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A volumetric technique for fossil body mass estimation applied to *Australopithecus afarensis*

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ABSTRACT

Fossil body mass estimation is a well established practice within the field of physical anthropology. Previous studies have relied upon traditional allometric approaches, in which the relationship between one/several skeletal dimensions and body mass in a range of modern taxa is used in a predictive capacity. The lack of relatively complete skeletons has thus far limited the potential application of alternative mass estimation techniques, such as volumetric reconstruction, to fossil hominins. Yet across vertebrate paleontology more broadly, novel volumetric approaches are resulting in predicted values for fossil body mass very different to those estimated by traditional allometry. Here we present a new digital reconstruction of *Australopithecus afarensis* (A.L. 288-1; 'Lucy') and a convex hull-based volumetric estimate of body mass. The technique relies upon identifying a predictable relationship between the 'shrink-wrapped' volume of the skeleton and known body mass in a range of modern taxa, and subsequent application to an articulated model of the fossil taxa of interest. Our calibration dataset comprises whole body computed tomography (CT) scans of 15 species of modern primate. The resulting predictive model is characterized by a high correlation coefficient ($r^2 = 0.988$) and a percentage standard error of 20%, and performs well when applied to modern individuals of known body mass. Application of the convex hull technique to *A. afarensis* results in a relatively low body mass estimate of 20.4 kg (95% prediction interval 13.5–30.9 kg). A sensitivity analysis on the articulation of the chest region highlights the sensitivity of our approach to the reconstruction of the trunk, and the incomplete nature of the preserved ribcage may explain the low values for predicted body mass here. We suggest that the heaviest of previous estimates would require the thorax to be expanded to an unlikely extent, yet this can only be properly tested when more complete fossils are available.

1. Introduction

Body mass is a critical constraint on an organism's ecology, physiology, and biomechanics, and is a required input parameter in many ecological and functional analyses. For paleontologists, it is thus highly desirable to reconstruct body mass for fossil species. Indeed, important studies concerning the evolution of brain size (McHenry, 1976), locomotor kinematics (Polk, 2004), and energetics (Steudel-Numbers, 2006) in hominins have all required reliable fossil body mass estimates.

The fossil record is, however, extremely fragmentary and the majority of specimens are known only from isolated elements. For this reason, the most common approach to mass estimation exploits a tight correlation between body mass and a given skeletal dimension or dimensions in a modern calibration dataset to derive a predictive equation. Within the field of physical anthropology, cranial metrics have been used in a predictive capacity, including orbital area (Kappelman, 1996), orbital height (Aiello and Wood, 1994), and facial breadth (Spocter and Manger, 2007). However, far more common are mass prediction equations based on postcranial elements, which Auerbach and Ruff (2004) subdivide into 'mechanical' and 'morphometric' methods on the basis of the chosen skeletal element. Mechanical techniques employ postcranial, mass supporting structures as a basis for predictive equations, including knee breadth (Squyres and Ruff, 2015), vertebral

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centrum area (McHenry, 1976), femoral head and neck breadth (Ruff et al., 1991), and humeral and radial head diameter (McHenry, 1992). Alternatively, morphometric techniques reconstruct fossil mass based on the direct assessment of body size and shape. For example, a series of studies (Ruff, 1994, 2000; Ruff et al., 2005) have found the combination of stature and biiliac breadth to provide relatively accurate estimates of body mass when applied to modern humans. Footprint area (as measured from fossil trackways) has even been used as a means of reconstructing hominin body mass (Dingwall et al., 2013; Masao et al., 2016).

Whilst bivariate and multivariate mass predictive equations benefit from their applicability to fragmentary material and the ability to generate large modern comparative datasets, there are associated disadvantages: which skeletal element to use, extrapolation, biasing by robust/gracile elements, and mass and inertia properties.

1.1. Which skeletal element to use?

When numerous skeletal elements are available for a particular fossil individual, it may be unclear which bony dimension ought to be used as a basis for mass prediction. If both a complete femur and tibia are available, for example, either could be considered a suitable mass-supporting structure upon which to base a fossil mass estimate. Yet previous research estimating body mass for non-primate fossil mammals demonstrates that estimates can span two orders of magnitude for the same individual depending on which limb bone or skeletal metric was used for prediction (Fariña et al., 1998). This example includes unusually proportioned mammals such as xenarthrans, and mass estimates for fossil hominins are not known to vary to such a degree (e.g., McHenry's [1992] estimates for the *A. afarensis* skeleton A.L. 288-1 based on different anatomical parts range between 11.8 and 37.1 kg). However, McHenry and Berger (1998) do highlight the potential for hominin mass estimates to vary considerably depending upon the use of forelimb or hind limb joint size as the basis for the predictive equation. Ultimately, a decision must still be made on which equation to use, taking into account the predictive power of the model (r^2 or percentage prediction error) and the existence of taphonomic damage or unusual morphology, for example, that may otherwise bias the result.

