation permitting a more direct comparison to previously published morphometric BMPEs.

Before generating panel regressions, Durbin-Watson tests (Durbin and Watson, 1950, 1951) were used to evaluate the degree of serial autocorrelation in both raw and natural log-transformed data. The Durbin-Watson statistic, d , is always a value between 0 and 4, with $d = 2$ indicating no autocorrelation. Values < 2 show positive autocorrelation, while values > 2 reveal negative autocorrelation. We expect the HGS data to exhibit positive autocorrelation (i.e., successive error terms are similar to one another), and d values less than 1 are typically treated as indicative of a problematic level of autocorrelation (Dougherty, 2011).

Panel regressions were performed using the 'plm' package in R (Croissant and Millo, 2008). There are two primary approaches for panel regression models, the "fixed effect" model and the "random effect" model. Both models are derived from a basic linear model:

$$y_{it} = a_{it} + b_{it}^T x_{it} + u_{it}$$

In which $i = 1, \dots, n$ are individuals, $t = 1, \dots, n$ are time intervals, a_{it} is the model intercept across individuals and time, b_{it}^T is the slope across individuals and time, and u_{it} is a random error term. The random error term can be broken down into two subcomponents: the individual error μ_i and the idiosyncratic error e_{it} . When independent variables are correlated with μ_i (i.e., the regressors are endogenous), the fixed effect model is preferred. When independent variables are not correlated with μ_i (i.e., the regressors are exogenous), the random effect model is preferred. With the HGS data, Hausman specification tests (Hausman, 1978) suggest that the fixed effect model is more appropriate. However, because the goal of this study is to generate a predictive (rather than descriptive) panel equation, we have chosen to utilize a random effect model. The fixed effect model treats the individual error term μ_i as an additional set of n parameters to be estimated and standardizes the variables for each individual by subtracting the mean (across time) of each term. This treatment generates some disadvantages, including the loss of many degrees of freedom in order to estimate the additional n set of μ_i parameters. More critically, standardization removes all individual-invariant variables and the intercept from the fixed effect model (Dougherty, 2011), which makes fixed effect models unsuitable for predictive applications (e.g., when longitudinal measurements for test cases are unavailable).

Because of the difficulty of determining sex in immature samples (Cunningham, Scheuer, & Black, 2016) and the similarity of skeletal proportions (such as the ratio of leg length to stature [Walker et al., 2017]) in immature humans, we present equations derived from a combined sample of males and females, and focus our analyses of accuracy on these equations.

2.2 | Predictive accuracy

As a test sample, we followed Walker et al. (2017) and used a global sample of 530 age- and sex-specific group annual means of human juveniles from Eveleth and Tanner (1976). Populations of African, Asian, New Guinean, and Indo-Mediterranean descent from 33 distinct geographic regions were aggregated into population means representing ages 6 to 12. Sample origins and descriptive statistics of these populations can be found in Walker et al. (2017), and we provide the transcribed Eveleth and Tanner (1976) dataset in the Supporting Information (SOM Table 3) as an easier-to-access resource for other researchers. Using this test sample facilitates comparisons of predictive accuracy to adult morphometric equations (e.g., those of Ruff, 1994; Ruff et al., 1997, 2005) that were previously evaluated by Walker et al. (2017).

The accuracy of these equations was assessed by calculating prediction error (PE: kg) as the difference between observed (BM_{obs}) and predicted body masses (BM_{pred}). With this metric, negative values

indicate overprediction, while positive values indicate underprediction. We calculated several additional accuracy metrics, including relative percentage prediction error (%PE), following Smith (1980, 1984):

$$\text{Relative \%PE} = (BM_{obs} - BM_{pred}) / BM_{pred} * 100$$

Mean percentage prediction error (%MPE) was calculated by averaging relative %PEs across all populations by age and sex. Following many other studies of prediction error (e.g., Aiello and Wood, 1994; Dagosto and Terranova, 1992; Delson et al., 2000; Elliott et al., 2016a, b; Yapuncich et al., 2015), we consider both a mean %PE less than $\pm 20\%$ and the majority of test cases with %PE less than $\pm 20\%$ to indicate an acceptable level of prediction error. Because prediction equations both under- and overpredict individual cases, we also summarize predictive accuracy using the absolute values of %PEs.

We also compared observed and predicted BMs of the Eveleth and Tanner test sample using non-parametric Mann-Whitney U -tests to test for significant differences in the group medians. Non-parametric tests were used since observed BMs were not normally distributed and predicted BMs often had greater variance than observed BMs. Ideally, particularly if the goal of prediction is to capture the central tendency of a population (Yapuncich, 2017b), a BMPE will generate a distribution of predicted BMs with a median that is not significantly different from the observed BMs.

Finally, we used generalized linear mixed models (GLMMs) with repeated measures to examine the relationship between prediction error, body mass, and three somatic variables available for the Eveleth and Tanner test sample (biacromial/bi-iliac breadth [BAB/BIB], lower limb length/stature [LL/ST], and triceps skinfold thickness [TST]). Following Walker et al. (2017), we employed a first-order, autoregressive covariance structure to account for serial autocorrelation with each population (Cnaan, Laird, & Slasor, 1997; Dobson and Barnett, 2008). The first set of GLMMs evaluate the relationship between body mass and the prediction errors of the raw and logged panel regressions, with body mass as a fixed effect. The second set of GLMMs evaluates the relationship between prediction errors and the somatic variables, with all possible interactions modeled as fixed effects and body mass modeled as a random effect. Although the panel regressions were generated from a pooled sample, we analyzed males and females separately in all GLMMs.

2.3 | Accuracy in extrapolation

Walker et al. (2017) used a juvenile test sample to examine the predictive accuracy of previously published morphometric BMPEs when extrapolating beyond the range of their adult reference samples. In this study, the Eveleth and Tanner (1976) test sample still requires extrapolation by the Ruff et al. (1997) female equation, putting this equation at a predictive disadvantage. It is therefore of interest to gauge the performance of the novel panel equations with a test sample that also requires extrapolation. To do so, we evaluated the predictive accuracy of the panel equations using the sex-specific mean adult measurements of BIB, ST, and BM for the 58 populations (26 female, 32 male) published in Ruff (1994), Ruff et al. (1997), and Ruff et al. (2005).

