Predicting body mass of bonobos (Pan paniscus) with human-based morphometric equations

5 authors, including:

Gabriel S Yapuncich
Duke University
53 PUBLICATIONS   **240** CITATIONS

SEE PROFILE

Christopher S. Walker
North Carolina State University
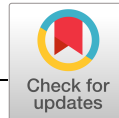**37** PUBLICATIONS   **481** CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:

Reassessing Primate Origins through Digital Investigation of Eocene Fossils from the Bridger Basin, Wyoming View project

The Upper Limb of Homo naledi View project

RESEARCH ARTICLE

Predicting body mass of bonobos (*Pan paniscus*) with human-based morphometric equations

Gabriel S. Yapuncich[1,2] | Aleah Bowie[1] | Raphaël Belais[3] | Steven E. Churchill[1,4] | Christopher S. Walker[2,1,4]

[1]Department of Evolutionary Anthropology, Duke University, Durham, North Carolina

[2]Department of Molecular Biomedical Sciences, College of Veterinary Medicine, North Carolina State University, Raleigh, North Carolina

[3]Lola ya Bonobo, Kinshasa, Democratic Republic of Congo

[4]Evolutionary Studies Institute, University of the Witwatersrand, Wits, South Africa

Correspondence
Christopher S. Walker, NCSU College of Veterinary Medicine, 1060 William Moore Dr., Raleigh, NC 27607.
Email: christopher_walker@ncsu.edu

Abstract

A primate's body mass covaries with numerous ecological, physiological, and behavioral characteristics. This versatility and potential to provide insight into an animal's life has made body mass prediction a frequent and important objective in paleoanthropology. In hominin paleontology, the most commonly employed body mass prediction equations (BMPEs) are "mechanical" and "morphometric": uni- or multivariate linear regressions incorporating dimensions of load-bearing skeletal elements and stature and living bi-iliac breadth as predictor variables, respectively. The precision and accuracy of BMPEs are contingent on multiple factors, however, one of the most notable and pervasive potential sources of error is extrapolation beyond the limits of the reference sample. In this study, we use a test sample requiring extrapolation—56 bonobos (*Pan paniscus*) from the Lola ya Bonobo sanctuary in Kinshasa, Democratic Republic of the Congo—to evaluate the predictive accuracy of human-based morphometric BMPEs. We first assess systemic differences in stature and bi-iliac breadth between humans and bonobos. Due to significant differences in the scaling relationships of body mass and stature between bonobos and humans, we use panel regression to generate a novel BMPE based on living bi-iliac breadth. We then compare the predictive accuracy of two previously published morphometric equations with the novel equation and find that the novel equation predicts bonobo body mass most accurately overall (41 of 56 bonobos predicted within 20% of their observed body mass). The novel BMPE is particularly accurate between 25 and 45 kg. Given differences in limb proportions, pelvic morphology, and body tissue composition between the human reference and bonobo test samples, we find these results promising and evaluate the novel BMPE's potential application to fossil hominins.

KEYWORDS
allometry, bi-iliac breadth, body size, hominin, panel regression, stature

1 | INTRODUCTION

Predicting body mass is a common objective in a variety of biological disciplines, as body mass can provide insight into an organism's life through its robust covariation with several ecological, physiological, and behavioral characteristics (Calder, 1984; Damuth & MacFadden, 1990; Fleagle, 1985; McNab, 1990; Peters, 1983; Schmidt-Nielsen, 1984). With respect to hominins, specifically, there exists a rich literature on both body mass prediction (e.g., Jungers, 1988; McHenry, 1974; Wolpoff, 1973) and the evolutionary implications

of body mass (e.g., Aiello & Wells, 2002; Aiello & Wheeler, 1995; Antón, Leonard, & Robertson, 2002; McHenry, 1994; Robson & Wood, 2008). Recently discovered small-bodied hominin species such as *Homo floresiensis* (Brown et al., 2004) and *Homo naledi* (Berger et al., 2010, 2015) have further diversified the range of body shapes and sizes within the hominin lineage and have generated renewed interest in the accurate prediction of body mass (Brassey, O'Mahoney, Chamberlain, & Sellers, 2018; Grabowski & Jungers, 2017; Grabowski, Hatala, Jungers, & Richmond, 2015; Holliday et al., 2018; Jungers, Grabowski, Hatala, & Richmond, 2016; Ruff, Burgess, Squyres, Junno, & Trinkaus, 2018; Will & Stock, 2015).

Although there are alternative methods (e.g., Brassey et al., 2018), univariate or multivariate linear regression remains the most common approach to predicting body mass in fossil taxa. These body mass prediction equations (BMPEs) describe the relationship between body mass and dimensions of skeletal or dental elements that are regularly fossilized (e.g., molar occlusal area, limb bone dimensions). For hominins, the most frequently employed BMPEs can be classified as either "mechanical" or "morphometric". Mechanical equations use dimensions of load-bearing skeletal elements as predictor variables (Almécija, Smaers, & Jungers, 2015; Burgess, McFarlin, Mudakikwa, Cranfield, & Ruff, 2018; Elliott, Kurki, Weston, & Collard, 2015a,b; Grine, Jungers, Tobias & Pearson, 1995; McHenry, 1992; Ruff et al., 2012; Ruff, 1991, 1994, 2000a; Squyres & Ruff, 2015), while morphometric equations use stature and living bi-iliac breadth (Ruff, 1991, 1994, 2000b; Ruff, Niskanen, Junno, & Jamison, 2005; Ruff, Trinkaus, & Holliday, 1997). Because these two types of equations rely on different predictor variables, direct comparisons of their performance have been relatively limited. Based on their comparisons of predictive accuracy, Auerbach and Ruff (2004) recommend morphometric over mechanical equations with the caveat that all predictor variables (stature and bi-iliac breadth) must be estimated with confidence.

While several theoretical and statistical issues make body mass prediction with linear regression models a deceptively complex procedure (Ruff, 2007; Smith, 2002; Yapuncich, 2018; Yapuncich, Gladman, & Boyer, 2015), extrapolation beyond the limits of the reference sample is one of the most problematic. In a strict sense, extrapolation violates the statistical assumption that the predicted sample belongs to the same population as the reference sample (Smith, 2009). However, rigid adherence to this assumption is not tenable in many paleontological cases, as the diversity of past species far exceeds those currently living (and therefore available for use as a reference sample). Thus, sample limitations may necessitate extrapolation, including predicting body masses from predictor values smaller or larger than those in the reference sample or predicting body mass in taxa outside the sample's phylogenetic bracket (*sensu* Witmer, 1995).

From a methodological standpoint, extrapolation often results in reduced precision (Aiello, 1992; Hens, Konigsberg, & William, 1998; Konigsberg, Hens, Jantz, & Jungers, 1998; Ruff, 2007) and accuracy (Walker, Yapuncich, Sridhar, Cameron, & Churchill, 2018; Yapuncich et al., 2015; Yapuncich, Churchill, Cameron, & Walker, 2018) of

predicted values. While precision and accuracy are important metrics for gauging the reliability of a BMPE, Gingerich (1990) advocates that BMPEs should also have a degree of generality and exhibit a "reasonable" degree of precision and accuracy across a wide range of taxa. Extrapolation provides an opportunity to evaluate the trade-offs between accuracy and generality to determine when differences (phylogenetic or otherwise) between the reference and test samples render BMPEs unreliable. We have used intentional extrapolation in previous work to determine if BMPEs developed with primate reference samples remain accurate with non-primate test samples (Yapuncich et al., 2015) and if morphometric equations based on adult humans work well in skeletally immature humans (Walker et al., 2018).

In this study, to test the hypothesis that extrapolating beyond the range of the BMPE reference sample (either body mass or phylogenetic bounds) will reduce predictive accuracy, we leverage a test sample requiring extrapolation—56 bonobos (*Pan paniscus*) from the Lola ya Bonobo sanctuary in Kinshasa, Democratic Republic of the Congo—to evaluate the predictive accuracy of human-based morphometric BMPEs. We predict that BMPEs based on skeletally immature humans, whose body masses overlap with those of bonobos, will be more accurate than BMPEs based on human adults, whose body masses largely do not overlap. We first assess systemic differences in stature and bi-iliac breadth between humans and bonobos, then develop a new prediction equation based on observed differences, and finally evaluate the predictive accuracy of multiple BMPEs with a variety of metrics.

