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Body mass estimation in hominoids: Age and locomotor effects

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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.

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

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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 post-mortem 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

Table 1
Sample.

Taxon	Immature		Adult		Source(s)[a]
	Male	Female	Male	Female	
Hylobates lar	8	13	15	14	MCZ
Symphalangus syndactylus	–	–	3	4	NMNH
Pongo pygmaeus	4	3	6	10	MCZ (8); NMNH (15)
Pongo abelii	3	3	2	5	NMNH
Pan paniscus	6	1	1	4	RMCA
Pan troglodytes	5	1	5	5	MCZ (1); PC (7); RMCA (6); NMNH (2)
Gorilla beringei	11	9	2	4	MSGP (23); NRM (5)
Gorilla gorilla	1	6	2	1	PC

[a] Sources: Mountain Gorilla Skeletal Project (MSGP), Harvard Museum of Comparative Zoology (MCZ), Swedish Museum of Natural History (NRM), Powell-Cotton Museum (PC), Royal Museum of Central Africa (RMCA), Natural Museum of Natural History (NMNH).

Table 2
Predictor abbreviations, and descriptions.

Predictor	Description
FHDSI	Femoral head superioinferior breadth
FDARTML	Distal femoral condyle mediolateral breadth
FDMETML	Distal femoral metaphysis mediolateral breadth
HHDSI	Humeral head superioinferior breadth
HDARTML	Distal humeral mediolateral breadth
HDMETML	Distal humeral metaphysis mediolateral breadth
TPLML	Proximal tibial plateau mediolateral breadth

breadths were measured on some individuals. Analyses of metaphyseal breadth included all individuals for which it was measured.

Regression analysis was performed for each predictor variable separately. There has been some debate over the most appropriate line fitting method for use in these types of analyses. While results from model I and model II line fitting techniques are similar when correlations between variables are reasonably high, most authors agree that model II techniques, such as reduced major axis (RMA), are better suited for studying scaling relationships, while least squares regression is most appropriate for developing predictive models, at least when applied to specimens within the size range of the reference sample (Smith, 1994; Sokal and Rolf, 1995). Therefore, although regression coefficients derived using the two methods were very similar (because correlations were generally quite high), all analyses of scaling differences were performed using RMA regression equations, while body mass prediction equations were generated using least squares regression. Following Ruff (2002, 2003), we only compare prediction and accuracy of different structural properties within taxonomic groups, rather than between groups, to minimize the potential confounding effects of phylogenetic relatedness. As this paper is focused on accurate body mass estimation, discussion of heritability or plasticity of various traits (while interesting) is beyond its scope.

Analysis took place in two main phases. First, in order to understand variation in body mass predictive equations better, we examined scaling patterns of skeletal dimensions relative to body mass in different age/taxon groups using RMA lines and analysis of covariance (ANCOVA). We then calculated and compared least squares body mass estimation equations for the same groups. Within each phase, we performed separate analyses on three samples: first, a subset of the sample containing only adults, second, the total sample of individuals representing the M2 dental stage through adulthood, including all individuals with the measurement in question (hereafter referred to as the “ontogenetic” sample), and third, the total sample of individuals with measureable metaphyses.

To examine joint scaling differences within adult hominoids, RMA equations were fitted to each skeletal predictor and ANCOVAs were used to test for differences in slope and elevation between African (*Pan, Gorilla*) and Asian (*Pongo*, *Hylobates, Symphalangus*) apes. There is evidence from previous studies that these groups differ from one another in systematic ways in at least some articular proportions (Godfrey et al., 1991; Ruff, 2002). African apes are closely related phylogenetically (Prado-Martinez et al., 2013) and share some similarities in locomotor behavior (Doran, 1996), while Asian apes vary in body size and are less closely genetically affiliated, but are nevertheless similar behaviorally in their use of brachiation and quadrumanous climbing, especially when contrasted with African apes (Fleagle, 1976). Using these African and Asian ape categories also facilitates comparison to previous studies, which subdivided apes in this fashion (Ruff, 2002, 2003).

A second set of RMA lines was fitted to the ontogenetic sample and the ANCOVAs re-calculated to test whether the addition of the immature data changed taxon specific scaling patterns. Additional analyses were performed between four finer subgroups (*Gorilla, Pan, Pongo,* and *Hylobates*/*Symphalangus*) to test if scaling differences were being driven by differences between genera within the broader groupings. For these, RMA ANCOVAs were followed by pairwise post hoc tests between groups with a family-wise error rate of 0.05 (Warton et al., 2011).

Since, in some cases, scaling patterns appeared to be slightly altered by the addition of the immature individuals, we further examined differences between adults and non-adults to test for systematic departure of the immature specimens from adult trends (for epiphyseal articular surface breadths). To do this, ANCOVAs were performed to test for slope and elevation differences between adults and immature individuals. Residuals for the immature specimens from the adult only regression lines were calculated, and sign tests used to test whether these residuals were significantly different from zero, as not all residuals were normally distributed. Lastly, the scaling relationships between metaphyseal breadths and body mass in the total taxonomic sample, as well as African and Asian apes, were examined in the immature sample.