TABLE 3 Relative percentage prediction error (%PE) for most accurate adult morphometric equation and HGS panel equations

Sex	Age (years)	n	Ruff et al. 1997 Female				HGS raw data				HGS logged data				
			Mean	SD	Range	%PE < 20%	Mean	SD	Range	%PE < 20%	Mean	SD	Range	%PE < 20%	
Female	6	24	25.06	15.19	8.10 to 77.54	42	22.43	10.05	8.87 to 52.83	46	3.30	4.60	-6.42 to 8.3	100	
	7	39	12.47	14.05	-5.23 to 50.09	82	13.05	9.71	-0.65 to 36.11	79	2.27	4.86	-10.56 to 10.98	100	
	8	41	4.41	11.47	-14.30 to 40.37	90	7.33	8.71	-10.67 to 36.39	93	1.68	5.38	-13.93 to 12.45	100	
	9	42	-2.14	9.07	-24.50 to 26.78	95	2.65	7.25	-18.25 to 26.3	98	1.10	5.43	-17.78 to 11.45	100	
	10	42	-6.53	8.03	-28.17 to 23.12	95	-0.06	6.93	-20.49 to 25.51	95	1.16	5.77	-17.33 to 15.77	100	
	11	41	-9.32	7.11	-32.96 to 11.37	98	-1.63	6.56	-24.83 to 16.85	98	1.02	6.09	-20.82 to 13.94	98	
	12	43	-10.55	6.54	-34.49 to 0.39	93	-1.70	6.52	-26.05 to 8.24	98	1.52	6.42	-22.25 to 12.74	98	
	Male	6	24	25.01	14.30	5.02 to 62.56	46	23.32	10.10	8.84 to 44.71	46	5.24	4.07	-2.22 to 15.8	100
		7	38	12.50	15.13	-4.94 to 64.22	84	13.94	11.59	0.86 to 53.57	82	3.98	6.04	-6.5 to 24.85	97
		8	39	4.50	11.47	-8.71 to 42.09	95	7.95	9.24	-3.6 to 37.95	95	3.15	5.72	-6.98 to 20.45	97
		9	39	-1.99	9.06	-17.15 to 21.37	95	3.29	7.61	-10.41 to 22.59	95	2.38	5.61	-9.78 to 15.23	100
		10	38	-5.62	8.20	-21.65 to 21.30	95	0.94	7.34	-14.39 to 25.13	97	2.20	6.20	-2.09 to 20.89	97
11		39	-7.58	8.12	-24.91 to 22.77	95	-0.13	7.84	-7.25 to 28.34	97	2.31	7.40	-14.04 to 27.01	97	
12	41	-8.37	8.30	-26.27 to 29.21	95	0.00	8.32	-18.16 to 37.28	98	3.09	8.17	-14.43 to 39	98		

3 | RESULTS

3.1 | Body mass prediction equations

In the HGS dataset, both stature and bi-iliac breadth exhibit substantial positive autocorrelation with body mass, whether using raw (ST: $d = 0.208$; BIB: 0.173) or logged data (ST: 0.195; BIB: 0.147).

For the raw data, a random effect panel regression model returned the following morphometric prediction equation:

$$BM = 0.480 * ST + 1.267 * BIB - 60.761$$

Both BIB and ST were significant factors ($p < 0.0001$), the adjusted r^2 is 0.750, and the sum of squared errors (SSE) = 47081.

For the logged data, a random effect panel regression model returned the following morphometric prediction equation:

$$\ln BM = 1.956 * \ln ST + 0.695 * \ln BIB - 8.313$$

Both BIB and ST were again significant factors ($p < 0.0001$), the adjusted r^2 is 0.935, and the SSE = 25.393. The difference in the r^2 values suggest that the equation derived from logged data will generate more precise (though not necessarily more accurate) predictions than the raw data equation.

3.2 | Accuracy as indicated by prediction error

Relative %PE and the percentage of test cases with $<20\%$ PE are presented in Table 3 for the raw and logged panel regressions. Metrics of predictive accuracy for the Ruff et al. (1997) female morphometric equation, identified by Walker et al. (2017) as the most accurate morphometric equation with the Eveleth and Tanner (1976) test sample, are also included for comparison. Figure 2 shows boxplots of relative %PE for all three equations.

There are some similarities in the accuracy of the raw data equation and the Ruff et al. (1997) equation as assessed. Both equations exhibit a pattern of underprediction among the youngest ages and overprediction at older ages (Table 3, Figure 2). However, at older ages,

the overprediction of the raw data equation is less substantial than the Ruff et al. (1997) equation. In contrast, the logged data equation does not exhibit any noticeable correlation between relative %PE and age. The logged data equation is most accurate among 6-year-olds and slightly overpredicts body mass among older ages.

In Walker et al. (2017), we did not calculate the percentage of test cases with PE $<20\%$ for previously published morphometric equations (Ruff, 1994; Ruff et al., 1997, 2005), but the Ruff et al. (1997) female equation performs well by that metric (Table 3). The equation has prediction errors within 20% for the majority of test cases for all ages except 6-year-old females and males. The performance of the raw data panel equation is very similar, as it also does not predict the majority of 6-year-olds with 20% prediction error. Among other age groups, the raw data exhibits either the same or greater predictive accuracy than the Ruff et al. (1997) equation (with the exception of 7-year-old males). The logged data panel equation has the best accuracy by this metric: predicting more than 95% of the test cases within $\pm 20\%$ of the observed body masses for all age and sex classes.

There are notable differences in the variances of prediction errors for all three equations (Table 3). The raw data panel equation exhibits the greatest variance of all three equations for all age groups. For the Ruff et al. (1997) equation, standard deviations of %PE are strongly negatively correlated with age (Pearson's $r = -0.94$, $p < 0.001$). Although variance of %PE is uniformly higher for the raw data panel equation, it also exhibits a significant negative correlation between %PE standard deviation and age (Pearson's $r = -0.80$, $p < 0.001$). Standard deviations of %PE for the logged data panel equation show the opposite pattern: a significant positive correlation with age (Pearson's $r = 0.83$, $p < 0.001$).

