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Evaluating morphometric body mass prediction equations with a juvenile human test sample: accuracy and applicability to small-bodied hominins

Christopher S. Walker^{a, b, c, *, 1}, Gabriel S. Yapuncich^{b, 1}, Shilpa Sridhar^b, Noël Cameron^{d, c}, Steven E. Churchill^{b, c}

^a Department of Molecular Biomedical Sciences, College of Veterinary Medicine, North Carolina State University, 1060 William Moore Drive, Raleigh, NC, 27607, USA

^b Department of Evolutionary Anthropology, Box 90383, Duke University, Durham, NC, 27708, USA

^c Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa

^d School of Sport, Exercise and Health Sciences, Loughborough University, Loughborough, LE11 3TU, United Kingdom

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ABSTRACT

Body mass is an ecologically and biomechanically important variable in the study of hominin biology. Regression equations derived from recent human samples allow for the reasonable prediction of body mass of later, more human-like, and generally larger hominins from hip joint dimensions, but potential differences in hip biomechanics across hominin taxa render their use questionable with some earlier taxa (i.e., *Australopithecus* spp.). Morphometric prediction equations using stature and bi-iliac breadth avoid this problem, but their applicability to early hominins, some of which differ in both size and proportions from modern adult humans, has not been demonstrated. Here we use mean stature, bi-iliac breadth, and body mass from a global sample of human juveniles ranging in age from 6 to 12 years ($n = 530$ age- and sex-specific group annual means from 33 countries/regions) to evaluate the accuracy of several published morphometric prediction equations when applied to small humans. Though the body proportions of modern human juveniles likely differ from those of small-bodied early hominins, human juveniles (like fossil hominins) often differ in size and proportions from adult human reference samples and, accordingly, serve as a useful model for assessing the robustness of morphometric prediction equations. Morphometric equations based on adults systematically underpredict body mass in the youngest age groups and moderately overpredict body mass in the older groups, which fall in the body size range of adult *Australopithecus* (~26–46 kg). Differences in body proportions, notably the ratio of lower limb length to stature, influence predictive accuracy. Ontogenetic changes in these body proportions likely influence the shift in prediction error (from under- to overprediction). However, because morphometric equations are reasonably accurate when applied to this juvenile test sample, we argue these equations may be used to predict body mass in small-bodied hominins, despite the potential for some error induced by differing body proportions and/or extrapolation beyond the original reference sample range.

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1. Introduction

As a frequent proxy for body size, body mass has broad implications for the study of allometry and can inform reconstructions of

a variety of associated ecological and physiological characteristics, including diet (Aiello and Wheeler, 1995), locomotion (Cant, 1992; Rubenson et al., 2007), predation risk (Isbell, 1994), life history (Robson and Wood, 2008), and energetic demands (Aiello and Wells, 2002; Churchill, 2006; Snodgrass and Leonard, 2009). Because body mass covaries with many ecological and biomechanical attributes, it has immense importance in the study of early hominin biology. However, body mass cannot be observed directly in fossil taxa, thus researchers frequently resort to predicting its

* Corresponding author.

E-mail address: christopher_walker@ncsu.edu (C.S. Walker).

¹ These authors contributed equally to this work.

value from morphological variables that are preserved in the paleontological or archeological records. As a result, the reliability of many assessments of hominin paleoecology are partially dependent on the accurate prediction of body mass.

For fossil hominins, two predominant approaches to body mass prediction have been employed: a “mechanical” method that uses dimensions of load-bearing skeletal elements such as femoral head diameter or knee breadth (Ruff et al., 1991, 2012; McHenry, 1992; Ruff, 1994, 2000a; Grine et al., 1995; Squires and Ruff, 2015; Elliott et al., 2016a,b), and a “morphometric” method that models the body as a cylinder, under the assumption that mass is proportional to the volume of the cylinder (Ruff, 1991, 1994, 2000b; Ruff et al., 1997, 2005). With the morphometric method, the diameter of the cylinder is represented by bi-iliac breadth, while the height of the cylinder is set equal to stature. In both approaches, predictor variables are regressed against known body masses of a reference sample using ordinary least squares (for bivariate regressions) or multiple regression (for multivariate regressions); this procedure is also known as “inverse calibration” (Konigsberg et al., 1998).

Mechanical prediction equations derived from recent human samples allow for the reasonable prediction of body mass in more recent, and generally larger, hominins (including many members of the genus *Homo*) from hip joint dimensions (e.g., Ruff et al., 1997; Ruff, 2010). Potential differences in hip abductor biomechanics across hominin taxa, however, render their use questionable with earlier, generally smaller, hominins such as *Australopithecus* spp. (Jungers, 1988a; McHenry, 1992; Ruff, 1995; Ruff et al., 1999; Auerbach and Ruff, 2004). Morphometric prediction equations do not require the assumption of similar lower limb biomechanics (though they do require the assumption that body proportions are broadly similar). Though multiple variables may be included in morphometric prediction equations (e.g., Schaffer, 2016), stature/bi-iliac breadth equations have been most widely applied to archeological and paleontological samples (e.g., Ruff and Walker, 1993; Ruff et al., 1997, 2006; Arsuaga et al., 1999; Trinkaus et al., 1999; Holt, 2003; Rosenberg et al., 2006; Vercellotti et al., 2008; Siegmund and Papageorgopoulou, 2011; Pomeroy and Stock, 2012) because the incorporated variables can often be gathered from skeletonized material. Accordingly, while not necessarily the most accurate possible morphometric equations (see Schaffer, 2016), stature/bi-iliac breadth equations (henceforth used synonymously with “morphometric equations” or “morphometric method”) are the most widely applicable and have been recommended over mechanical methods when the variables can be reconstructed with confidence (Auerbach and Ruff, 2004).