Body mass prediction equations were calculated for the adult only and the ontogenetic sample for each articular breadth predictor in the total sample, African and Asian apes, and within each genus. Prediction equations based on metaphyseal breadths were calculated for the total sample and African and Asian apes (sample sizes were not sufficient for individual genus calculations). Within each of these groups, equations were evaluated using the percent standard error of the estimate (%SEE), a measure of predictive precision, and mean percent prediction error (%PE), a measure of predictive accuracy calculated as [(actual-predicted)/predicted] *100. These have been explained in greater detail elsewhere (see Ruff, 2003) and were calculated for three samples: adults only, the ontogenetic sample (all epiphyseal articular breadths), and juveniles (metaphyseal breadths).

To facilitate comparisons of articular to metaphyseal dimensions for body mass estimation in non-adults, %PE was also calculated separately for the immature specimens using the ontogenetic reference sample equations for articular breadths. Mean percent prediction errors of 10–20% were considered “good” here, as this represents the general range of error characterizing the best body mass estimators in other similar studies of primates and other mammals (Ruff, 2003; Dagosto et al., 2018; Perry et al., 2018). It has been argued that a %PE of about 10% may be close to the biological limit for estimating individual body masses from skeletal material (Ruff, 2003).

To more directly assess the effect of choice of equation on estimated body mass and aid in recommendations for reference sample use in cases of uncertain taxonomic or locomotor group affiliation, we also calculated the actual difference in kg between body masses estimated for the same individual from the total sample, African or Asian ape samples, and genus samples (the latter two as appropriate based on phylogenetic affiliation). Masses were estimated for each individual from these three types of reference samples, and the average percent difference of the more specific estimates from the total sample estimate was calculated over the entire range of points. The more similar the results from the different equations, the less important the choice of reference sample should be in influencing estimated body mass.

Exponentiating logged body mass estimates back into their original units creates a log detransformation bias which, although it may be slight, should be corrected for (Smith, 1993). For this study, detransformed body masses were adjusted using the quasimaximum likelihood estimator (QMLE) method (Smith, 1993; Ruff, 2003). Family-wise error rate for each analysis was set at 0.05. All raw measurements and body masses used in analyses are found in the Supplementary Online Material (SOM) Table S1. Statistics were performed in R, with RMA regressions and ANCOVAs calculated using the smatr package (Warton et al., 2011; R Core Team, 2014).

3. Results and preliminary discussion

3.1. Scaling patterns of joints and metaphyses

3.1.1. Adult joints Scaling patterns of adult articular breadths on body mass in the total sample, and in African and Asian apes separately, are shown in Figure 1, with RMA slopes and intercepts given in Table 3 and more detailed statistics in SOM Table S1. Slopes are close to 0.33 (isometry) and 95% confidence intervals (CI) include isometry for FHDSI in all samples, but are slightly positively allometric in all other groups and measurements, with 95% CIs excluding isometry in all but the distal femoral and proximal tibial breadths in African apes (Table 3, SOM Table S2).

While adult sample sizes are not large enough to perform tests of scaling differences between species within genera, different species of *Gorilla*, *Pan*, and *Pongo* do not appear to show substantially different relationships between joint size and body mass based on inspection of the data. While previous studies have shown that *Symphalangus* are not ontogenetically scaled versions of *Hylobates lar* in long bone lengths relative to body mass, as well as in other aspects of shape (Jungers and Cole, 1992), in the current study, they did not appear to deviate from *Hylobates* in joint size relative to body size (Fig. 1). Because sample sizes for *Symphalangus* are small, and to extend the body size range represented by gibbons and siamangs, the two genera are therefore pooled for all further analyses.

Slopes are not significantly different between African and Asian apes in any skeletal variable examined. Neither femoral nor humeral head SI breadths are different in elevation between these groups, but African apes have significantly greater elevations in FDARTML, HDARTML, and TPLML (Fig. 1, Table 3, SOM Table S2). These elevation differences are more pronounced in knee breadths than in distal humeral breadth. In general, scaling patterns appear to be much more similar across taxa in femoral and humeral head diameters than in knee breadths.

3.1.2. Ontogenetic sample joints The addition of immature individuals generally does not substantially change slopes or intercepts for the total or Asian ape sample, although there are slightly larger differences in the African apes (Table 3). Consistent with this, scaling patterns are similar to those in the adult-only sample: FHDSI again scales isometrically in all groups, while all other variables are positively allometric, with 95% confidence intervals excluding isometry (Table 3, SOM Table S3). Unlike in the adult-only sample, African and Asian apes have significantly different slopes in HHDSI, with humeral head breadth increasing more quickly with body mass in African apes. In all other variables, elevations are significantly higher in African apes than in Asian apes, including in femoral head breadth (Table 3). Because overall patterns for the femoral head appear similar, this is likely at least partially the result of an increase in sample size. Again, though, knee breadths differ more between groups than other joint dimensions.