Although human-based BMPEs are frequently applied to hominin fossils (Berger et al., 2015; Grabowski & Jungers, 2017; Grabowski et al. 2015; Holliday et al., 2018; Will & Stock, 2015), the body proportions of several hominin taxa differ markedly from extant humans (Holliday et al., 2018; Jungers et al., 2016; McHenry, 1992; Richmond, Aiello, & Wood, 2002; Ruff, 2010; Ruff & Walker, 1993). Despite these differences, evaluating the accuracy of human-based BMPEs with nonhuman test samples is exceedingly rare (Ruff, 1987). This study provides a rare evaluation of the predictive accuracy of morphometric BMPEs using a nonhuman test sample. Our test sample of bonobos has the potential to be informative for hominin evolution as bonobos often serve as a referential model for the morphology and ecology of the last common ancestor of humans and chimpanzees (Zihlman, Cronin, Cramer, & Sarich, 1978; Wrangham & Pilbeam, 2002; but see Sayers, Raghanti, & Lovejoy, 2012).

2 | METHODS

All data were collected as part of a project approved by Duke University (IACUC #A261-13-10) and adhered to the legal requirements of the Ministry of Research and the Ministry of Environment in D.R. Congo. Animal husbandry and care practices complied with the policies of Lola ya Bonobo, as well as the Pan-African Sanctuary Alliance, The Primate Veterinary Healthcare Manual, and the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

2.1 | Sample & measurements

Body mass (BM), stature (ST), and living bi-iliac breadth (BIB; Figure 1) were measured during routine health check-ups on 56 bonobos at the Lola ya Bonobo sanctuary in Kinshasa, Democratic Republic of the Congo. Summary statistics of measurements and demographic information are shown in Table 1, and measurements for each individual are available in File S1. Measurements were taken by the sanctuary's veterinary team (including R. Belais) as part of a thorough physical examination of anesthetized individuals for a routine health and wellness check-up. BM (kg) was taken using a standard metric floor scale. ST (cm) was taken as crown-heel length using a metric tape measure. Each bonobo was placed in a supine position with hind limbs fully extended. ST was then measured as the straight-line distance, along the surface of the examination table,
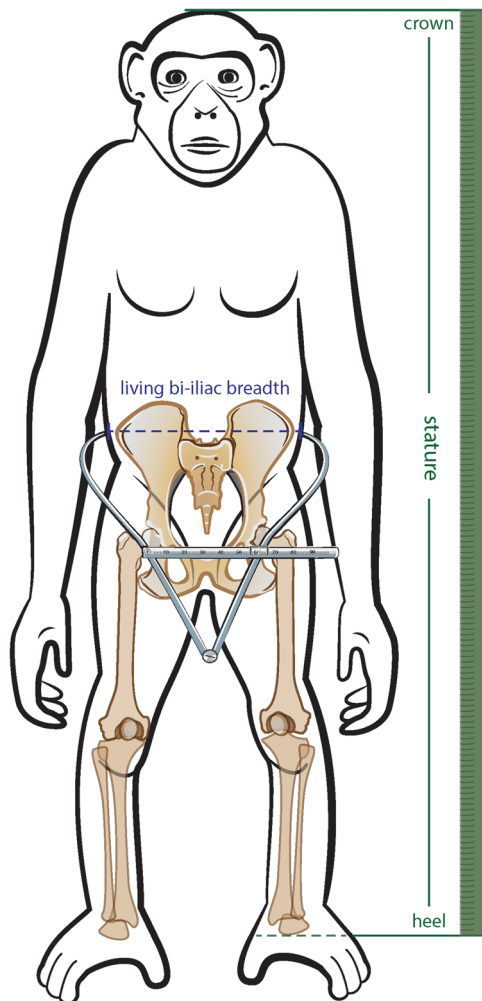

FIGURE 1 Predictor variable measurements. Living bi-iliac breadth (BIB), measured with spreading calipers, is the mediolateral diameter of the trunk at the level of the greatest lateral projection of the iliac blades. Stature (ST), measured with a metric tape, is the straight-line distance between the superior cranium (crown) and plantar surface of the heel

from the level of the top of the crown to the level of the plantar surface of the heel. BIB (cm) was taken as the mediolateral distance across the trunk at the level of the greatest lateral projection of the iliac blades (palpated) and measured with spreading calipers. All bonobos were semi-free-ranging within the sanctuary and include individuals ranging from 2 to 31.5 years old.

2.1.1 | Statistical analyses

To evaluate potential differences in the scaling relationships between the predictor variables (ST and BIB) and BM in adult humans and bonobos, analyses of covariance (ANCOVA) of ST and BIB were performed in PAST (Hammer, Harper, & Ryan, 2001) with body mass as a covariate. For the ANCOVAs, 58 sex-specific adult means were used for the human sample. The majority of these values came from Ruff (1994), with Aleut female body mass adjusted following Ruff et al. (1997), and male and female Finn population mean incorporated from Ruff et al. (2005). The bonobo sample was partitioned into three different age classes: juvenile, subadult, and adult. The minimum age at first menstrual cycle (indicative of reproductive maturity) among Lola ya Bonobo females is 7 years (Tan & Hare, 2013). Accordingly, all bonobos under 7 years of age ($n = 10$ females, 6 males) were classified as juveniles. Bonobos continue to experience somatic growth until approximately 11 years of age (Leigh & Shea, 1995, 1996), so individuals at and between 7 and 11 years old ($n = 9$ females, 10 males) were classified as subadults. Lastly, bonobos 12 years of age and older were considered fully adult ($n = 6$ females, 15 males), with skeletal maturation presumably complete. Thus, the combination of bonobo juvenile and subadult age classes is roughly equivalent to the skeletally immature human sample, while the adult bonobo and adult human age classes should represent individuals with full epiphyseal fusion. A more liberal ANCOVA was conducted by including subadults and adults and a more conservative ANCOVA was conducted including only adults. In these tests, p-values less than 0.05 were considered statistically significant.

Body mass for each bonobo was predicted using three different equations. First, we evaluated the adult female human equation from Ruff et al. (1997), which was the most accurate adult based BMPE when applied to immature humans aged 6 to 12 years old (Walker et al., 2018):

$$BM = 0.522 \times ST + 1.809 \times BIB - 75.5 \qquad (1)$$

Second, we evaluated the immature human logged data panel equation from Yapuncich et al. (2018), which was the most accurate equation from that study:

$$\ln BM = 1.956 \times \ln ST + 0.695 \times \ln BIB - 8.313 \qquad (2)$$

Finally, based on the scaling differences revealed by ANCOVAs (see Section 3), we developed a novel BMPE based on BIB in skeletally immature humans reported in the Harpenden Growth Study (HGS;

TABLE 1 Descriptive statistics (mean, standard deviation [SD], and range) for Lola ya Bonobo individuals

Sex	Age class	n	Age (years)			Stature (cm)			Bi-iliac breadth (cm)			Body mass (kg)		
			Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Female	All	25	9.76	6.06	2–27	102.36	19.57	63–124	19.21	3.75	11.8–24	23.00	10.61	5–38
	Juvenile	10	4.50	1.41	2–6.5	81.80	13.37	63–106	15.39	2.21	11.8–19	11.55	4.92	5–20
	Subadult	9	9.67	1.15	8–11	115.56	6.77	102–124	21.61	1.47	19–24	29.06	3.94	22–33
	Adult	6	18.67	4.50	14–27	116.83	5.71	108–123	21.97	2.59	17–24	33.00	4.82	25–38
Male	All	31	11.76	6.30	3–31.5	112.68	15.41	67–132	21.22	2.64	15.5–25	30.73	10.49	8–52
	Juvenile	6	4.83	1.33	3–6	85.83	12.51	67–100	16.63	1.03	15.5–18.4	13.17	3.66	8–17
	Subadult	10	9.00	1.49	7–11	116.5	6.55	108–127	21.75	1.71	19.5–24.2	30.80	5.92	24–39
	Adult	15	16.37	5.84	12–31.5	120.87	5.84	112–132	22.71	1.06	21–25	37.70	4.91	31–52

Tanner, Whitehouse, & Takaishi, 1966 a,b). From the full HGS data set, Yapuncich et al. (2018) utilized a subset consisting of 3,468 observations of individuals age 4 to 18 years ($n = 74$ females, 99 males). Although we did not have access to data on individual ancestry, other studies have described the HGS sample as being solely of European descent (e.g., Marshall & Tanner, 1969, 1970). In the HGS data utilized here, body mass ranges from 14.1 to 84.6 kg, stature ranges from 96.8 to 194.3 cm, and bi-iliac breadth ranges from 15.3 to 32.6 cm. More extensive descriptive statistics for the HGS sample are provided in Yapuncich et al. (2018; their Tables 1 and 2). The BIB-only prediction equation was generated using panel regression with a random effect model in the R package *plm* (Croissant & Millo, 2007) following the methods of Yapuncich et al. (2018):

$$\ln BM = 2.065 \times \ln BIB - 2.887 \qquad (3)$$

Panel regression models are intended to be applied to data representing repeated measures of subjects over a series of regular intervals (Baltagi, 2013; Dougherty, 2011) such as the HGS data, and, by accounting for serial autocorrelation, provide robust estimates of model parameters. Following Yapuncich et al. (2018), variables were natural log-transformed to stabilize the variance.