Overall, prediction errors indicate that the logged data panel equation is the most accurate of the three examined equations.

3.3 | Accuracy as indicated by two-sample tests

Results of the Mann-Whitney U-tests comparing the distributions of body masses observed in the Eveleth and Tanner (1976) test sample

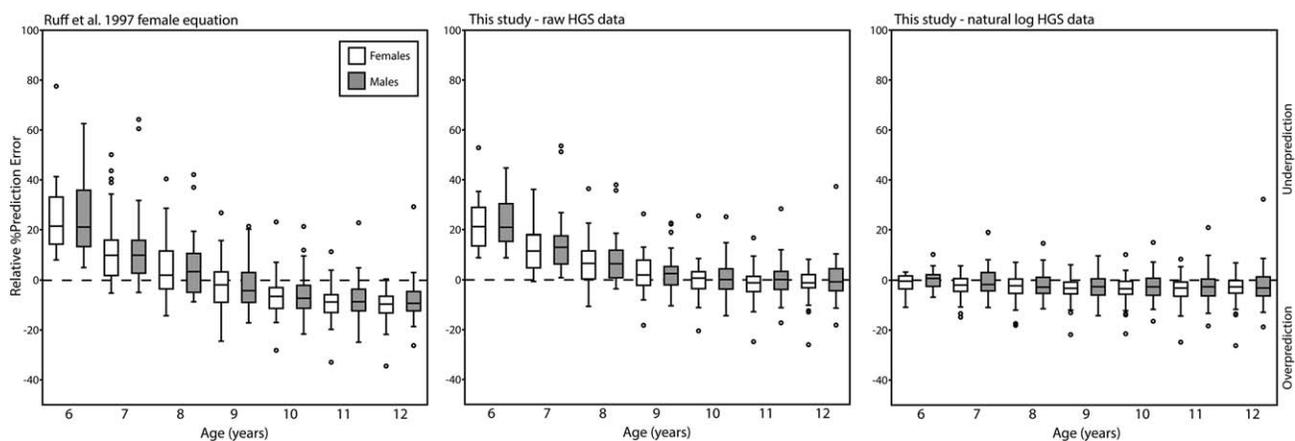


FIGURE 2 Relative % prediction error boxplots by age and sex for the three examined equations (Ruff et al., 1997 female, raw data panel, and natural log-transformed data panel equations). Boxes include 25–75% quartiles; whiskers extend to farthest points <1.5 interquartile range; circles indicate outliers; dashed line demarcates over- and underprediction

TABLE 4 Observed and predicted body mass (BM) distributions for test sample and evaluated prediction equations

Sex	Age (years)	n	Eveleth and Tanner, 1976 test sample				Ruff et al., 1997 Female				HGS raw data				HGS logged data						
			Median Observed BM (kg)	SD	Range	Median Predicted BM (kg)	SD	Range	Mann-Whitney U	p value	Median Predicted BM (kg)	SD	Range	Mann-Whitney U	p value	Median Predicted BM (kg)	SD	Range	Mann-Whitney U	p value	
Female	6	24	19.7	1.7	16.2-21.9	15.9	2.6	9.4-20.3	65.0	***	16.3	2.1	10.9-19.7	58.0	***	19.0	1.3	15.7-21.2	212.0	0.114	
	7	39	21.9	2.2	17.5-24.8	19.8	3.5	12.3-25.1	518.0	*	19.6	2.9	13.3-23.8	400.0	***	21.3	1.9	16.9-24.2	646.5	0.267	
	8	41	23.5	2.6	19.0-28.1	23.5	4.0	14.5-30.2	772.0	0.528	22.4	3.3	14.9-28.1	623.0	*	23.1	2.3	18.1-27.6	756.0	0.426	
	9	42	26.1	3.2	20.5-31.6	27.2	4.5	17.4-34.7	769.5	0.316	25.8	3.7	17.4-31.8	818.0	0.567	25.9	2.8	19.7-30.8	834.0	0.670	
	10	42	30.7	3.8	23.7-35.9	31.7	4.9	19.9-39.6	627.0	*	29.8	4.0	19.5-36.0	881.0	0.994	29.2	3.3	21.2-34.6	841.0	0.721	
	11	41	34.0	4.6	26.0-40.7	37.3	5.6	24.4-45.3	517.0	**	34.2	4.5	23.3-40.8	778.0	0.554	33.1	4.0	23.9-39.3	794.0	0.666	
	12	43	37.0	5.2	27.9-46.1	42.5	5.7	29.0-50.9	515.0	***	38.9	4.7	27.8-45.4	867.0	0.627	37.5	4.4	27.6-44.3	844.5	0.492	
	Male	6	24	20.4	1.5	16.7-22.4	16.1	2.7	10.5-20.9	63.5	***	16.4	2.2	11.8-20.1	45.0	***	19.1	1.4	16.3-21.5	178.5	*
		7	38	22.5	2.2	18.0-25.9	20.0	3.5	11.4-25.5	466.0	**	19.7	2.9	12.4-24.1	364.5	***	21.4	2.0	16.6-24.4	559.0	0.091
		8	39	24.1	2.5	20.0-28.6	23.4	3.9	14.4-30.1	687.0	0.466	22.7	3.2	14.8-28.0	559.0	*	23.4	2.3	18.0-27.6	650.5	0.281
		9	39	27.2	3.0	22.0-32.2	27.8	4.3	18.2-34.7	655.0	0.294	26.1	3.6	18.1-31.9	687.0	0.471	26.1	2.8	20.2-30.9	677.0	0.408
		10	38	29.6	3.5	23.9-35.1	31.2	4.6	21.3-39.0	526.0	*	29.1	3.8	20.8-35.5	714.5	0.938	28.6	3.2	22.1-34.2	648.5	0.444
11		39	33.0	4.3	25.3-39.4	34.8	5.0	24.1-42.9	503.0	*	32.3	4.1	23.2-38.9	751.0	0.928	31.5	3.6	23.8-37.5	693.0	0.499	
12	41	36.5	4.7	27.2-43.3	39.9	5.2	28.0-47.4	526.0	**	36.4	4.3	26.5-42.6	834.5	0.958	35.0	4.0	26.4-41.4	707.0	0.225		

