Body mass estimation in hominoids: Age and locomotor effects

M. Loring Burgess [a, *], Shannon C. McFarlin [b], Antoine Mudakikwa [c], Michael R. Cranfield [d], Christopher B. Ruff [a]

[a] Center for Functional Anatomy and Evolution, Johns Hopkins University School of Medicine, Baltimore, MD, USA
[b] Department of Anthropology, Center for the Advanced Study of Human Paleobiology, The George Washington University, Washington, DC, USA
[c] Rwanda Development Board, Department of Tourism and Conservation, Kigali, Rwanda
[d] Mountain Gorilla Veterinary Project, University of California at Davis, CA, USA

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ABSTRACT

While there are a number of methods available for estimation of body mass in adult nonhuman primates, very few are available for juveniles, despite the potential utility of such estimations in both analyses of fossils and in museum collection based research. Furthermore, because of possible scaling differences, adult based body mass estimation equations may not be appropriate for non-adults. In this study, we present new body mass estimation equations for both adult and immature nonhuman hominoids based on joint and metaphyseal dimensions. Articular breadths of the proximal and distal femur, distal humerus and tibial plateau, and metaphyseal breadths of the distal femur and humerus were collected on a reference sample of 159 wild *Pan*, *Gorilla*, *Pongo*, *Hylobates*, and *Symphalangus* specimens of known body mass from museum and research collections. Scaling of dimensions with body weight was assessed in both the adult and the ontogenetic sample at several taxonomic levels using reduced major axis regression, followed by regression of each dimension against body mass to generate body mass estimation equations. Joint dimensions were found to be good predictors of body mass in both adult and immature hominoids, with percent prediction errors of 10–20%. However, subtle scaling differences between taxa impacted body mass estimation, suggesting that phylogeny and locomotor effects should be considered when selecting reference samples. Unlike patterns of joint growth in humans, there was little conclusive evidence for consistently larger joints relative to body mass in the non-adult sample. Metaphyseal breadths were strong predictors of body mass and, with some exceptions, gave more precise body mass estimates for non-adults than epiphyseal breadths.

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1. Introduction

The relationship of body size to a variety of important variables, such as life history, locomotion, energetic requirements, and organ structure and function, has long been recognized (Huxley, 1932; Gould, 1966; Schmidt-Nielsen, 1975, 1977; Clutton-Brock et al., 1977; Jungers, 1984; Alexander, 1985; Fleagle, 1985). Because of this, considerable effort has been devoted to developing means of estimating body mass from skeletal remains in both humans and nonhuman primates for use in paleontological and archaeological studies (Dagosto and Terranova, 1992; Hartwig-Scherer and Martin, 1992; McHenry, 1992; Ruff, 1994, 2003; Grabowski et al., 2015;

Squyres and Ruff, 2015). Although body mass prediction is unavoidably associated with some error (Smith, 1996), such estimations are important, as body mass is generally considered the most reasonable size parameter against which to evaluate other characteristics and is readily measured in living animals for comparisons (Schmidt-Nielsen, 1977; Jungers, 1984). Of the many available estimation methods, those based on weight-bearing elements, because they are more closely functionally related to body mass, appear to be relatively more accurate and precise than those based on craniodental measurements (Ruff et al., 1989). In particular, limb bone diaphyseal cross-sectional variables and articular dimensions have been shown to be good predictors of body mass across a variety of mammalian taxa, including primates (Anyonge, 1993; Egi, 2001; Ruff, 2003; Grabowski et al., 2015).

Of the available resources for estimating body mass in primates from postcranial elements, almost none consider non-adults in detail (but see Hartwig-Scherer and Martin [1992] for nonhuman

* Corresponding author.
    E-mail address: mburge15@jhmi.edu (M.L. Burgess).

primates, and Ruff [2007] for humans). This is unfortunate, because associated body masses are relatively rare in the museum collections of extant primates that are often used for ontogenetic studies, and there are many immature fossil hominins and apes for which estimated body mass at time of death would be useful (e.g., Walker et al., 1993; Nakatsukasa et al., 2007; Ruff, 2007). Equations based on adults are not necessarily suitable for use on immature specimens. Ontogenetic and static adult scaling patterns are often quite different (Shea, 1981; Jungers and Susman, 1984), and equations based on joint dimensions in human adults seem to overestimate body mass in immature individuals, as joints tend to "grow ahead" of body mass and are thus relatively larger in juveniles (Ruff et al., 1994; Ruff, 2002, 2003).

This study focuses on body mass estimation in adult and immature hominoids. Previous work has used a variety of dimensions as body mass estimators, including diaphyseal cross-sectional properties, joint measurements, and derived variables such as estimated bone weights and surface areas (Hartwig-Scherer and Martin, 1992; McHenry, 1992; Ruff, 2003). We concentrate here on articular dimensions because they are easily measurable, less environmentally plastic than some other variables (Trinkaus et al., 1994; Lieberman et al., 2001), and should be less sensitive to developmental changes in behavior and activity level than diaphyseal cross-sectional properties (Ruff et al., 2013; Sarringhaus and MacLatchy, 2016).