2.1.2 | Predictive accuracy

We gauged the accuracy of these three equations with several metrics frequently used in studies of body mass prediction (e.g., Aiello & Wood, 1994; Dagosto & Terranova, 1992; Delson et al., 2000; Elliott et al., 2015a,b; Yapuncich et al., 2015). First, we calculated the prediction error (PE: kg) for each individual 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. Second, following Smith (1980, 1984), we calculated the relative percentage prediction error (%PE):

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

Third, we calculated the mean percentage prediction error (%MPE) by averaging relative %PE by age and sex. Following other

studies using these accuracy metrics (Aiello & Wood, 1994; Dagosto & Terranova, 1992; Delson et al., 2000; Elliott et al., 2015a,b; Yapuncich et al., 2015), we consider both a median %PE less than ±20% or conditions in which the majority of test cases have less than ±20%PE to indicate acceptably low error. Finally, we compared observed and predicted BMs using nonparametric two-tailed Mann-Whitney U-tests (to account for nonnormality of observed BMs) to test for significant differences in the group medians. $p < .05$ were considered statistically significant. With this metric, a prediction equation should generate a distribution of predicted BMs that does not have a significantly different median than the observed BMs. This is particularly true if the goal of prediction is to capture the central tendency of a population (Yapuncich, 2018).

2.1.3 | Bonobo-specific prediction equations

After evaluating the accuracy of human-based prediction equations with the Lola ya Bonobo sample, multiple regression was used to generate a bonobo-specific morphometric body mass prediction equation with the adult data, since there are currently no published morphometric equations for bonobos. To generate this equation, BIB, ST, and BM values were natural log-transformed. Adult male and female samples were combined, as the level of sexual dimorphism (calculated as [ln (female BM) − ln(male BM)]*100) is only 13%, less than the 20% threshold suggested by Yapuncich et al. (2015) to necessitate separate prediction equations. The precision of this equation was gauged with the correlation coefficient (r^2), mean squared error (MSE), and percent standard error of the estimate (%SEE).

3 | RESULTS

3.1 | Differences in scaling relationships of stature and bi-iliac breadth

Results from both ANCOVAs are presented in Table 2 and Figure 2 plots ST and BIB against body mass. In both the liberal (adults and subadults) and conservative (adults only) ANCOVAs, neither somatic variable shows significant differences in slope. However, in both

TABLE 2 ANCOVAs for stature and bi-iliac breadth with BM as a covariate

Sample	Variable	Equal variance*	df	Homogeneity of intercepts		Homogeneity of slopes	
				F	p-Value	F	p-Value
Adults and subadults	Stature	Y	96	193.2	***	0.759	.39
	Bi-iliac breadth	Y	96	0.351	.56	2.279	.14
Adults only	Stature	Y	77	175.5	***	0.832	.37
	Bi-iliac breadth	N	77	1.116	.29	1.651	.20

Abbreviations: ANCOVA, analyses of covariance; BM, body mass.

*Levene's test for equal variance.

***$p < .001$.

ANCOVAs, the intercepts of the ST versus BM regressions differ significantly, indicating that at a given body mass, bonobos are significantly shorter than humans. There are no significant differences observed in the intercepts of the BIB versus BM regressions, although BIB does not have the same level of variance in the bonobo and human samples (thus violating an assumption of the ANCOVA). For a prediction equation intended for application across multiple taxa, the significant differences recovered between the intercepts of ST versus BM suggest that accuracy will decrease when ST is included in the prediction equation. These results motivated the development of a new prediction equation (Equation 3) generated from BIB of skeletally immature humans of the HGS data set, which overlap in body mass and bi-iliac breadth with the bonobos.

3.1.1 | Accuracy as indicated by prediction error

Figure 3 shows boxplots of prediction error for all three human-based BMPEs when applied to different bonobo age classes. Relative %PE and the percentage of test cases with <20% PE are presented by sex and age class in Table 3. There are noticeable differences in the predictive accuracy of these three equations, particularly in their predictive accuracy among juvenile bonobos. Not surprisingly, Equation 1 (based on adult female humans) has poor predictive accuracy when applied to the Lola ya Bonobo sample and under-predicted body mass across all three age classes. The equation was most accurate among subadult female bonobos, with a median relative %PE of 19.1 and 6 out of 9 individuals predicted within 20% of their observed body weight (Table 3). The equation strongly
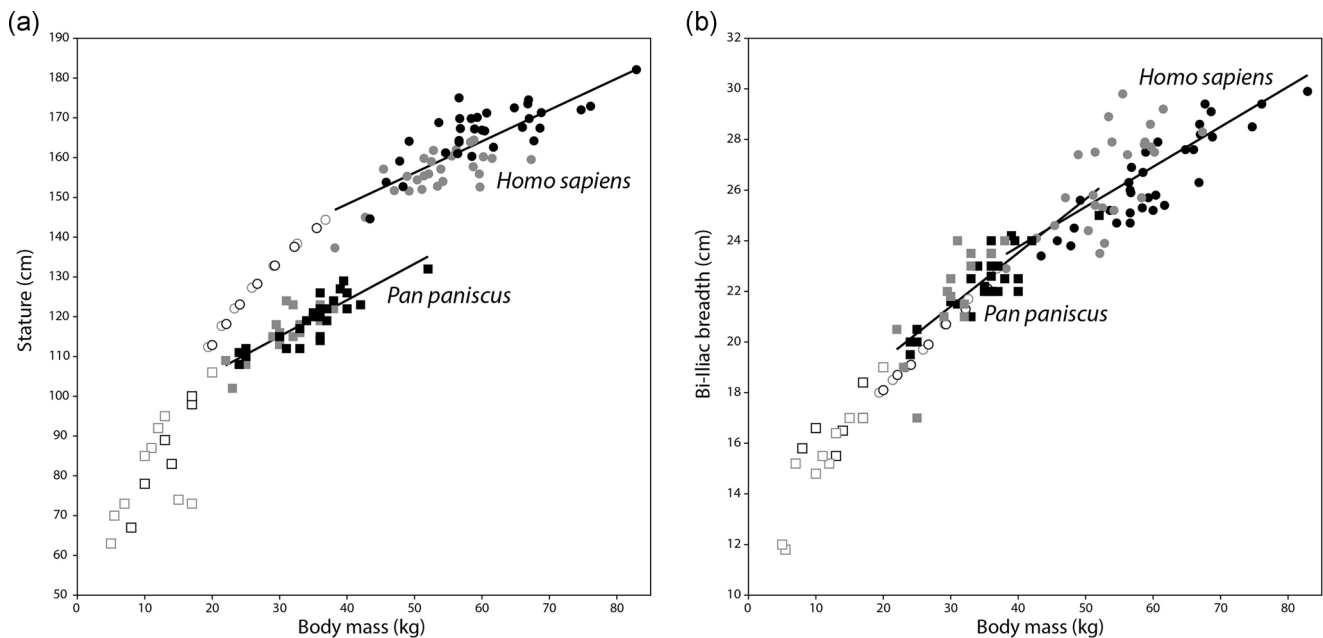