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TABLE 5 Parameter estimates, standard errors (SE), denominator degrees of freedom (Den df), t ratios, and probabilities (Pr > |t|) for GLMM models

Sex	Model term	Estimate	SE	Den df	t ratio	Pr > t	
Model 1a—Raw data							
Females	Intercept	4.63	0.60	186.4	7.77	***	
	BM	−0.13	0.02	263.9	−7.04	***	
Males	Intercept	5.03	0.68	192.4	7.35	***	
	BM	−0.13	0.02	251.7	−6.07	***	
Model 1b—Logged data							
Females	Intercept	−0.78	0.41	184.0	−1.89	n.s.	
	BM	0.04	0.01	269.8	3.56	***	
Males	Intercept	−0.92	0.50	192.4	−1.85	n.s.	
	BM	0.06	0.02	255.1	4.06	***	
Model 2a—Raw data							
Females	Intercept	−4.38	10.99	60.9	−0.40	n.s.	
	TST	0.21	0.16	62.1	1.38	n.s.	
	LL/ST	−43.96	16.33	62.9	−2.69	**	
	(TST-9.75135) [†] (LL/ST-0.46934)	−6.57	9.15	64.0	−0.72	n.s.	
	BAB/BIB	17.15	5.85	47.3	2.93	**	
	(TST-9.75135) [†] (BAB/BIB-1.36152)	2.51	2.10	55.4	1.20	n.s.	
	(LL/ST-0.46934) [†] (BAB/BIB-1.36152)	649.98	375.77	65.9	1.73	n.s.	
	(TST-9.75135) [†] (LL/ST-0.46934) [†] (BAB/BIB-1.36152)	228.57	132.80	58.2	1.72	n.s.	
	Males	Intercept	7.69	8.62	59.9	0.89	n.s.
		TST	0.19	0.13	61.4	1.51	n.s.
LL/ST		−44.95	15.90	69.2	−2.83	**	
(TST-8.18642) [†] (LL/ST-0.47043)		−13.45	8.28	63.3	−1.62	n.s.	
BAB/BIB		9.35	5.06	56.6	1.85	n.s.	
(TST-8.18642) [†] (BAB/BIB-1.39453)		2.06	1.58	61.2	1.31	n.s.	
(LL/ST-0.47043) [†] (BAB/BIB-1.39453)		501.46	220.28	65.3	2.28	*	
(TST-8.18642) [†] (LL/ST-0.47043) [†] (BAB/BIB-1.39453)		146.14	108.23	61.5	1.35	n.s.	
Model 2b—Logged data							
Females		Intercept	−14.63	6.60	58.1	−2.22	*
	TST	0.20	0.09	60.8	2.18	*	
	LL/ST	−9.09	9.60	59.1	−0.95	n.s.	
	BAB/BIB	1.78	5.41	60.7	0.33	n.s.	
	TST [†] LL/ST	12.49	3.79	58.3	3.30	**	
	TST [†] BAB/BIB	0.75	1.22	53.5	0.61	n.s.	
	LL/ST [†] BAB/BIB	305.79	221.66	60.0	1.38	n.s.	
	TST [†] LL/ST [†] BAB/BIB	149.96	79.06	58.2	1.90	n.s.	
	Males	Intercept	−1.19	6.32	62.0	−0.19	n.s.
		TST	0.20	0.09	63.5	2.16	*
LL/ST		−20.02	11.71	69.2	−1.71	n.s.	
(TST-8.18642) [†] (LL/ST-0.47043)		−6.08	6.06	64.4	−1.00	n.s.	
BAB/BIB		6.88	3.88	59.2	1.77	n.s.	
(TST-8.18642) [†] (BAB/BIB-1.39453)		0.69	1.16	64.0	0.59	n.s.	
(LL/ST-0.47043) [†] (BAB/BIB-1.39453)		237.43	163.55	68.2	1.45	n.s.	
(TST-8.18642) [†] (LL/ST-0.47043) [†] (BAB/BIB-1.39453)		88.86	79.90	65.2	1.11	n.s.	

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

and body masses predicted by each of the examined equations are presented in Table 4.

As reported by Walker et al. (2017), the Ruff et al. (1997) female equation generates distributions of predicted body masses with medians that are significantly smaller than the medians of the distributions of observed body masses at the youngest ages (Table 4). For 8- and 9-year-old females and males, there are no significant differences in the medians of the observed and predicted body mass distributions. From this inflection point, the medians of the predicted body mass

distributions become increasingly and significantly larger than the medians of the observed body mass distributions. The inflection points between under- and overprediction can also be seen in the prediction error boxplots in Figure 2.

With the raw data panel equation, there are fewer age classes that exhibit significant differences between the medians of the observed and predicted body mass distributions (Table 4). For both females and males from ages 6 to 7, the raw data panel equation generates distributions with medians that are significantly less than the medians of the observed body

TABLE 6 Relative percentage prediction error (%PE) for most accurate adult morphometric equation and HGS panel equations applied to adult test sample

Sex	Ruff et al., 1997 Female				HGS raw data				HGS logged data			
	Mean	SD	Range	%PE < 20%	Mean	SD	Range	%PE < 20%	Mean	SD	Range	%PE < 20%
Female	-0.57	6.44	-11.31 to 14.16	100	10.33	7.17	-2.58 to 28.33	92	14.57	7.48	1.14 to 32.04	84
Male	1.38	6.64	-12.88 to 13.46	100	12.36	12.36	-3.96 to 27.26	81	13.32	7.48	-2.10 to 25.83	81

masses. At all other ages, there are not significant differences between the medians of the observed and predicted body mass distributions.