Because scaling relationships are generally similar in the adult-only and ontogenetic samples, we use the larger ontogenetic samples to further investigate differences between genera. Accordingly, ANCOVAs were carried out between gibbons and siamangs, orangutans, chimpanzees, and gorillas for the ontogenetic sample (Fig. 2). Again, there are no significant slope differences between any groups (SOM Table S3). While humeral and femoral head breadths show more similar scaling across genera than the other joint measurements, gorillas have significantly higher elevations for FHDSI than other genera, and chimpanzees have lower elevations for HHDSI than the other great ape genera. The lower elevation for chimpanzee humeri likely explains the higher slope for African versus Asian apes. Overall, however, the differences between proximal joints are much less pronounced than those in the distal joints. In knee and elbow breadths, chimpanzees and orangutans are similar to one another, while gorillas have relatively broader and gibbons and siamangs relatively narrower measurements. These differences are significant in FDARTML and HDARTML, but only chimpanzees and lesser apes are significantly different in TPLML.

As in broader African-Asian ape comparisons, in most cases, immatures do not appear to depart systematically from the generic adult sample lines (Fig. 3). Only the residuals for immature *Hylobates* distal humeral breadths and *Pan* distal femoral and proximal humeral breadths are significantly different from zero, and slopes and elevations are not significantly different (with the exception of humeral head and distal femoral and proximal tibial breadths, which have some differences in *Pan* and *Hylobates*, Fig. 3). In general, there is little suggestion of consistent differences either across taxa within a measurement or across measurements within taxa. In most cases, immatures are relatively evenly distributed around adult trend lines, although often with more data scatter. Some of the youngest/smallest individuals, especially in *Pan*, fall substantially below adult lines for some, although not all, joints. This inconsistency likely reflects differences in articular surface morphology and development. Although these two youngest *Pan* individuals had erupted their second molars, these results suggest that some joint measurements (e.g., TPLML) may not be appropriate for body mass estimation for individuals early in this developmental stage.

3.1.3. Metaphyseal breadths Metaphyseal breadths scale strongly with body mass in all groups assessed (Fig. 4, SOM Table S4). Consistent with adult results for corresponding articular breadth measurements, there appear to be larger differences between groups for the distal femur than the distal humerus. Slopes differ