FIGURE 2 Biplots of (a) stature and body mass and (b) bi-iliac breadth and body mass, both with reduced major axis regressions through adults and subadults (filled shapes). Adult & subadult (filled squares) and juvenile (open squares) *P. paniscus* from Lola ya Bonobo test sample. Immature *H. sapiens* (open circles) are age- and sex-specific mean values calculated from a worldwide sample of 33 populations from ages 6–12 reported in Eveleth and Tanner (1976) and summarized in Walker et al. (2018). Means from Eveleth and Tanner (1976) are used for visualization purposes only, since incorporating the 3468 observations in the HGS immature human data set would overwhelm the figure. Adult *H. sapiens* (filled circles) represent population means from (Ruff, 1994; Ruff et al., 1997; 2005). Gray shapes indicate females; black shapes indicate males
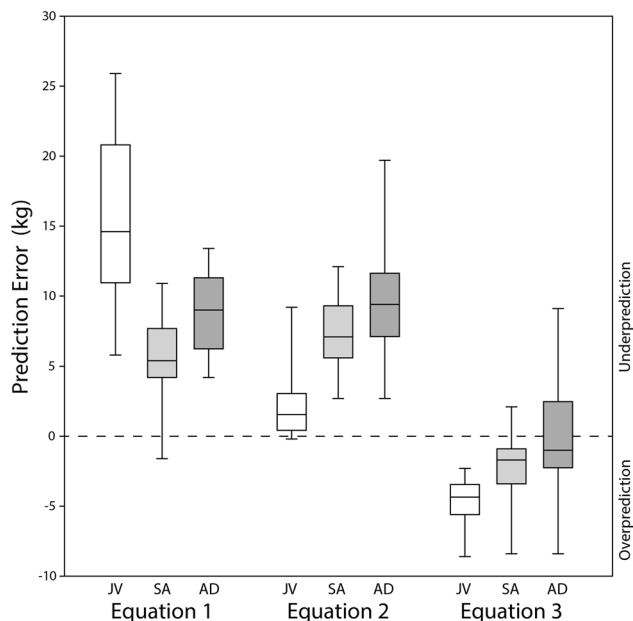
FIGURE 3 Prediction error boxplots by age class for three examined equations. Equation 1: Ruff et al. (1997) adult female; Equation 2: Yapuncich et al. (2018) logged immature panel; Equation 3: logged BIB panel equation of this study. JV, juvenile *P. paniscus* (*n* = 10 females, 6 males); SA, subadult *P. paniscus* (*n* = 9 females, 10 males); AD, adult *P. paniscus* (*n* = 6 females, 15 males). Boxes include 25–75% quartiles; whiskers extend to farthest points <1.5 interquartile range; dashed line demarcates over- and underprediction

underpredicted body mass among juvenile bonobos of both sexes (Figure 3 and Table 3).

Equation 2, derived from a large sample of skeletally immature humans, also performed poorly when applied to bonobos (Table 3). Equation 2 was least accurate when predicting the body masses of adults of both sexes, with median relative %PEs of 39.8 in females and 46.1 in males (Table 3), leading to underpredictions of approximately 10 kg on average (Figure 3). In contrast to Equation 1, Equation 2 was most accurate for juvenile bonobos (Figure 3), with median relative %PEs of 6.9 and 22.3 in females and males, respectively (Figure 3 and Table 3). The equation predicted the body masses for 8 of 10 juvenile females and 2 of 6 juvenile males within 20% of their observed BM.

Equation 3, the novel BIB panel equation developed for this study, was substantially more accurate for bonobos than either of the previously published BMPEs (Table 3), with a slight tendency to overpredict body mass (Figure 3). More than half of the bonobos (41 of 56) were predicted within ±20% of their observed BM and accuracy was particularly high among adult bonobos (median relative %PEs of −4.1 in females and 6.5 in males). Compared to its performance among adults, Equation 3 had lower predictive accuracy among juvenile bonobos (median relative %PEs of −29.4 in females and −24.2 in males). Comparing the percentage of individuals predicted within ±20% of their observed BM, Equation 3 had equal or greater accuracy than the

TABLE 3 Relative percentage prediction error (%PE) for morphometric prediction equations

| Sample	n	Equation 1; Ruff et al. (1997)					Equation 2; Yapuncich et al. (2018)					Equation 3 (this study)				
		Mean	Median	SD	Range	%PE< |20%|	Mean	Median	SD	Range	%PE< |20%|	Mean	Median	SD	Range	%PE<|20%|
Females (all)	25	2250.4	19.1	11531.1	−637.5–57592.3	32	30.5	28.7	27.8	−2.4–119.2	40	−14.8	−12.6	18.2	−54.4–29.2	56
Females (juveniles)	10	5578.5	−151.0	18277.4	−637.5–57592.3	0	25.1	6.9	42.4	−2.4–119.2	80	−30.5	−29.4	13.2	−54.4–12.1	20
Females (subadults)	9	26.5	19.1	26.3	−5.0–89.8	67	29.0	28.7	11.3	11.6–44.1	22	−8.5	−8.6	9.9	−22.7–6.9	78
Females (adults)	6	39.6	25.6	37.8	15.3–115.0	33	41.6	39.8	6.6	33.6–49.9	0	1.7	−4.1	15.3	−12.6–29.2	83
Males (all)	31	−50.9	28.2	291.4	−1396.8–165.3	10	38.4	39.2	13.7	12.1–62.3	6	−4.0	−2.8	16.6	−51.9–21.4	87
Males (juveniles)	6	−390.1	−238.7	580.9	−1396.8–165.3	0	23.9	22.3	11.2	12.1–43.4	33	−29.5	−24.2	15.8	−51.9–15.8	33
Males (subadults)	10	27.2	27.7	11.7	6.9–48.6	20	32.7	32.0	8.7	21.8–48.7	0	−5.2	−6.0	5.4	−12.2–4.3	100
Males (adults)	15	32.7	30.8	12.4	12.0–57.5	7	48.0	46.1	9.8	31.6–62.3	0	7.0	6.5	8.6	−5.9–21.4	87
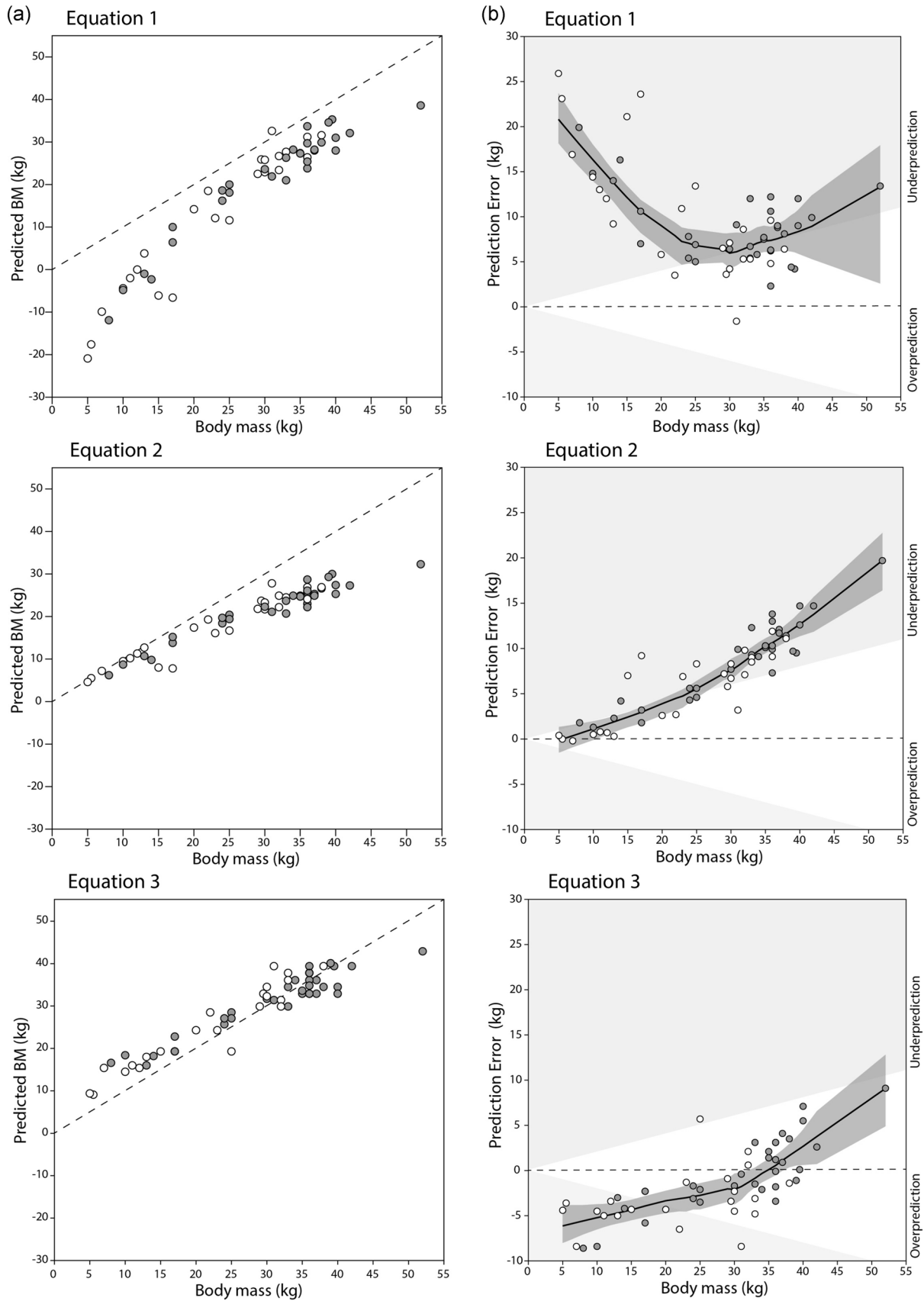
FIGURE 4 Continued.

other equations for all bonobo sex and age classes with the exception of juvenile females (Table 3).