For all ages and sexes, the medians of the distributions of body masses predicted by the logged data panel equation are not significantly different from the medians of the observed body mass distributions (Table 4). The ranges and standard deviations of predicted body masses are also more constrained when body mass is predicted with either of the panel equations. Mann-Whitney *U* tests comparing the standard deviations of body masses predicted by the panel equations reveal that they are not significantly larger than those of the observed body masses (raw data equation: $U = 82$, $p = 0.467$; logged data equation: $U = 85.5$, $p = 0.556$). In contrast, the standard deviations of predicted body masses are significantly larger than those of the observed body masses for the Ruff et al. (1997) equation ($U = 47$, $p = 0.016$).

Similar to the signal recovered by analyses of prediction error, comparisons of the distributions of predicted and observed body masses strongly suggest that the logged data panel equation is the most accurate of the three examined equations.

3.4 | Generalized linear mixed models

Parameter estimates for the general linear mixed models are presented in Table 5. Additional descriptors of the GLMMs are presented in the Supporting Information, including the main and total effects for each parameter (SOM Table 4) and conditional model plots for the second model (SOM Figure 2). The first set of GLMMs model body mass as a fixed effect in order to look at the relationship between body mass and prediction error. For the raw data panel equation, there is a significant negative relationship between body mass and prediction error for both females ($p < 0.001$) and males ($p < 0.001$). For the logged data panel equation there is a significant positive relationship between body mass and prediction error for both females ($p < 0.001$) and males ($p < 0.001$).

The second set of GLMMs model body mass as a random effect and three somatic variables (BAB/BIB, LL/ST, and TST) as fixed effects to examine the relationship between the prediction error and the somatic variables when accounting for body mass. For the raw data panel equation, there is a significant negative relationship between prediction error and LL/ST ($p < 0.01$) in both females and males. For females, BAB/BIB has a significant positive relationship with prediction error ($p < 0.01$). For males, the interaction between LL/ST and BAB/BIB is significantly positively correlated with prediction error ($p = 0.026$).

Linear mixed models do not recover similar significant relationships between prediction error and the somatic variables for the logged data

panel equation. Instead, there is a significant positive relationship between TST and prediction error for both females ($p = 0.033$) and males ($p = 0.035$). The interaction between TST and LL/ST also exhibits a significant positive relationship in females ($p = 0.001$).

For the raw data panel equation, BAB/BIB has the strongest total effect in females (0.725), while LL/ST has the strongest total effect in males (0.435) (SOM Table 4). For the logged data panel equation, BAB/BIB also had the strongest total effect in females (0.666), while mass had the strongest total effect for males (0.512).

3.5 | Accuracy in extrapolation

Because the Eveleth and Tanner (1976) test sample requires extrapolation by the Ruff et al. (1997) female equation, we also evaluated the predictive accuracy of the panel equations using adult measurements. The relative %PEs for all three equations are presented in Table 6.

Not surprisingly, the Ruff et al. (1997) female equation generates the most accurate predictions, and is most accurate for females in the test sample. Both of the juvenile panel equations tend to underpredict adult body mass (Table 6; SOM Figure 3); the direction of these prediction errors is reciprocal to the overprediction of juvenile body mass by the adult equations (Walker et al., 2017). Mann-Whitney *U* tests reveal that the juvenile equations do not capture the central tendencies of the adult populations well, as medians are significantly different for both sexes when predicted by either juvenile equation (raw panel equation: females, $U = 162$, $p < 0.001$; males, $U = 259$, $p < 0.001$; logged panel equation: females, $U = 121$, $p < 0.001$; males, $U = 266$, $p < 0.001$).

4 | DISCUSSION

4.1 | Predictive accuracy of panel regressions

Results of both accuracy analyses (prediction error and nonparametric tests of observed and predicted body masses) suggest that the morphometric panel regressions developed for this study generate reliable predictions of body mass in human juveniles. The logged data panel equation is particularly accurate for all ages in the Eveleth and Tanner (1976) test sample: across all age and sex classes, the mean |%PE| is only 2.47 and 99% of the test cases are predicted within $\pm 20\%$ of their observed body mass (Table 3). Crucially, there are no significant differences in the medians of observed and predicted body masses, and the ranges of the predicted body masses are comparable to the ranges of observed body masses (Table 4). These similarities between observed and