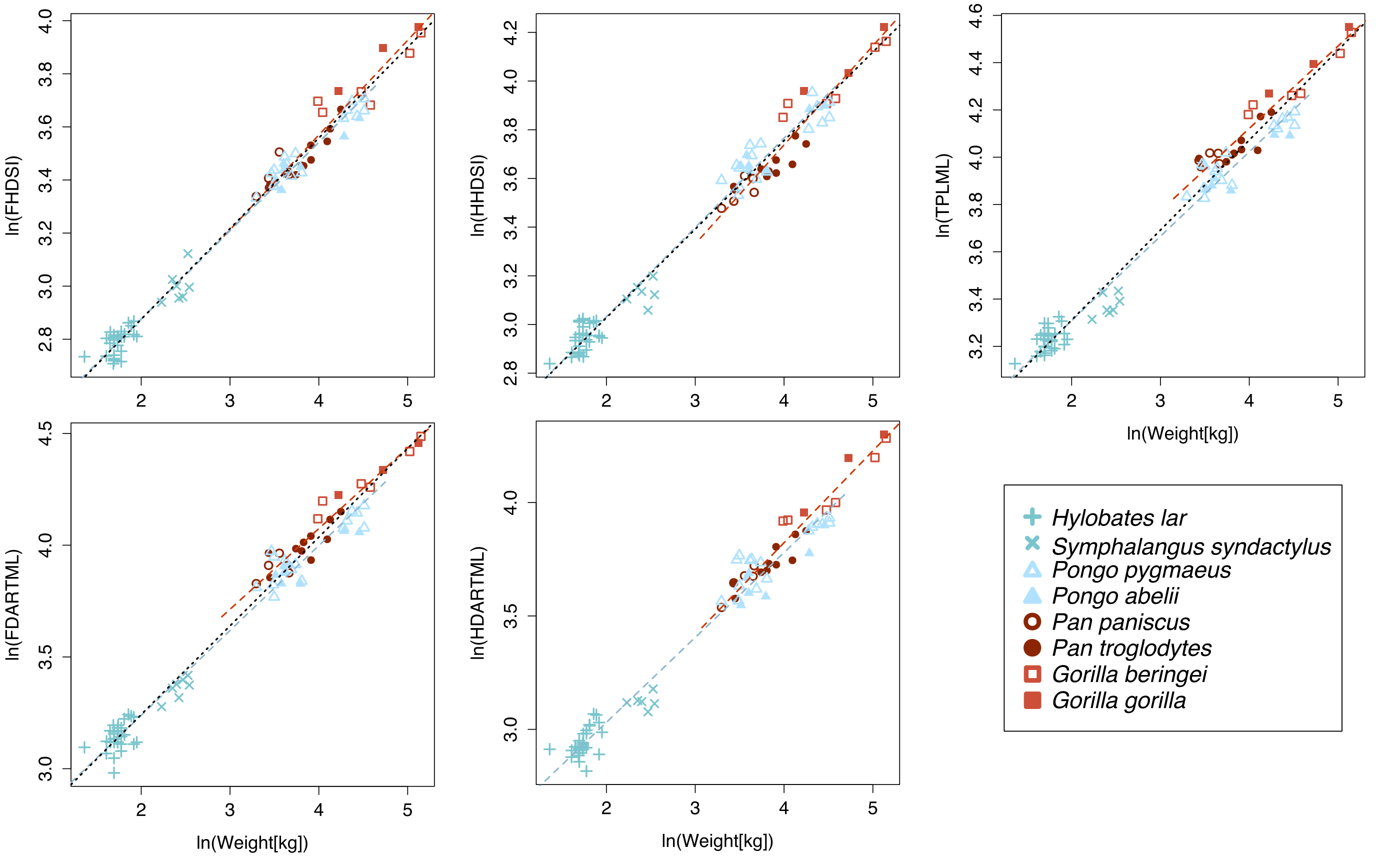

Figure 1. Plots of skeletal predictors against body mass in adults only, with RMA regression lines fit to African and Asian apes, and the total sample (ln = natural log). Black dotted line = total sample, red dashed line = African apes, blue dashed line = Asian apes. Regression statistics are given in Table 3 and SOM Table S2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3
Comparison of RMA slopes and intercepts between adult and ontogenetic samples.

Predictor (ln)[a]	Total sample				African apes				Asian apes			
	Adult		Ontogenetic		Adult		Ontogenetic		Adult		Ontogenetic	
	Slope	Intercept	Slope	Intercept	Slope	Intercept	Slope	Intercept	Slope	Intercept	Slope	Intercept
FHDSI[e]	0.34[b]	2.19	0.34[b]	2.20	0.36[b]	2.14	0.35[b]	2.20	0.33[b]	2.21	0.33[b]	2.22
FDARTML[c,e]	0.40	2.45	0.39	2.48	0.36[b]	2.63	0.39	2.52	0.38	2.48	0.37	2.52
HHDSI[d]	0.36	2.30	0.36	2.30	0.41	2.11	0.43	2.00	0.37	2.30	0.37	2.30
HDARTML[c,e]	0.39	2.26	0.38	2.30	0.41	2.20	0.39	2.26	0.37	2.28	0.36	2.33
TPLML[c,e]	0.38	2.55	0.38	2.58	0.35[b]	2.73	0.39	2.57	0.36	2.59	0.35	2.62

[a] See Table 2 for abbreviations; ln = natural log.
[b] 95% CI for slope includes isometry.
[c] Elevation differences between African and Asian apes (adult sample, $p < 0.05$).
[d] Slope differences between African and Asian apes (ontogenetic sample, $p < 0.05$).
[e] Elevation differences between African and Asian apes (ontogenetic sample, $p < 0.05$).

significantly between African and Asian apes for distal femoral breadths, but there are no slope or elevation differences in the distal humerus.

3.2. Body mass estimation

3.2.1. Choice of predictor variable Table 4 shows body mass estimation equations from joint measurements in the total sample, African and Asian apes, and within each genus for the adult-only sample and the combined ontogenetic sample. For convenience, QMLE values are provided for each equation. For both the adult and the ontogenetic reference sample, the order of %SEE and %PE for different properties within each taxonomic group is very similar. Equations are therefore compared on the basis of %PE, as the two parameters are generally representative of each other. As expected based on previous studies, most predictors are relatively good body mass estimators, with %PE generally around 10–15% for the adults and somewhat higher for the ontogenetic sample equations.