To visualize the accuracy of each equation across the range of observed body masses (rather than by age class), the predicted body masses (Figure 4a) and prediction errors (Figure 4b) are plotted against observed body mass for all Lola ya Bonobo individuals. Equation 1 consistently underpredicts body mass, reaching the highest accuracy in individuals between 30 and 35 kg (Figure 4). However, even in this body mass range, Equation 1 predicts relatively few individuals within ±20% of their observed BM (Figure 4b). Equation 2 also consistently underpredicts body mass, though not to the same degree as Equation 1, and achieves its highest level of accuracy between 5 and 10 kg (Figure 4b). Equation 3 generates slight overpredictions at low body masses and slight underpredictions at high body masses (Figure 4a). However, for individuals between 25 and 45 kg, Equation 3 is very accurate, predicting 11 of 13 females and 21 of 22 males within ±20% of their observed BM.

3.1.2 | Accuracy as indicated by two-sample tests

The results of the Mann–Whitney U-tests comparing the distributions of predicted and observed body masses are presented in Table 4. With the bonobo test sample, Equation 1 generates distributions of predicted BMs that are significantly different from observed BMs for the majority of sex and age groups (Table 4). Among juvenile bonobos, there are no significant differences between observed body masses and those predicted with Equation 2 (Table 4), but there are significant differences among subadults and adults (as well as the aggregated sample). Equation 3 performs the best by this metric, as there are only significant differences between observed and predicted BMs among juvenile male bonobos (Table 4). Compared to Equation 1, ranges and standard deviations of predicted BMs are more constrained with the two-panel equations, and Equation 2 generates a slightly tighter distribution of predicted body masses than Equation 3. As with the prediction error results, Mann-Whitney U tests suggest that Equation 3 is the most accurate of the three BMPEs examined here.

3.1.3 | Bonobo-specific prediction equations

With the Lola ya Bonobo adult sample ($n = 21$), multiple regression returned the following morphometric BMPE:

$$\ln BM = 0.555 \times \ln BIB + 1.868 \times \ln ST - 7.080 \qquad (4)$$

The adjusted r^2 for Equation 4 is 0.790, the MSE is 0.004, and the %SEE is 6.549. A quasi-maximum likelihood estimator (QMLE) of 1.002 should be used to correct for bias when detransforming predicted body masses (Smith, 1993; Sprugel, 1983). Stature was a significant factor in the regression model ($p < .001$) but bi-iliac breadth is not ($p < .06$). We limited the model to just the significant factor, and ordinary least squares regression of stature against body mass returned the following equation:

$$\ln BM = 2.507 \times \ln ST - 8.408 \qquad (5)$$

Equation 5 has an r^2 of 0.774, an MSE of 0.004, a %SEE of 7.263, and a QMLE of 1.002.

4 | DISCUSSION

By requiring extrapolation beyond the bounds of the reference sample, bonobos represent a challenging test sample for human-derived morphometric BMPEs. Humans and bonobos differ in body tissue composition (Zihlman & Bolter, 2015), relative limb proportions (Corruccini & McHenry, 1979; McHenry & Corruccini, 1981), and pelvic morphology (e.g., Hammond & Almécija, 2017; Lovejoy, Suwa, Spurlock, Asfaw, & White, 2009), all of which are factors that should reduce the accuracy of human-derived morphometric BMPEs.

In this study, we predicted that BMPEs derived from a reference sample of immature humans (Equations 2 and 3) would have higher predictive accuracy than those derived from an adult human reference sample (Equation 1). Based on several accuracy metrics, the most reliable BMPE is Equation 3, a panel equation derived from natural-log transformed bi-iliac breadth of skeletally immature humans (Figure 3 and Table 3). Since multivariate BMPEs often have greater accuracy than univariate equations (Gingerich, 1990; Jungers, 1990; Mendoza, Janis, & Palmqvist, 2006; Yapuncich et al., 2015), it is somewhat surprising that the equations which include both stature and bi-iliac breadth (Equations 1 and 2) have lower predictive accuracy than the univariate Equation 3. The inaccuracies of these equations are likely caused by differences in the relationship between stature and body mass in humans and bonobos (Table 2; Figure 2). ANCOVAs reveal that adult bonobos are significantly shorter than humans at a given body mass (Figure 2a). In contrast, despite marked differences in pelvic morphology, the relationship between bi-iliac breadth and body mass is comparable between these two species (Figure 2b).

FIGURE 4 (a) Biplots of observed and predicted body mass and (b) local regression (LOESS) of prediction error to observed body mass (smoothing factor = 0.5) for *P. paniscus* individuals from Lola ya Bonobo. Equation 1; Ruff et al. (1997) adult female; Equation 2; Yapuncich et al. (2018) logged immature panel; Equation 3 logged BIB panel equation of this study. White circles indicate females; gray circles indicate males. In (a), the dotted line represents a line of equivalence so that values below the line are underpredicted and values above the line are overpredicted. In (b), under- and overprediction are indicated. The dark gray region indicates 95% confidence interval of each regression. Light gray regions approximate prediction errors >20%. LOESS regressions were performed in PAST (Hammer et al., 2001)

TABLE 4 Observed and predicted body mass (BM) distributions for Lola ya Bonobo sample

Sample	n	Lola ya Bonobo test sample Median Observed BM (kg)	Equation 1; Ruff et al. (1997) Median Predicted BM (kg)	SD	Range	Mann-Whitney U	p-Value	Equation 2; Yapuncich et al. (2018) Median Predicted BM (kg)	SD	Range	Mann-Whitney U	p-Value	Equation 3; this study Median Predicted BM (kg)	SD	Range	Mann-Whitney U	p-Value
Females (all)	25	25.0	18.5	16.7	−20.9–32.6	195.0	*	19.3	7.6	4.6–27.8	204.5	*	28.5	9.7	9.1–39.4	263.0	.34
Females (juveniles)	10	11.5	−5.2	10.1	−20.9–14.2	7.0	**	8.7	3.7	4.6–17.4	37.5	.36	15.7	4.6	9.1–24.3	26.0	.08
Females (subadults)	9	30.0	25.8	5.9	12.1–32.6	19.0	.06	23.3	3.4	16.1–27.8	11.0	*	31.4	4.5	24.3–39.4	28.0	.29
Females (adults)	6	17.0	27.0	7.4	11.6–31.6	16.0	.81	24.1	3.8	16.7–26.9	2.0	*	35.4	7.4	19.3–39.4	16.0	.81
Males (all)	31	35.0	26.3	12.6	−11.9–38.6	252.0	**	23.7	6.5	6.2–32.3	215.5	***	32.9	7.4	16.0–42.9	455.0	.72
Males (juveniles)	6	13.5	−0.6	7.9	−11.9–10.0	1.5	*	10.2	3.3	6.2–15.2	11.0	.30	18.3	2.4	16.0–22.8	4.0	*
Males (subadults)	10	31.5	24.9	6.5	16.2–34.6	24.0	.05	23.0	3.8	18.4–29.3	12.0	**	32.6	5.2	25.7–40.1	39.0	.43
Males (adults)	15	36.0	28.2	4.7	21.0–38.6	15.5	***	25.3	3.1	20.7–32.3	1.0	***	34.5	3.5	29.9–42.9	73.0	.11

*p < .05.
***p < .01.
****p < .001.

TABLE 5 Body masses of select hominin fossil taxa predicted with Equation 3

Taxon	Specimen	BIB (cm)[a]	Living BIB (cm)[b]	Predicted BM (kg)	Previous BM (kg)[c]	Previous BM (kg)[d]
Australopithecus afarensis	AL 288-1	25.3	26.6	48.8	26.0	45.4
Australopithecus africanus	STS 14	25	26.3	47.5	22.8	39.3
Homo erectus	BSN 49/P27	28.8	30.7	65.6	29.4	73.0
Australopithecus sediba	MH2	25	26.3	47.5	29.1	41.0

Abbreviation: BIB, bi-iliac breadth.
[a]Kibii et al. (2011) for *A. sediba*, Ruff (2010) for all other taxa.
[b]BIB converted to living BIB following Ruff et al. (2005).
[c]Grabowski et al. (2015).
[d]Ruff et al. (2018) male/female mean.