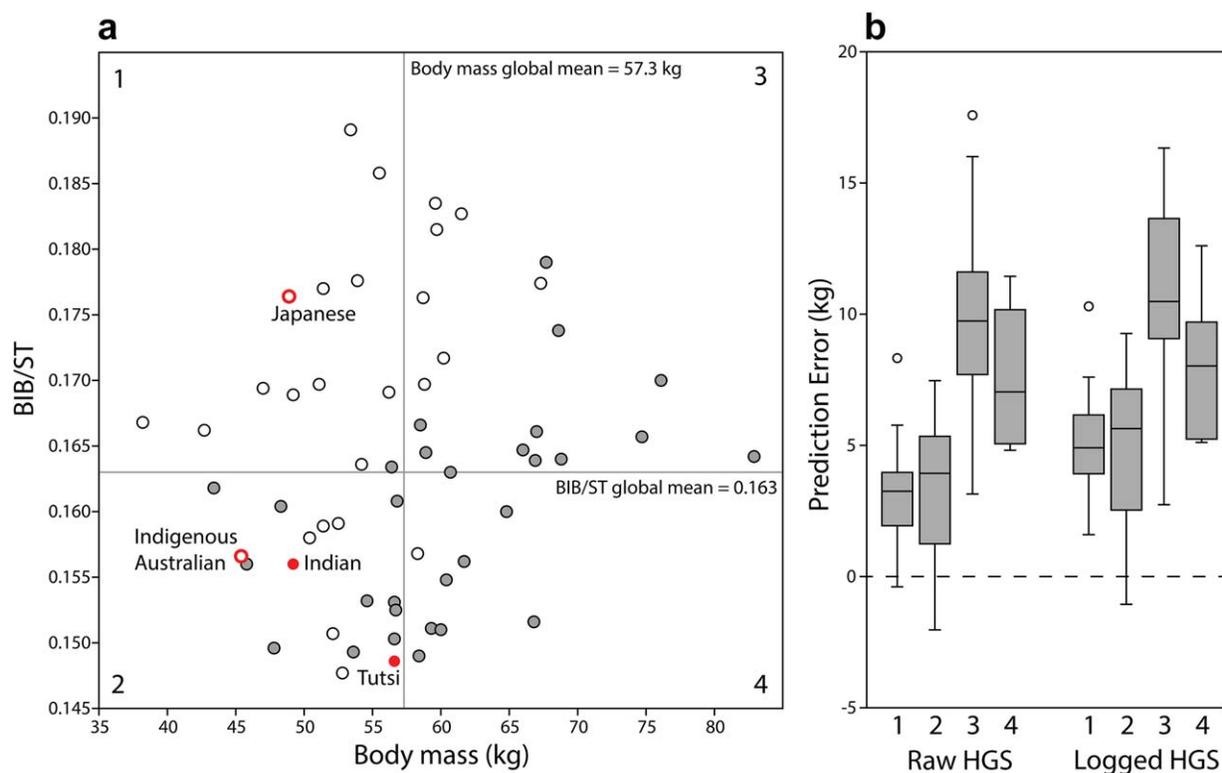


FIGURE 3 (a) Weight and bi-iliac (BIB)/stature (ST) ratios for adult populations published in Ruff (1994), Ruff et al. (1997), and Ruff et al. (2005). Red circles indicate populations overpredicted by panel equations; open circles indicate females; filled circles indicate males. (b) Prediction error boxplots for adult populations in each quadrant indicated in A. Groups 1 and 2 include all populations with body masses less than the global mean. Groups 2 and 4 include all populations with BIB/ST ratios less than the global mean. Boxes include 25–75% quartiles; whiskers extend to farthest points <1.5 interquartile range; circles indicate outliers; dashed line demarcates over- and underprediction

predicted body masses suggest that the logged data panel equation will accurately predict population parameters (including metrics of central tendency and variance). Because the accuracy of previously published mechanical juvenile BMPEs (Robbins et al., 2010; Robbins Schug et al., 2013; Ruff, 2007) has been evaluated with different test samples, it is not possible to directly compare the predictive accuracy for those equations and the morphometric panel equations presented in this study. However, we would note that the morphometric panel equations do have the lowest average |PE| of all the juvenile equations evaluated here or in Robbins Schug et al., (2013) (SOM Table 5).

Based on %PE, the raw data panel equation is more accurate than the Ruff et al. (1997) female equation, with a mean of $|\%PEs| = 6.88$ compared to a mean of $|\%PEs| = 9.72$. The raw data panel equation also predicts slightly more test cases within $\pm 20\%$ of the observed body mass (87% vs. 86%) (Table 3). When predicted with the raw panel data equation, median body masses exhibit significant differences with observed body masses among fewer age classes than predictions made by the Ruff et al. (1997) female equation (Table 4). While the Ruff et al. (1997) female equation switches from under- to overprediction as age increases, the raw data panel equation steadily decreases the amount of underprediction as age increases (Figure 1). Thus, median body masses predicted by the raw data panel equation are more accurate among older age groups than those predicted by the Ruff et al. (1997) female equation (Table 4).

In addition to having the highest mean %PE, the Ruff et al. (1997) female equation also has the greatest variance in the predicted body masses (Table 4), resulting in %PEs with the greatest variance of all examined equations (Table 3, Figure 1). In fact, body masses predicted by the Ruff et al. (1997) have significantly greater mean variance ($t = -2.625$, $p = 0.016$) than that observed in the Eveleth and Tanner (1976) test sample, while body masses predicted by the raw data ($t = -0.809$, $p = 0.429$) and logged data ($t = 0.564$, $p = 0.578$) panel equations do not. Increasing the variance of predicted body masses is an undesirable property for a prediction equation, and may be a partial result of failing to stabilize the variance of the predictor variables (i.e., not log-transforming stature and bi-iliac breadth). Because log-transformation stabilizes the variance of bi-iliac breadth more than stature (Figure 1), it is not surprising that the increase in predicted BM variance is most pronounced for the Ruff et al. (1997) female, which weights BIB more heavily than the raw or logged data panel equations (BIB coefficients of 1.809, 1.267, and 0.695 respectively).

The three examined equations exhibit heterogeneous trends in %PE variance (Table 3). For both the Ruff et al. (1997) female and raw data panel equations, variances of %PEs are greatest at younger ages (and smaller body masses) and decrease as age (and body mass) increases. This trend can be considered a methodological artifact: since %PE is calculated as the difference between observed and predicted body masses relative to predicted body mass, errors of the same

magnitude will produce a larger %PE at a smaller body mass than at a larger body mass. It is therefore notable that the logged data panel equation does not exhibit the same trend. Instead, standard deviations of %PEs modestly increase as age and body mass increase (Table 3). This trend is much more biologically intuitive, since increasing age makes it more likely that individuals will deviate from any number of ontogenetic allometries (e.g., stature, bi-iliac breadth, biacromial breadth, body fat percentage) (Bogin, 1988; Tanner, 1988), and these deviations may decrease predictive accuracy.

Results from the linear mixed models underscore the impact that other body proportions can have on prediction error (Table 5)². For the raw data panel equation, the parameter estimates and effects of the linear mixed models (SOM Table 4) are similar to the relationships between additional somatic variables and prediction error recovered by Walker et al. (2017) for the Ruff et al. (1997) female equation. In this study, LL/ST has a significant positive relationship with the prediction errors of the raw data panel equation. As discussed by Walker et al. (2017), younger juveniles in the Eveleth and Tanner (1976) dataset exhibit lower LL/ST ratios than older juveniles (reflecting relatively shorter lower limbs), so that more of their stature is composed of the torso. These proportions cause an underprediction of body mass (positive PE) at younger ages. The similarities in the parameters for the linear mixed models for both the Ruff et al. (1997) female equation and the raw data panel equation suggest that extrapolation beyond the range of the reference sample is not the primary causal factor for the predictive inaccuracies of these equations. Rather, the results of the linear mixed models suggest that ontogenetic changes in body proportions have a strong influence on prediction error. This interpretation is consistent with the model-fitting analyses of Schaffer (2016), who demonstrated that included additional somatic variables increases the explanatory power of regression models.