1.2. Extrapolation

Whilst typically less extreme in paleoanthropology compared to other disciplines of vertebrate paleontology, body mass estimations are often conducted on fossil specimens lying outside the range of body sizes occupied by the modern calibration dataset. Potential dwarfism (Brown et al., 2004; Vančata, 2005; Holliday and Fransiscus, 2009; Stein et al., 2010; Herridge and Lister, 2012) and gigantism (Millien and Bovy, 2010; Bates et al., 2015) are recurrent themes for fossil mass reconstructions, yet by their very nature they require an extrapolation of a predictive relationship beyond the modern range. In such instances, extrapolated predictions should be regarded as extremely speculative (Smith, 2002) due to a lack of evidence that the linear model holds beyond the extant dataset and a rapid widening of confidence intervals around the prediction.

1.3. Biasing by robust/gracile elements

Underlying the theory of bivariate/multivariate mass prediction is the assumption that the relationship between mass and a given skeletal dimension identified in modern species also holds for the fossil species of interest. In some instances, however, we can intuitively appreciate that species may be characterized by unusually proportioned skeletal elements (the elongated canines of sabertoothed cats or the robust hind the limb bones of some moa birds, for example). When placed into the context of the rest of the body, such enlarged/reduced features are obvious. Should such structures be used as a basis for mass estimation, however, unfeasibly large/small fossil species will be reconstructed (Braddy et al., 2008 versus Kaiser and Klok, 2008; Brassey et al., 2013). This is a particular concern when dealing with isolated elements in the absence of complete skeletons, where relative robustness/gracility cannot be known. In physical anthropology, for example, the mass estimation of *Gigantopithecus* on the basis of molar size (Conroy, 1987) or mandible size (Fleagle, 2013) is vulnerable to this problem.

1.4. Mass and inertia properties

Currently, traditional allometric predictive relationships produce a solely scalar value for body mass (i.e., X species weighed Y kg). Whilst these single values may be of use in subsequent ecological analyses or evolutionary models, they are not informative with regards to how said mass is distributed around the body. Inertial properties (including mass, center of mass, and moments of inertia) are essential when conducting biomechanical simulations such as multibody dynamic analyses of locomotion and feeding. Previous biomechanical analyses of fossil hominins have therefore reconstructed inertial parameters on the basis of modern human and chimpanzee values (Crompton et al., 1998; Kramer and Eck, 2000; Sellers et al., 2004), due to a lack of viable alternatives.

1.5. Volumetric techniques

For the above reasons, volumetric mass estimation techniques have become increasingly popular within the field of vertebrate paleontology (see Brassey, 2017 and references therein). Historically, volume based estimates required the sculpting of scale models and the estimation of volume via fluid displacement (Gregory, 1905; Colbert, 1962; Alexander, 1985). However, as part of the recent shift towards 'virtual paleontology' (Sutton et al., 2014; as characterized by the increased application of digital imaging techniques such as computed tomography, laser scanning, and photogrammetry), three-dimensional (3D) computational modeling of fossil species is becoming increasingly common. As articulated skeletons are digitized faster and with greater accuracy, volumetric mass estimation techniques now involve the fitting of simple geometric shapes (Gunga et al., 1995, 1999) or more complex contoured surfaces (Hutchinson et al., 2007; Bates et al., 2009) to digital skeletal models within computer-aided design (CAD) packages. Volumetric approaches overcome many of the limitations associated with traditional allometric mass estimation methods, including the need to extrapolate predictive models and rely upon single elements, whilst also allowing inertial properties to be calculated if desired.

Both physical sculpting and digital CAD 'sculpting' of 3D models inevitably involves some degree of artistic interpretation, however. By attempting to reconstruct the external appearance of an extinct species, assumptions must be made regarding the volume and distribution of soft tissues beyond the extent of the skeleton. Whilst those undertaking such modeling necessarily rely upon their experience as anatomists to inform reconstructions, previous research has found resulting mass estimates to be sensitive to the individual carrying out the procedure (Hutchinson et al., 2011). The convex hulling technique applied in the present paper was therefore developed with the aim of incorporating many of the benefits associated with volumetric mass estimation, whilst overcoming the subjectivity inherent in 'sculpted' models (Sellers et al., 2012).

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