We expected Equation 1 to be less accurate than the other equations with the bonobo test sample, since application to bonobos requires extrapolation beyond both the body mass and phylogenetic ranges of the adult human reference sample. However, Equation 1 was more accurate than Equation 2 among subadult and adult bonobos according to the percentage of individuals predicted within ±20% of their observed BM (Table 3) and the Mann–Whitney U-tests (Table 4). The increased accuracy of Equation 1 relative to Equation 2 may reflect the weighting of the coefficients in each equation. In Equation 1, stature has a smaller coefficient than BIB, while in Equation 2, stature has a larger coefficient than BIB. With significant differences in stature observed among bonobos and humans (Table 2), the relative weight of the stature and BIB coefficients means that stature does not introduce as much inaccuracy in Equation 1.

Equation 2 is the most accurate equation for juvenile bonobos but underpredicts body mass for subadult and adult individuals (Figure 2; Tables 3 and 4). As discussed above, this underprediction arises from the interspecific differences in the scaling relationships between body mass and stature in humans and bonobos (Figure 3 and Table 3), as well as the weight of stature as a predictor variable in Equation 2.

The higher accuracy of Equation 3, when applied to the Lola ya Bonobo sample, suggests this equation should generate reliable predictions of body mass in bonobos, particularly for subadults and adults, and has the potential to generate reliable predictions of body mass in other hominoid species (a potential that should be empirically tested with data from other species). The equation achieves its highest accuracy with the Lola sample between 25 and 45 kg (Figure 4). Grabowski et al. (2015) argue this is an important range for understanding body mass change throughout hominin evolution, although Ruff et al. (2018) predict most fossil hominins to have slightly larger body masses (30–70 kg). Thus, the interspecific reliability of Equation 3 seems to make it a good candidate for the reliable prediction of body mass for some fossil hominins. However, rather than providing a distinct best option, this study underlines several general challenges of body mass prediction and introduces several caveats to the broad application of Equation 3 among fossil taxa.

First, these analyses highlight the importance of evaluating the scaling relationships between potential variables and body mass before developing BMPEs (as in Burgess et al., 2018; Grabowski

et al., 2015; Yapuncich & Boyer, 2014). ANCOVAs reveal that the scaling relationships of stature and body mass are significantly different between humans and bonobos (Figure 2 and Table 3), which likely generates systematic biases in predicted body masses for both Equations 1 and 2. Evaluating the scaling relationships of the predictor variables before testing the accuracy of each equation, it was possible to predict that BIB would be a more reliable predictor than STAT for this bonobo sample.

Second, these analyses demonstrate that variables can contribute differently to predictive accuracy depending on the level of inquiry. BIB alone is more accurate than the combination of BIB and STAT when applied to bonobos with human-derived Equation 3 (Figure 3 and Table 3), but the preferred bonobo-derived equation (Equation 5) relies solely on STAT. Essentially, BIB substantially increases predictive accuracy interspecifically, but is not informative intraspecifically. Because scaling relationships often differ at interspecific and intraspecific levels (Gould, 1971), strong correlations at the interspecific level may not be present at the intraspecific level.

Third, accurate predictor variables can be capricious. Pelvic morphology differs substantially between bonobos and humans, and bonobo pelves are longer craniocaudally and shorter dorsoventrally relative to human pelves. Given these differences in pelvic morphology, there is no *prima facie* argument that BIB should be a reliable predictor of body mass across these species. Nonetheless, BIB performs very well with the bonobo test sample (Figure 3; Table 3 and 4). This interspecific accuracy may suggest that Equation 3 could reasonably be applied to fossil taxa as well. However, the pelves of many fossil hominins differ substantially from the pelves of both bonobos and humans, as they are often very mediolaterally broad (Ruff, 2010), which would lead to strongly overpredicted body masses. Indeed, the predicted body masses for *Australopithecus afarensis* (AL 288-1), *Australopithecus africanus* (STS 14), *Australopithecus sediba* (MH2), and *Homo erectus* (BSN 49/P27) are more than double the predicted body masses reported by Grabowski et al. (2015) and are higher (though more comparable) than male/female mean body masses predicted by Ruff et al. (2018; Table 5). Equation 3 may work well for particular taxa when extrapolating beyond the phylogenetic bounds of the human reference sample, but that characteristic does not necessarily mean the equation will be accurate when generalized to all taxa phylogenetically bracketed by humans and bonobos.

Finally, as we have previously argued for BMPEs more generally (Yapuncich et al., 2018), Equation 3 should only be applied when the predictor values can be estimated with a reasonable degree of confidence. Stature is difficult to measure from skeletal remains and stature prediction equations (e.g., Jungers, 1988; Konigsberg et al., 1998; McHenry, 1974) are not necessarily tested with other hominoid species. By relying solely on bi-iliac breadth, Equation 3 sidesteps the methodological problems associated with predicting stature. However, since BIB measurements were taken on living individuals in the reference sample for Equation 3, application to skeletonized specimens requires converting osteological BIB to living BIB (as in Ruff et al., 2005). It is possible that using predicted values (which have their own uncertainty) in BMPEs may decrease precision so much that predicted body masses are not particularly informative (Martin, 1990).

Despite these complications, Equation 3 is the most accurate of the three evaluated equations for predicting bonobo body mass. This equation generally overpredicts the body mass of smaller and younger individuals, underpredicts the body mass of the largest individuals, and is most accurate (prediction error <20%, with few exceptions) for individuals larger than 17 kg. While Equation 3 generates accurate results in bonobos, the pronounced bi-iliac breadth of many fossil hominins renders the application of this novel BMPE to fossil taxa more fraught.

ACKNOWLEDGMENTS

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

ORCID

Gabriel S. Yapuncich http://orcid.org/0000-0001-7371-5857
Christopher S. Walker http://orcid.org/0000-0002-5173-2784

REFERENCES

Aiello, L. C. (1992). Allometry and the analysis of size and shape in human evolution. *Journal of Human Evolution*, 22, 127–147. https://doi.org/10.1016/0047-2484(92)90034-7

Aiello, L. C., & Wood, B. A. (1994). Cranial variables as predictors of hominine body mass. *American Journal of Physical Anthropology*, 95, 409–426. https://doi.org/10.1002/ajpa.1330950405

Aiello, L. C., & Wheeler, P. (1995). The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Current Anthropology*, 36, 199–221. https://doi.org/10.1086/204350

Aiello, L. C., & Wells, J. C. (2002). Energetics and the evolution of the genus *Homo*. *Anthropology*, 31, 323–338. https://doi.org/10.1146/annurev.anthro.31.040402.085403

Almécija, S., Smaers, J. B., & Jungers, W. L. (2015). The evolution of human and ape hand proportions. *Nature Communications*, 6, 7717. https://doi.org/10.1038/ncomms8717

Antón, S. C., Leonard, W. R., & Robertson, M. L. (2002). An ecomorphological model of the initial hominid dispersal from Africa. *Journal of Human Evolution*, 43, 773–785. https://doi.org/10.1006/jhev.2002.0602

Auerbach, B. M., & Ruff, C. B. (2004). Human body mass estimation: A comparison of "morphometric" and "mechanical" methods. *American Journal of Physical Anthropology*, 125, 331–342. https://doi.org/10.1002/ajpa.20032

Baltagi, B. H. (2013). *Econometric analysis of panel data* (5th Edition.). West Sussex, UK: Wiley. https://doi.org/10.1002/9781118445112.stat03160

Berger, L. R., de Ruiter, D. J., Churchill, S. E., Schmid, P., Carlson, K. J., Dirks, P. H., & Kibii, J. M. (2010). *Australopithecus sediba*: A new species of *Homo*-like australopith from South Africa. *Science*, 328, 195–204. https://doi.org/10.1126/science.1184944

Berger, L. R., Hawks, J., de Ruiter, D. J., Churchill, S. E., Schmid, P., Delezene, L. K., … Zipfel, B. (2015). *Homo naledi*, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. *eLife*, 4, e09560. https://doi.org/10.7554%2FeLife.09560

Brassey, C. A., O'Mahoney, T. G., Chamberlain, A. T., & Sellers, W. I. (2018). A volumetric technique for fossil body mass estimation applied to *Australopithecus afarensis*. *Journal of Human Evolution*, 115, 47–64. https://doi.org/10.1016/j.jhevol.2017.07.014

Brown, P., Sutikna, T., Morwood, M., Soejono, R. P., Jatmiko, E., Saptomo, W. E., & Due, R. A. (2004). A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature*, 431(1072), 1055–1061. https://doi.org/10.1038/nature02999

Burgess, M. L., McFarlin, S. C., Mudakikwa, A., Cranfield, M. R., & Ruff, C. B. (2018). Body mass estimation in hominoids: Age and locomotor effects. *Journal of Human Evolution*, 115, 36–46. https://doi.org/10.1016/j.jhevol.2017.07.004

Calder, W. A. (1984). *Size, function, and life history*. Cambridge, MA: Harvard University Press.