The linear mixed model of somatic variables and prediction error for the logged data panel equation does not highlight the same somatic variables as the raw data panel equation. Instead, the effect of triceps skinfold thickness (as an imperfect measure of fat mass) is the most notable significant factor (Table 5); TST exhibits a significant positive relationship with prediction errors of the logged data panel equation among both females and males. TST does not have a significant relationship with the prediction errors of either the Ruff et al. (1997) female equation or the raw data panel equation. Because other studies have demonstrated that fat mass has a strong effect on the accuracy of body mass prediction (Lorkiewicz-Muszyńska et al., 2013; Schaffer, 2016), Walker et al. (2017) were cautious to conclude that the absence of a significant relationship between TST and prediction error as evidence that fat mass is not an important consideration when predicting body mass. The significant relationships between TST and prediction for the logged data panel equation are therefore encouraging, as this correlation may

indicate these prediction errors reflect more subtle variation in body composition, rather than simply gross differences in body proportions.

4.2 | Accuracy in extrapolation

Given the reference samples of these equations, large-bodied populations (e.g., male Finns, Danish, Lau) require the greatest amount of extrapolation. The large underpredictions of body mass in these populations are consistent with using an ordinary least squares regression model to extrapolate beyond the upper bound of the model's reference sample. Using the raw data panel equation, the body masses for 93% of the adult test populations are underpredicted. Four populations (Japanese females, Indigenous Australian females, Tutsi males, and Indian males) are overpredicted. Using the logged data panel equation, the body masses for 97% of the adult populations are underpredicted. Only two populations (Tutsi males and Indian males) are overpredicted. All four populations of the populations overpredicted by the panel equations are also overpredicted by the Ruff et al. (1997) female equation. These populations all exhibit mean BMs that are less than the global mean of 57.3 kg (Figure 3a). With the exception of Japanese females, they also exhibit BIB/ST ratios that are less than the global mean (0.163) (Figure 3a), indicating that these populations are taller than expected given bi-iliac breadth. When the adult populations are grouped by their BM and BIB/ST values relative to the respective global means, the effect of extrapolation beyond the body mass range of the reference sample is evident. Prediction errors for those groups with BMs less than the global mean are substantially less than those with BMs greater than the global mean (Figure 3b). Differences in prediction error are much less pronounced when comparing groups with BIB/ST less than the global mean to those with BIB/ST greater than the global mean (Figure 3b). Those populations with both BM and BIB/ST values greater than the global mean have the greatest mean prediction error (i.e., they are strongly underpredicted).

Overall, when applied to an adult test sample, the juvenile panel equations generate %PEs ($\leq 25\%$) that are of comparable magnitude to the most accurate %PEs generated by Ruff et al. (1997) female equation when applied to juveniles (Walker et al., 2017). While we do not recommend applying the juvenile panel equations to individuals that are suspected to be large-bodied, the most probable outcome is modest underprediction (~ 5 kg) of body mass.

4.3 | Limitations and application in archeological, forensic, and paleontological contexts

While the precision and accuracy of both panel equations suggest they will generate reliable predictions of immature human body mass in forensic and archeological contexts, it is worth noting several limitations of these equations. Each limitation highlights an opportunity for improvement in future studies.

The first limitation is driven by the ability to accurately reconstruct the predictor variables utilized by morphometric BMPEs from unfused, immature bones. The juvenile panel regressions are derived anthropometric measurements taken on living individuals, so there is a negligible

²GLMM results should be interpreted with some reservations as the prediction errors for the panel equations are leptokurtotic. Common data transformations, such as Box-Cox, did not induce normality for PEs. Other metrics of predictive accuracy (i.e., %PE) also do not exhibit normality.

degree of random error for the predictor variables. However, since immature individuals lack epiphyseal fusion, we expect a higher degree of error when estimating morphometric predictor variables from skeletonized remains. While there are published methods for predicting juvenile stature from unfused skeletal elements (e.g., Robbins Schug et al., 2013), an inability to reconstruct juvenile bi-iliac breadth accurately would strongly constrain the practical application of the panel equations presented in this study.

In humans, fusion of the pelvis typically occurs between 11 and 15 years in females and 14–17 years in males (Cunningham et al., 2016; Stevenson, 1924; Verbruggen and Nowlan, 2017). Applied to the Eveleth and Tanner (1976) test sample, the panel regressions are substantially more accurate for 11- and 12-year-old females than the Ruff et al. (1997) female equation (Tables 3 and 4), which demonstrates how reducing the degree of extrapolation can improve the predictive accuracy. Additionally, Watson, Fagan, & Dobson (2011a) and Watson, O'Higgins, Fagan, & Dobson (2011b) have developed and validated geometric morphometric methods to reconstruct juvenile pelvises from osteological elements. Although it is beyond the scope of this study, it would be worthwhile to evaluate the accuracy of morphometric BMPEs after reconstruction. Ultimately, as with all prediction equations, the panel equations presented in this study should not be applied when predictor variables cannot be inferred with confidence. While this qualification may limit their utility for fully skeletonized young juveniles, we believe these equations are preferable to adult-derived BMPEs for older juveniles or when the individual or population of interest is suspected to be smaller-bodied than modern adult humans.

Related to the first limitation, the second limitation stems from a reliance on predictor variables that may themselves be predicted when these equations are applied to skeletonized remains. A number of prediction equations exist for inferring stature (Hens et al., 1998; Jungers, 1988; Konigsberg et al., 1998; Raxter, Auerbach, & Ruff, 2006; Raxter, Ruff, & Auerbach, 2007; Robbins Schug et al., 2013; Ruff, 2007; Ruff et al., 2012), and Ruff (2010) presented an equation for converting

osteological BIB to living BIB. However, as noted by Martin (1990), incorporating predicted values (which have their own error) into downstream prediction equations may generate so much uncertainty that predicted body masses are useless. As we have pointed out previously (Walker et al., 2017), one remedy for morphometric BMPEs would be to predict body mass from long bone lengths directly (as in Ruff, 2007), rather than inferring stature from long bone lengths, and then predicting body mass from inferred stature.