In comparisons of corresponding measurements from different bones, the proximal femur consistently has lower %PE than the proximal humerus, but this is not necessarily true of distal articular breadths of the same bones. Femoral head superioinferior breadth is the best body mass predictor in the total sample and within Asian apes, consistent with the lack of significant differences between Asian ape genera in scaling of this dimension. The slightly higher %PE for FHDSI in African apes is likely due to the elevation differences found between gorillas and chimpanzees (see above), but the

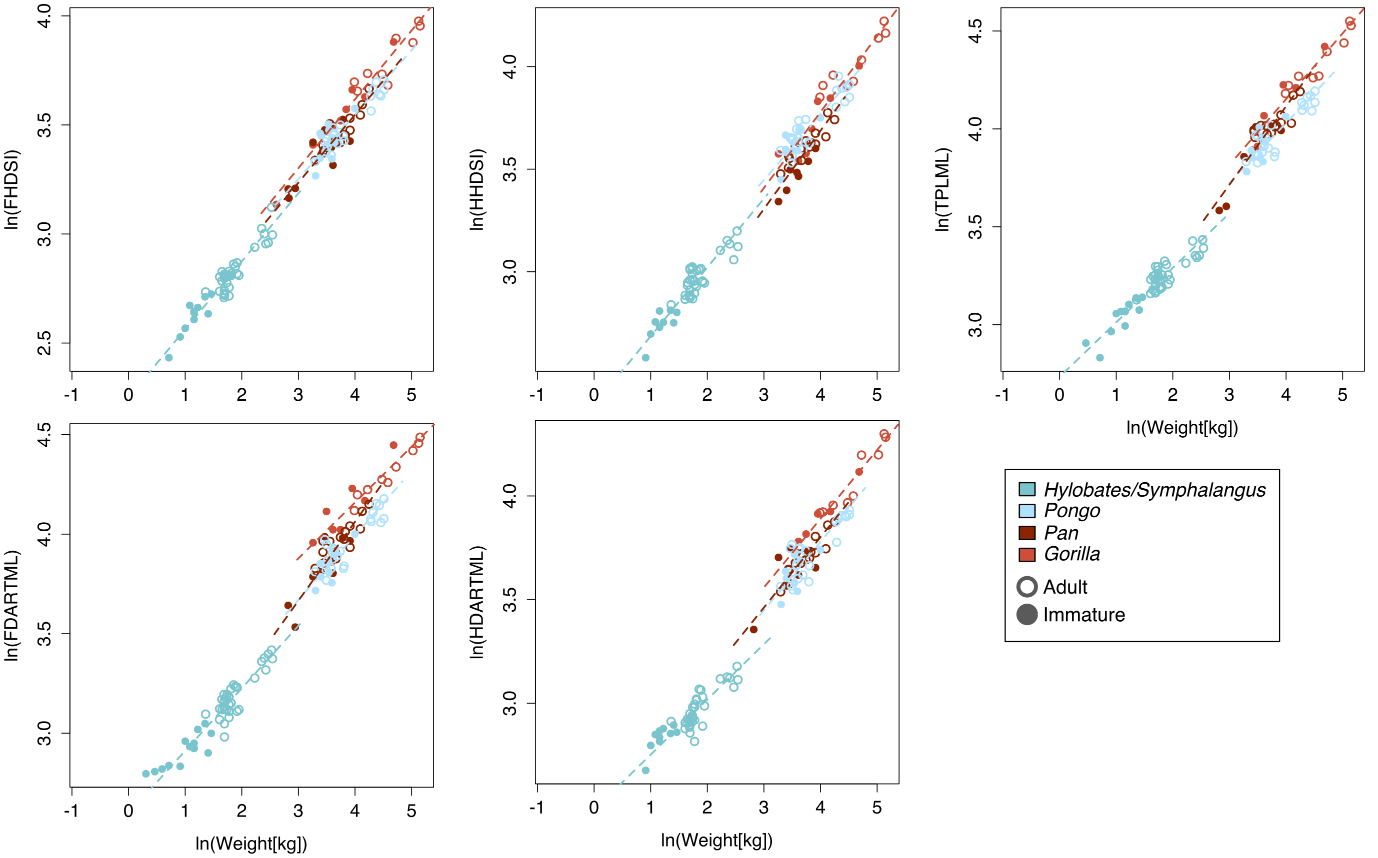

Figure 2. Plots of skeletal predictors against body mass in combined ontogenetic sample, with RMA regression lines fit to genera (across whole age ranges; ln = natural log). RMA regression lines fit to African and Asian apes not shown. No slopes were different between genera, but significant elevation differences were found in each predictor ($p < 0.05$). FHDSI = *Gorilla* higher elevation than all others; HHDSI = *Pan* lower elevation than all others; FDARTML and HDARTML = *Gorilla* higher elevation than all others, *Hylobates* lower elevation than all others; TPLML = *Hylobates* lower elevation than *Pan*. See SOM Table S3 for regressions statistics.

femoral head is still a good body mass predictor for this group (%PE = 12.9%).

Knee and elbow joint dimensions are less precise predictors than femoral and humeral head breadths in Asian apes, but are somewhat better for African apes, with HDARTML outperforming FDARTML. This is likely related to differences shown above between genera in both distal dimensions, which were relatively broader in gorillas than chimpanzees and relatively narrower in gibbons and siamangs than in orangutans. These differences were less pronounced in the humerus than in the femur. The tibial plateau is similarly a relatively poor predictor of body mass in the total adult sample, despite being the most “locomotor-blind” measurement in previous studies of broader taxonomic groupings (Ruff, 2003). However, it performs better within African and Asian ape groups, consistent with observed scaling differences between the two.