Corruccini, R. S., & McHenry, H. M. (1979). Morphological affinities of *Pan paniscus*. *Science*, 204, 1341–1343. https://doi.org/10.1126/science.451545

Croissant, Y., & Millo, G. (2007). Plm: Linear models for panel data. R package version 03-1. Retrieved from http://doi.org/CRAN R-projectorg

Dagosto, M., & Terranova, C. J. (1992). Estimating the body size of Eocene primates: A comparison of results from dental and postcranial variables. *International Journal of Primatology*, 13, 307–344. https://doi.org/10.1007/BF02547818

Damuth, J., & MacFadden, B. J. (1990). *Body size in mammalian paleobiology*. Cambridge: Cambridge University Press.

Delson, E., Terranova, C. J., Jungers, W. L., Sargis, E. J., Jablonski, N. G., & Dechow, P. C. (2000). Body mass in Cercopithecidae (Primates Mammalia): Estimation and scaling in extinct and extant taxa (83, pp. 1–159). New York, NY: Anthropological Papers of the American Museum of Natural History.

Dougherty, C. (2011). *Introduction to econometrics* (4th edition.). Oxford, UK: Oxford University Press.

Elliott, M., Kurki, H., Weston, D. A., & Collard, M. (2015a). Estimating body mass from skeletal material: New predictive equations and methodological insights from analyses of a known-mass sample of humans. *Archaeological and Anthropological Sciences*, 8, 731–750. https://doi.org/10.1007/s12520-015-0252-5

Elliott, M., Kurki, H., Weston, D. A., & Collard, M. (2015b). Estimating body mass from postcranial variables: An evaluation of current equations using a large known-mass sample of modern humans. *Archaeological and Anthropological Sciences*, 8, 689–704. https://doi.org/10.1007/s12520-015-0251-6

Eveleth, P., & Tanner, J. (1976). *Worldwide variation in human growth.* Cambridge, UK: Cambridge University Press.

Fleagle, J. G. (1985). Size and scaling in primate biology. In W. J. Jungers (Ed.), *Size and adaptation in primates*. New York, NY: Plenum Press. https://doi.org/10.1007/978-1-4899-3647-9_1

Gingerich, P. D. (1990). Prediction of body mass in mammalian species from long bone lengths and diameters. *Contributions from the University of Michigan Museum of Paleontology*, 28, 79–92.

Gould, S. J. (1971). Geometric similarity in allometric growth: A contribution to the problem of scaling in the evolution of size. *The American Naturalist*, 105, 113–136. https://doi.org/10.1086/282710

Grabowski, M., & Jungers, W. L. (2017). Evidence of a chimpanzee-sized ancestor of humans but a gibbon-sized ancestor of apes. *Nature Communications*, 8, 880. https://doi.org/10.1038/s41467-017-00997-4

Grabowski, M., Hatala, K. G., Jungers, W. L., & Richmond, B. G. (2015). Body mass estimates of hominin fossils and the evolution of human body size. *Journal of Human Evolution*, 85, 75–93. https://doi.org/10.1016/j.jhevol.2015.05.005

Grine, F., Jungers, W., Tobias, P., & Pearson, O. (1995). Fossil *Homo* femur from Berg Aukas, northern Namibia. *American Journal of Physical Anthropology*, 97, 151–185. https://doi.org/10.1002/ajpa.1330970207

Hammer, Ø., Harper, D. A., & Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4, 1–9.

Hammond, A. S., & Almécija, S. (2017). Lower ilium evolution in apes and hominins. *The Anatomical Record*, 300, 828–844. https://doi.org/10.1002/ar.23545

Hens, S. M., Konigsberg, L. W., & William, J. L. (1998). Estimation of African ape body length from femur length. *Journal of Human Evolution*, 34, 401–411. https://doi.org/10.1006/jhev.1997.0209

Holliday, T. W., Churchill, S. E., Carlson, K. J., DeSilva, J. M., Schmid, P., Walker, C. S., & Berger, L. R. (2018). Body size and proportions of *Australopithecus sediba*. *Paleoanthropology*, 406–422. https://doi.org/10.4207/PA.2018.ART118

Jungers, W. L. (1988). New estimates of body size in australopithecines. In F. E. Grine (Ed.), *Evolutionary history of the "robust" australopithecines* (pp. 115–125). New York, NY: Aldine de Gruyter.

Jungers, W. L. (1990). Problems and methods in reconstructing body size in fossil primates. In J. Damuth & B. J. MacFadden (Eds.), *Body size in mammalian paleobiology: estimation and biological implications* (pp. 103–118). Cambridge: Cambridge University Press.

Jungers, W. L., Grabowski, M., Hatala, K. G., & Richmond, B. G. (2016). The evolution of body size and shape in the human career. *Philosophical Transactions of the Royal Society B*, 371, 20150247. https://doi.org/10.1098/rstb.2015.0247

Kibii, J. M., Churchill, S. E., Schmid, P., Carlson, K. J., Reed, N. D., De Ruiter, D. J., & Berger, L. R. (2011). A partial pelvis of *Australopithecus sediba*. *Science*, 333, 1407–1411. https://doi.org/10.1126/science.1202521

Konigsberg, L. W., Hens, S. M., Jantz, L., & Jungers, W. L. (1998). Stature estimation and calibration: Bayesian and maximum likelihood perspectives in physical anthropology. *American Journal of Physical Anthropology*, 107, 65–92. https://doi.org/10.1002/(SICI)1096-8644(1998)107:27+⟨65::aid-ajpa4⟩3.0.co;2-6

Leigh, S. R., & Shea, B. T. (1995). Ontogeny and the evolution of adult body size dimorphism in apes. *American Journal of Primatology*, 36, 37–60. https://doi.org/10.1002/ajp.1350360104

Leigh, S. R., & Shea, B. T. (1996). Ontogeny of body size variation in African apes. *American Journal of Physical Anthropology*, 99, 43–65. https://doi.org/10.1002/(sici)1096-8644(199601)99:1⟨43::aid-ajpa3⟩3.0.co;2-0

Lovejoy, C. O., Suwa, G., Spurlock, L., Asfaw, B., & White, T. D. (2009). The pelvis and femur of *Ardipithecus ramidus*: The emergence of upright walking. *Science*, 326, 71e1–71e6. https://doi.org/10.1126/science.1175831

Marshall, W. A., & Tanner, J. M. (1969). Variations in the pattern of pubertal changes in girls. *Archives of Disease in Childhood*, 44, 291–303. https://doi.org/10.1136/adc.44.235.291

Marshall, W. A., & Tanner, J. M. (1970). Variations in the pattern of pubertal changes in boys. *Archives of Disease in Childhood*, 45, 13–23. https://doi.org/10.1136/adc.45.239.13

Martin, R. A. (1990). Estimating body mass and correlated variables in extinct mammals: Travels in the fourth dimensions. In J. Damuth & B. J. MacFadden (Eds.), *Body size in mammalian paleobiology: Estimation and biological implications* (pp. 49–68). Cambridge, UK: Cambridge University Press.

McHenry, H. M. (1974). How large were the australopithecines? *American Journal of Physical Anthropology*, 40, 329–340. https://doi.org/10.1002/ajpa.1330400304

McHenry, H. M. (1992). Body size and proportions in early hominids. *American Journal of Physical Anthropology*, 87, 407–431. https://doi.org/10.1002/ajpa.1330870404

McHenry, H. M. (1994). Behavioral ecological implications of early hominid body size. *Journal of Human Evolution*, 27, 77–87. https://doi.org/10.1006/jhev.1994.1036

McHenry, H. M., & Corruccini, R. S. (1981). *Pan paniscus* and human evolution. *American Journal of Physical Anthropology*, 54, 355–367. https://doi.org/10.1002/ajpa.1330540309

McNab, B. K. (1990). The physiological significance of body size. In J. Damuth & B. J. MacFadden (Eds.), *Body size in mammalian paleobiology: estimation and biological implications* (pp. 11–23). Cambridge, UK: Cambridge University Press.