Even when measurements of bi-iliac breadth and stature are available, some methodological difficulties remain for researchers who wish to apply the morphometric method to fossil hominins. First, osteological measurements of some fossil taxa fall outside the range of extant human samples, so that predicted body masses for these taxa require extrapolation. Extrapolation greatly increases uncertainty around predicted values (Aiello, 1992; Hens et al., 1998; Konigsberg et al., 1998; Ruff, 2007) and may violate a fundamental assumption of the prediction process – that predicted values belong to the same population as the reference population (Smith, 2009). Second, many fossil hominins have different proportions than those observed in recent human samples (Johanson et al., 1982; McHenry and Berger, 1998; Asfaw et al., 1999; Richmond et al., 2002; Morwood et al., 2005; Lovejoy et al., 2009; Berger et al., 2010; Churchill et al., 2013; Schmid et al., 2013; Berger et al., 2015), which may reduce accuracy when prediction equations are applied to fossil taxa. Ruff et al. (2005) examined the effect of certain proportional indices on the predictive accuracy of the morphometric method, including relative sitting height (= sitting height/stature \times 100) and biacromial/bi-iliac breadth. They found

that “only biacromial/bi-iliac breadth has a significant effect on prediction bias ($p < 0.01$)” (Ruff et al., 2005: 386), and that this effect was restricted to males. Additionally, Ruff (2000b) evaluated the reliability of the morphometric method by predicting the body masses of Olympic athletes, a sample that also deviates from the body proportions of non-athlete populations in a variety of ways. Ruff (2000b) demonstrated that the morphometric method produced fairly accurate body mass predictions for the athletic sample, particularly for individuals in events that emphasized a general combination of agility, endurance, strength, and speed (e.g., decathletes). Continued evaluation of morphometric methods with samples that exhibit a range of proportions may reveal additional correlations between prediction error and body proportions.

Several previous studies have addressed issues of body mass prediction in small-bodied hominins by evaluating mechanical and morphometric equations in small-bodied archeological samples (Kurki et al., 2010) or by developing and testing prediction equations for application to juveniles (Ruff, 2007; Sciulli and Blatt, 2008; Robbins et al., 2010; Robbins Schug et al., 2013). However, most juvenile prediction equations follow the mechanical method, utilizing femoral metaphyseal breadth (Ruff, 2007), femoral head breadth (Ruff, 2007), and femoral midshaft second polar moments of area (Robbins et al., 2010; Robbins Schug et al., 2013). Ruff (2007) published juvenile morphometric equations that used bi-iliac breadth and long bone lengths (rather than stature); the accuracy of these equations has yet to be evaluated with a novel test sample.

While published juvenile mechanical equations have proven to be reasonably accurate when predicting body masses of small-bodied hominins, no previous study has tested the accuracy of morphometric prediction equations with a small-bodied human sample. This line of investigation is particularly important since predictions from morphometric equations have been used as a comparative baseline to assess mechanical equations (Auerbach and Ruff, 2004; Kurki et al., 2010). Here we use mean stature, bi-iliac breadth, and body mass from a global sample of human juveniles to evaluate the accuracy of morphometric body mass prediction equations when applied to small-bodied fossil hominins and examine the effect of juvenile body proportions (specifically lower limb length/stature and biacromial/bi-iliac breadth) on predictive accuracy. Treating human juveniles as a small-bodied fossil hominin proxy, we focus on two potential sources of error with possible repercussions for the application of morphometric prediction equations to the hominin fossil record: 1) extrapolation error due to differing body sizes between test and reference samples and 2) differing body proportions between test and reference samples. With respect to body size, human juveniles largely overlap with the estimated statures and masses of *Australopithecus* (and some specimens attributed to *Homo*), allowing for a direct assessment of extrapolation error over a range of sizes (e.g., Eveleth and Tanner, 1976; Grabowski et al., 2015). Body proportions in human juveniles and small-bodied fossil hominins, however, are particularly variable (Eveleth and Tanner, 1976; Johanson et al., 1982; Berge, 1998; McHenry and Berger, 1998; Asfaw et al., 1999; Bogin, 1999; Richmond et al., 2002; Ruff, 2002; Bogin et al., 2002; Morwood et al., 2005; Green et al., 2007; Lovejoy et al., 2009; Berger et al., 2010; Kibii et al., 2011; Schmid et al., 2013; Churchill et al., 2013; DeSilva et al., 2013; Berger et al., 2015; Marchi et al., 2017; Feuerriegel et al., 2017). Body proportions change during growth and development, differ across human juvenile populations, and even diverge within juvenile populations according to environmental factors (Eveleth and Tanner, 1976; Berge, 1998; Bogin, 1999; Bogin et al., 2002; Ruff, 2002; Temple et al., 2011). Small-bodied fossil hominin body proportions are similarly diverse, particularly with respect to measures central to morphometric prediction equations – limb length and hip breadth (Jungers, 1982;

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