Metaphyseal breadths are reasonably good body mass predictors, with %PE of about 15–20% in most cases (Table 5). Distal humeral mediolateral metaphyseal breadth in Asian apes has the lowest %PE (11.4%) and the highest FDMETML in the total sample (22.9%). The poorer prediction for the latter is likely related to the differential scaling of the knee joint in African apes (particularly gorillas) and Asian apes (Fig. 4). Distal humeral mediolateral metaphyseal breadth in African apes is also among the poorer predictors. This may be because of differences between African ape genera, where chimpanzees seem to have relatively smaller HDMETML breadths than gorillas at similar sizes. Unfortunately, sample sizes for chimpanzees are too small to test this directly, but to explore this further, an additional equation was fit for distal humeral metaphyseal breadths in the gorilla sample only (Table 5 footnote). This equation is more comparable to the Asian ape HDMETML equations in accuracy and precision (%SEE = 14.6, %PE = 11.1) than the total African ape sample is. We recommend using this equation for estimating body mass from the distal humerus in gorillas. Because we cannot be sure if chimpanzees and gorillas truly differ in distal humeral metaphyseal breadths or if this is a sampling artifact, to be conservative, we recommend using the African ape equation for chimpanzees until further information is available.

3.2.2. Choice of reference sample: age range If a specimen is clearly an adult, it is most appropriate to use the adult-only equations, as these generally have the lowest %PE and %SEEs. However, for an immature specimen, either of two options is available, depending upon the developmental status of the individual and the material available: using the metaphyseal breadth equations or using the epiphyseal equations for the ontogenetic sample (in older juveniles). Note that use of the latter equations permits estimations from the proximal femur and humerus. Within each taxonomic group, %PEs for epiphyseal articular breadths are somewhat inflated in the ontogenetic equations compared to the adult-only equations for the same predictors. When applied only to juveniles, prediction errors calculated using the ontogenetic reference sample equations tend to be intermediate, between those of the adult equations for the same dimensions (applied to adults) and those of the equations for the corresponding metaphyseal dimension, although generally more similar to the former (Table 4). The proximal femoral and humeral ontogenetic equations using epiphyseal (articular) breadths are thus reasonable choices for body mass prediction in juveniles.