Mendoza, M., Janis, C. M., & Palmqvist, P. (2006). Estimating the body mass of extinct ungulates: A study on the use of multiple regression. *Journal of Zoology*, 270, 90–101. https://doi.org/10.1111/j.1469-7998.2006.00094.x

Peters, R. H. (1983). *The ecological implications of body size.* Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511608551

Richmond, B. G., Aiello, L. C., & Wood, B. A. (2002). Early hominin limb proportions. *Journal of Human Evolution*, 43, 529–548. https://doi.org/10.1016/S0047-2484(02)90594-4

Robson, S. L., & Wood, B. (2008). Hominin life history: Reconstruction and evolution. *Journal of Anatomy*, 212, 394–425. https://doi.org/10.1111/j.1469-7580.2008.00867.x

Ruff, C. (1987). Structural allometry of the femur and tibia in Hominoidea and *Macaca*. *Folia Primatologica*, 48, 9–49. https://doi.org/10.1159/000156283

Ruff, C. (2007). Body size prediction from juvenile skeletal remains. *American Journal of Physical Anthropology*, 133, 698–716. https://doi.org/10.1002/ajpa.20568

Ruff, C., Niskanen, M., Junno, J.-A., & Jamison, P. (2005). Body mass prediction from stature and bi-iliac breadth in two high latitude populations, with application to earlier higher latitude humans. *Journal of Human Evolution*, 48, 381–392. https://doi.org/10.1016/j.jhevol.2004.11.009

Ruff, C. B. (1991). Climate and body shape in hominid evolution. *Journal of Human Evolution*, 21, 81–105. https://doi.org/10.1016/0047-2484(91)90001-C

Ruff, C. B. (1994). Morphological adaptation to climate in modern and fossil hominids. *American Journal of Physical Anthropology*, 37, 65–107. https://doi.org/10.1002/ajpa.1330370605

Ruff, C. B. (2000a). Body size, body shape, and long bone strength in modern humans. *Journal of Human Evolution*, 38, 269–290. https://doi.org/10.1006/jhev.1999.0322

Ruff, C. B. (2000b). Body mass prediction from skeletal frame size in elite athletes. *American Journal of Physical Anthropology*, 113, 507–517. https://doi.org/10.1002/1096-8644(200012)113:4.⟨507::aid-ajpa5⟩3.0.co;2-f.

Ruff, C. B. (2010). Body size and body shape in early hominins – Implications of the Gona pelvis. *Journal of Human Evolution*, *58*, 166–178. https://doi.org/10.1016/j.jhevol.2009.10.003

Ruff, C. B., & Walker, A. (1993). Body size and body shape. In A. Walker & R. Leakey (Eds.), *The Nariokotome Homo erectus skeleton* (pp. 234–265). Cambridge, MA: Harvard University Press. https://doi.org/10.1007/978-3-662-10382-1_11

Ruff, C. B., Trinkaus, E., & Holliday, T. W. (1997). Body mass and encephalization in Pleistocene *Homo*. *Nature*, *387*, 173–176. https://doi.org/10.1038/387173a0

Ruff, C. B., Burgess, L. M., Squyres, N., Junno, J.-A., & Trinkaus, E. (2018). Lower limb articular scaling and body mass estimation in Pliocene and Pleistocene hominins. *Journal of Human Evolution*, *115*, 85–111. https://doi.org/10.1016/j.jhevol.2017.10.014

Ruff, C. B., Holt, B. M., Niskanen, M., Sladék, V., Berner, M., Garofalo, E., & Tompkins, D. (2012). Stature and body mass estimation from skeletal remains in the European Holocene. *American Journal of Physical Anthropology*, *148*, 601–617. https://doi.org/10.1002/ajpa.22087

Sayers, K., Raghanti, M. A., & Lovejoy, C. O. (2012). Human evolution and the chimpanzee referential doctrine. *Annual Review of Anthropology*, *41*, 119–138. https://doi.org/10.1146/annurev-anthro-092611-145815

Schmidt-Nielsen, K. (1984). *Scaling: Why is animal size so important?* Cambridge: Cambridge University Press. https://doi.org/10.1017/cbo9781139167826

Smith, R. J. (1980). Rethinking allometry. *Journal of Theoretical Biology*, *87*, 97–111. https://doi.org/10.1016/0022-5193(80)90222-2

Smith, R. J. (1984). Determination of relative size: The "criterion of subtraction" problem in allometry. *Journal of Theoretical Biology*, *108*, 131–142. https://doi.org/10.1016/S0022-5193(84)80174-5

Smith, R. J. (1993). Bias in equations used to estimate primate body mass. *Journal of Human Evolution*, *36*, 423–459. https://doi.org/10.1006/jhev.1993.1036

Smith, R. J. (2002). Estimation of body mass in paleontology. *Journal of Human Evolution*, *43*, 271–287. https://doi.org/10.1006/jhev.2002.0573

Smith, R. J. (2009). Use and misuse of the reduced major axis for line-fitting. *American Journal of Physical Anthropology*, *140*, 476–486. https://doi.org/10.1002/ajpa.21090

Sprugel, D. G. (1983). Correcting for bias in log-transformed allometric equations. *Ecology*, *64*, 209–210. https://doi.org/10.2307/1937343

Squyres, N., & Ruff, C. B. (2015). Body mass estimation from knee breadth, with application to early hominins. *American Journal of Physical Anthropology*, *158*, 198–208. https://doi.org/10.1002/ajpa.22789

Tan, J., & Hare, B. (2013). Bonobos share with strangers. *PLOS One*, *8*, e51922. https://doi.org/10.1371/journal.pone.0051922

Tanner, J. M., Whitehouse, R. H., & Takaishi, M. (1966a). Standards from birth to maturity for height, weight, height velocity, and weight velocity: British children, 1965. Part I. *Archives of Disease in Childhood*, *41*, 454–471. https://doi.org/10.1136/adc.41.219.454

Tanner, J. M., Whitehouse, R. H., & Takaishi, M. (1966b). Standards from birth to maturity for height, weight, height velocity, and weight velocity: British children, 1965. Part II. *Archives of Disease in Childhood*, *41*, 613–635. https://doi.org/10.1136/adc.41.220.613

Walker, C. S., Yapuncich, G. S., Sridhar, S., Cameron, N., & Churchill, S. E. (2018). Evaluating morphometric body mass prediction equations with a juvenile human test sample: Accuracy and applicability to small-bodied hominins. *Journal of Human Evolution*, *115*, 65–77. https://doi.org/10.1016/j.jhevol.2017.03.009

Will, M., & Stock, J. T. (2015). Spatial and temporal variation of body size among early *Homo*. *Journal of Human Evolution*, *82*, 15–33. https://doi.org/10.1016/j.jhevol.2015.02.009

Witmer, L. (1995). The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In J. Thomason (Ed.), *Functional morphology in vertebrate paleontology* (pp. 19–33). Cambridge, UK: Cambridge University Press.

Wolpoff, M. H. (1973). Posterior tooth size, body size, and diet in South African gracile australopithecines. *American Journal of Physical Anthropology*, *39*, 375–393. https://doi.org/10.1002/ajpa.1330390306

Wrangham, R., & Pilbeam, D. (2002). African apes as time machines. In B. M. F. BMF Galdikas, N. E. Briggs, L. K. Sheeran, G. L. Shapiro & J. Goodall (Eds.), *All apes great and small* (pp. 5–17). Boston, MA: Springer. https://doi.org/10.1007/0-306-47461-1_2

Yapuncich, G. S. (2018). Alternative methods for calculating percentage prediction error and their implications for predicting body mass in fossil taxa. *Journal of Human Evolution*, *115*, 140–145. https://doi.org/10.1016/j.jhevol.2017.03.001

Yapuncich, G. S., & Boyer, D. M. (2014). Interspecific scaling patterns of talar articular surfaces within primates and their closest living relatives. *Journal of Anatomy*, *224*, 150–172. https://doi.org/10.1111/joa.12137

Yapuncich, G. S., Gladman, J. T., & Boyer, D. M. (2015). Predicting euarchontan body mass: A comparison of tarsal and dental variables. *American Journal of Physical Anthropology*, *157*, 472–506. https://doi.org/10.1002/ajpa.22735

Yapuncich, G. S., Churchill, S. E., Cameron, N., & Walker, C. S. (2018). Morphometric panel regression equations for predicting body mass in immature humans. *American Journal of Physical Anthropology*, *166*, 179–195. https://doi.org/10.1002/ajpa.23422

Zihlman, A. L., Cronin, J. E., Cramer, D. L., & Sarich, V. M. (1978). Pygmy chimpanzee as a possible prototype for the common ancestor of humans, chimpanzees and gorillas. *Nature*, *275*, 744–746. https://doi.org/10.1038/275744a0

Zihlman, A. L., & Bolter, D.R. (2015). Body composition in *Pan paniscus* compared with *Homo sapiens* has implications for changes during human evolution. *Proceedings of the National Academy of Sciences*, *112*, 7466–7471. https://doi.org/10.1073/pnas.1505071112

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.