A third limitation stems from the lack of ancestral diversity in the reference sample. The Harpenden Growth Study was conducted in Britain from 1948 to 1971 (Tanner, 1981); while we did not have access to the ancestral data for the individuals included in the sample for this study, other studies analyzing HGS data have described the sample as being of solely European descent (e.g., Marshall and Tanner, 1969, 1970). As emphasized by Schaffer (2016), it is beneficial to develop population-specific prediction equations to increase accuracy in forensic contexts. However, despite the ancestral homogeneity of the HGS reference sample, it is notable that the logged data panel equation presented here is extremely accurate when applied to the Eveleth and Tanner (1976) dataset, which is comprised of a globally representative sample.

Finally, while the panel equations do not require prediction of age, they do assume that test cases follow similar ontogenetic allometries as the reference sample. Deviations from these growth trajectories are likely to generate systematic biases in the predicted body masses. This is important to consider in paleontological contexts and the potential application of panel equations to fossil hominins. Grabowski, Hatala, Jungers, & Richmond (2015) argued that body masses for many fossil hominins have been overpredicted, and Walker et al. (2017) noted a systematic overprediction of human juveniles in the estimated range of australopith body mass. These biases can be visualized by applying locally weighted smoothing regressions (Figure 4). The Ruff et al. (1997) female equation is characterized by underprediction at the smallest body masses (15–25 kg) and overprediction at larger body

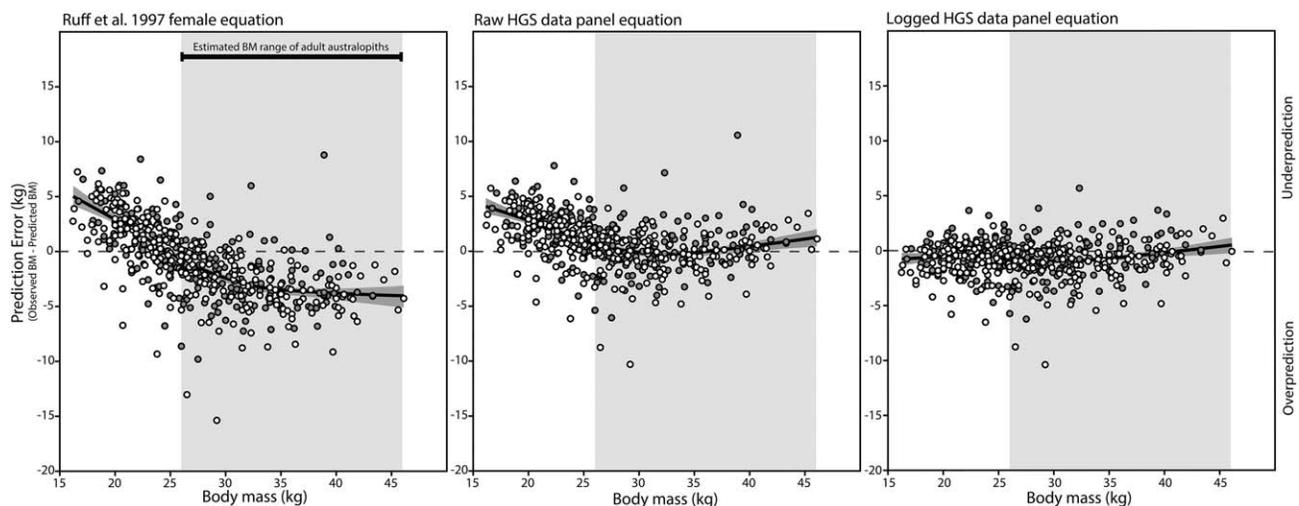


FIGURE 4 Local regression (LOESS) of prediction error to observed body mass (smoothing factor = 0.5) for the Ruff et al. (1997) female, raw HGS data panel, and natural log-transformed HGS data panel equations. Equations applied to Eveleth and Tanner (1976) juvenile test sample. The 95% confidence interval of regression is indicated by dark gray region. White circles indicate females; gray circles indicate males

masses (25–45 kg). The raw data panel equation also tends to underpredict at smaller body masses (15–30 kg), but does not overpredict larger body masses. The logged data panel equation is accurate across the full range of body masses, with only a slight trend toward underprediction among the largest body masses. A test sample that is more phylogenetically diverse than human juveniles would be a robust test of the generality of the panel equations.

5 | CONCLUSIONS

Panel regression is an underutilized, but useful, methodological approach for generating body mass prediction equations that account for serial autocorrelation of longitudinal observations and thus do not require inferences of the target individual's age (Robbins Schug et al., 2013). Both of the novel morphometric prediction equations presented in this study perform reliably across a range of ages and both sexes tested, but the logged data panel equation performs substantially better than either the raw data panel equation or the Ruff et al. (1997) female equation. The raw data panel equation is modestly more accurate than the Ruff et al. (1997) female morphometric equation, as it has a lower mean [%PE] and generates distributions of predicted body masses that are not significantly different from observed body masses for more age classes than the Ruff et al. (1997) female equation.

The logged data panel equation performs notably better than the other equations evaluated in this study. As assessed by prediction error, this equation is very accurate (mean [%PE] = 2.47) across all age classes. The distributions of body masses predicted by the logged data panel equation are not significantly different from the distributions of observed body masses for either sex or any age. The substantial improvement in predictive accuracy highlights the importance of log-transforming data in order to stabilize the variance of predictor variables. Overall, the logged data panel equation presented in this study should prove useful in archaeological, forensic, and paleontological predictive contexts in which bi-iliac breadth and stature can be estimated with confidence, particularly when the target individual or population appears to be smaller-bodied than modern adult humans.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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