Relative articular size does vary with locomotor behavior in primates and other mammals, however, because of its effects on both the transmission of joint reaction force and the degree of joint excursion (Jungers, 1988, 1991a; Godfrey et al., 1991, 1995; Rafferty and Ruff, 1994; Ruff, 2002). For example, the relatively large humeral and femoral heads of nonhuman hominoids relative to cercopithecoids are related to increased mobility of these joints, in particular in abduction (Hammond, 2014). A previous study found that some articular proportions were less affected by locomotor differences within catarrhine primates than others (Ruff, 2003). However, because of a paucity of specimens with known body masses, Ruff's (2003) study could not test for such effects within hominoids. One goal of the present study is to update these previously published adult body size estimation equations for hominoids using a much larger sample of individuals of known body mass and to compare articular scaling patterns between finer taxonomic/locomotor groups. We also examine the effects of patterns of joint growth on the estimation of body mass in immature individuals and the extent to which adult scaling relationships apply during ontogeny. Finally, we construct new equations for estimating body mass in immature nonhuman primates using long bone metaphyseal breadths, which have been shown to be good body mass predictors in humans (Ruff, 2007).

2. Materials and methods

2.1. Sample

The study sample comprised 157 wild collected individuals distributed among eight species, including all of the extant nonhuman ape genera (Table 1). Mandibular molar eruption and epiphyseal fusion were used to classify individuals into "immature" ($n = 74$) and "adult" ($n = 83$) categories. Immatures are represented by individuals of all dental stages, from partial emergence of the deciduous dentition (i.e., young infants) to more advanced stages of emergence of the permanent dentition (i.e., through the juvenile and subadult periods). Adults are defined as those individuals having both third mandibular molar eruption and complete postcranial epiphyseal fusion. All specimens have associated body masses. For the museum specimens, these come from

museum records indicating body mass recorded at the time of collection of the specimen. Individuals were excluded if their body masses were clearly estimated, as suggested by extensive rounding of measurement data, or if associated specimen data indicated that organs or skin had been removed prior to weight measurement. Two *Gorilla gorilla gorilla* specimens from the Powell-Cotton Museum had both an initial weight measurement and a separate weight measurement for the skin. In both cases, nothing in museum records indicated that the individual had been skinned or otherwise altered prior to the initial weight measurement. It was therefore assumed that the initial value was the total weight of the specimen (rather than the initial measurement plus the weight of the skin), and this value was used for analysis. This accounts for some slight differences in values for this taxon compared to a previous study that included some of the same individuals (Jungers and Susman, 1984).

In the case of the *Gorilla beringei* sample, body weights were collected by the Mountain Gorilla Veterinary Project during postmortem examinations. Depending on individual size, weights are typically collected using several methods. A tabletop scale was used to collect weights to the nearest 0.01 kg for small individuals (~2—5 kg). For gorillas of roughly 5—30 kg, the gorilla was held by a researcher and a floor scale used to weigh them, subsequently subtracting the researcher's weight from the total to obtain the weight of the specimen. For the largest gorillas (>30 kg), weights were measured to the nearest 1.0 kg using a hanging scale, with weights of supporting materials (such as ropes or stretchers) again subtracted from the total. These methods present obvious difficulties for data collection from fully adult individuals, hence, reliable body weight measurements from adults are less well represented in the sample. To minimize the effect of tissue autolysis, only those body weights collected within 48 h of death were used in the current analysis. One individual was necropsied three days after death, but closely matches other individuals close to its recorded weight in metaphyseal breadths and so was included. No individuals used in the sample were described to have been in an emaciated state at death.

2.2. Measurements and analyses

Previous studies of body mass estimation in anthropoid primates found that supero-inferior (SI) head breadths of the femur and humerus, distal humeral and femoral mediolateral (ML) articular breadths, and proximal tibial plateau ML breadths were all good body mass predictors, although they varied in the degree to which they were sensitive to taxonomic/locomotor differences (Ruff, 2003). The current study therefore focuses on these predictors. In addition to these articular breadths, ML metaphyseal breadths of the distal femur and humerus were taken on individuals with unfused epiphyses. Abbreviations and definitions of all measurements can be found in Table 2 (see Ruff [2002] for illustrations and more detailed explanations). Measurements were taken with digital calipers to the nearest 0.1 mm.

Not all measurements were available for all specimens, especially immature individuals, which varied in both preservation and formation of epiphyses across developmental time. Sample sizes for each individual predictor therefore are always less than the maximum sample size of individuals. It was found that, in general, joints were not fully formed enough for measurement of articular breadths until individuals had erupted their second permanent molars. Therefore, all analyses of ontogenetic scaling of joint articular surface dimensions were limited to individuals with erupted M2s. Metaphyseal breadths were measured at all ages until fusion of the epiphyses. Since this takes place after second molar eruption for the joints in question, both metaphyseal and articular