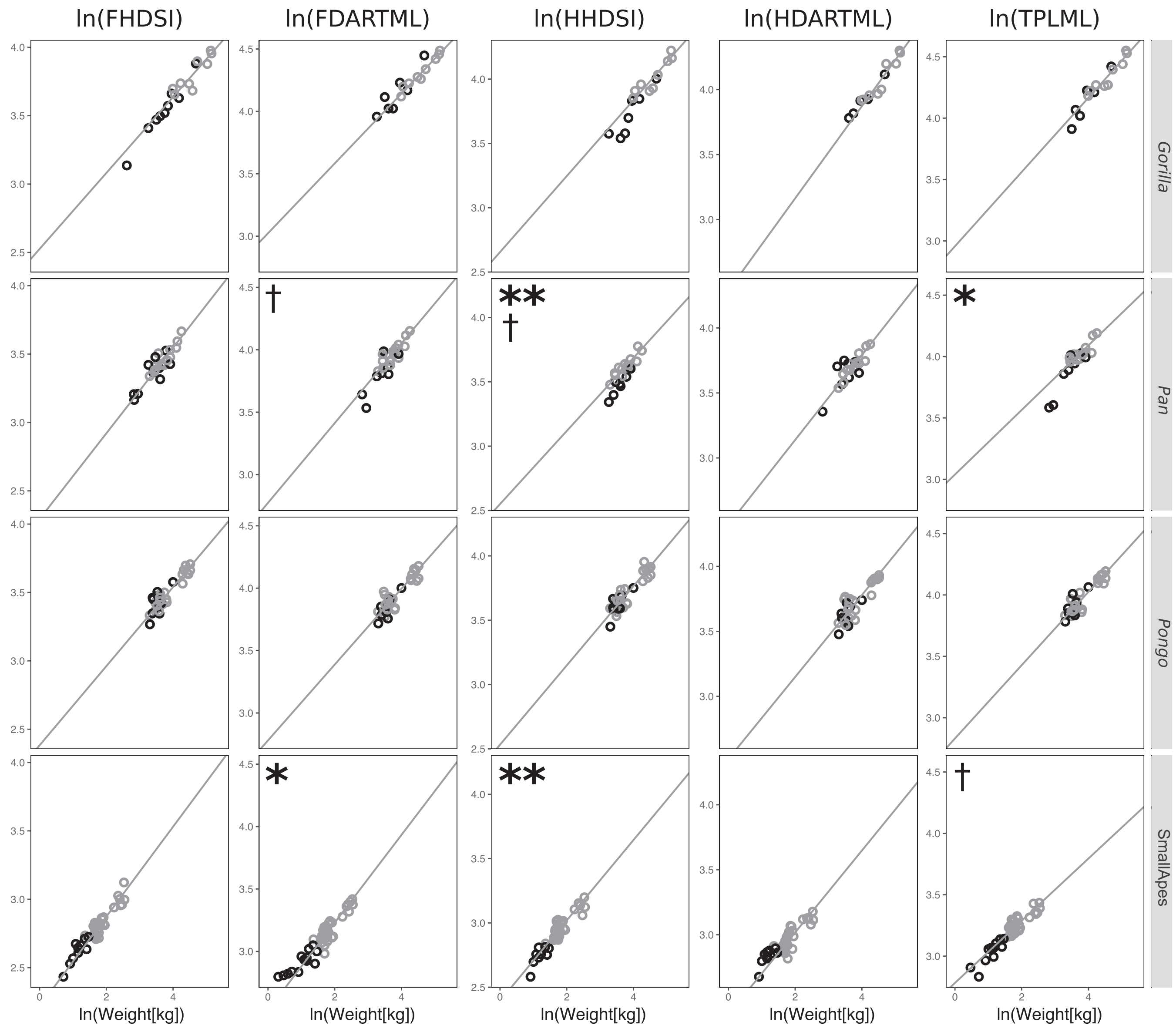

Figure 3. Plots of skeletal predictors against body mass in each genus with immatures compared to adult RMA regression line (ln = natural log). Gray = adult, black = immature. *Significant slope difference between adults and immature (ANCOVA, $p < 0.05$). **Significant elevation difference. †Immature residuals calculated from adult regression line are significantly different from zero (Sign tests, $p < 0.05$).

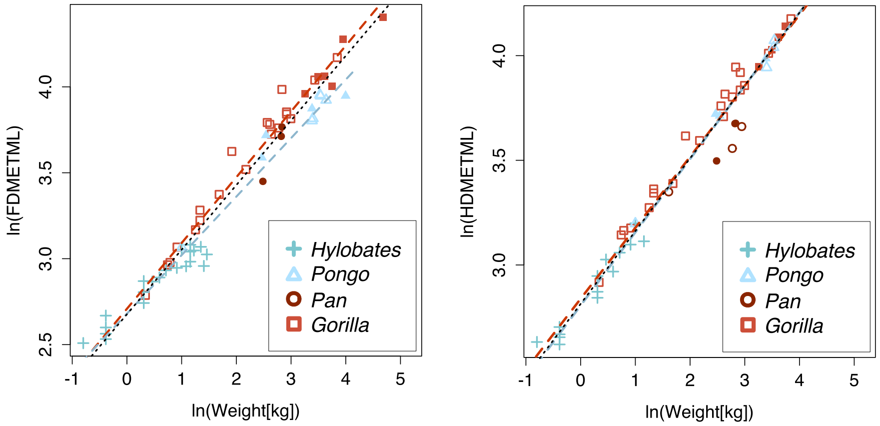

Figure 4. Plots of metaphyseal measurements against body mass with RMA lines fit to African and Asian apes, and the total sample (ln = natural log). Slopes are significantly different between two groups in FDMETML, but not in HDMETML. Regression statistics given in SOM Table S4.

Table 4
OLS body mass prediction equations from joint dimensions for adult and total ontogenetic samples.[a]

Sample	Predictor (ln)	Adults							Total ontogenetic reference sample							
		n	R^2	Slope	Int.	%SEE	%PE	QMLE	*n*	R2	Slope	Intercept	%SEE	%PE	QMLE	Imm. %PE[b]
Total sample	FHDSI	83	0.98	2.90	−6.34	15.4	11.8	1.010	123	0.98	2.90	−6.36	17.3	13.1	1.013	16.5
	FDARTML	83	0.98	2.49	−6.06	18.8	14.0	1.015	121	0.97	2.51	−6.18	22.8	16.6	1.021	23.6
	HHDSI	82	0.98	2.72	−6.21	18.8	14.4	1.015	114	0.97	2.72	−6.22	20.4	15.4	1.017	17.5
	HDARTML	82	0.98	2.55	−5.73	18.6	13.9	1.015	113	0.97	2.61	−5.96	21.6	16.2	1.019	23.5
	TPLML	82	0.97	2.59	−6.57	20.2	15.1	1.017	116	0.97	2.62	−6.72	20.9	15.5	1.018	18.1
African apes	FHDSI	24	0.91	2.68	−5.56	17.7	12.9	1.013	43	0.91	2.75	−5.87	19.5	14.8	1.016	16.8
	FDARTML	24	0.93	2.67	−6.88	15.7	11.0	1.011	40	0.86	2.37	−5.70	23.1	17.0	1.022	23.7
	HHDSI	24	0.91	2.34	−4.75	18.4	13.5	1.014	38	0.89	2.17	−4.11	18.9	14.5	1.015	14.4
	HDARTML	24	0.94	2.40	−5.17	14.2	10.7	1.009	37	0.90	2.40	−5.23	18.7	13.6	1.015	18.9
	TPLML	23	0.92	2.75	−7.32	16.8	12.8	1.012	37	0.92	2.47	−6.19	17.8	13.3	1.013	13.0
Asian apes	FHDSI	59	0.98	2.98	−6.56	13.9	11.1	1.008	80	0.98	2.97	−6.57	15.5	12.0	1.010	15.6
	FDARTML	59	0.97	2.60	−6.41	18.2	13.3	1.014	81	0.98	2.68	−6.71	19.4	14.0	1.016	16.5
	HHDSI	58	0.98	2.69	−6.16	17.8	13.8	1.014	76	0.98	2.69	−6.15	17.2	13.5	1.013	12.6
	HDARTML	58	0.97	2.63	−5.97	19.7	14.4	1.016	76	0.97	2.73	−6.32	21.6	16.1	1.019	22.7
	TPLML	59	0.97	2.76	−7.14	18.2	13.5	1.014	79	0.98	2.80	−7.31	18.9	14.0	1.015	16.8
Hylobates	FHDSI	36	0.81	2.74	−5.90	13.9	10.9	1.008	47	0.90	3.04	−6.76	14.3	11.1	1.009	11.9
	FDARTML	36	0.76	2.48	−6.03	15.9	12.0	1.011	50	0.89	3.00	−7.70	18.5	13.4	1.014	16.7
	HHDSI	35	0.72	2.71	−6.19	16.7	12.2	1.012	44	0.85	2.74	−6.31	16.1	12.1	1.011	11.7
	HDARTML	35	0.69	2.64	−6.00	17.4	12.1	1.013	45	0.77	3.30	−8.00	20.2	14.5	1.017	21.5
	TPLML	36	0.71	3.33	−8.96	17.6	13.6	1.013	48	0.88	3.36	−9.08	17.3	13.7	1.013	14.0
Pongo	FHDSI	23	0.91	3.29	−7.66	13.6	10.8	1.008	33	0.83	3.09	−7.00	17.6	13.2	1.013	19.5
	FDARTML	23	0.78	2.91	−7.64	21.7	14.8	1.019	31	0.79	2.75	−7.02	20.0	13.9	1.017	10.6
	HHDSI	23	0.81	2.92	−7.02	20.0	16.0	1.017	32	0.81	2.83	−6.69	19.0	15.1	1.015	13.2
	HDARTML	23	0.74	2.73	−6.34	23.9	17.5	1.023	31	0.74	2.61	−5.88	22.7	17.6	1.021	16.6
	TPLML	23	0.84	3.06	−8.34	18.6	12.6	1.015	31	0.81	2.95	−7.89	18.9	13.3	1.015	15.7
Pan	FHDSI	15	0.82	2.89	−6.26	13.4	9.5	1.008	25	0.81	2.88	−6.27	18.2	12.8	1.014	17.8
	FDARTML	15	0.74	2.69	−6.92	16.2	10.8	1.011	24	0.79	2.24	−5.13	17.7	12.8	1.013	14.3
	HHDSI	15	0.82	3.19	−7.79	13.1	10.0	1.008	22	0.74	2.25	−4.35	15.4	12.0	1.010	10.2
	HDARTML	15	0.85	2.83	−6.76	11.8	8.5	1.006	23	0.71	2.47	−5.46	19.6	12.9	1.016	21.0
	TPLML	14	0.66	3.08	−8.66	17.4	12.6	1.013	22	0.81	2.24	−5.28	17.4	12.5	1.013	11.1
Gorilla[c]	FHDSI	9	0.80	3.22	−7.65	23.9	16.5	1.023	18	0.95	3.08	−7.14	17.7	12.7	1.013	9.4
	FDARTML	9	0.96	3.50	−10.47	10.4	6.8	1.005	16	0.90	3.39	−10.07	20.8	15.0	1.018	23.3
	HHDSI	9	0.85	3.13	−7.95	20.2	14.6	1.017	16	0.90	2.56	−5.65	20.7	15.7	1.018	14.7
	HDARTML	9	0.89	2.66	−6.29	17.0	12.3	1.012	14	0.93	2.91	−7.33	14.4	10.1	1.009	7.2
	TPLML	9	0.90	3.14	−9.06	16.1	11.9	1.011	15	0.92	2.85	−7.84	17.1	13.0	1.013	14.8

[a] See text and Table 2 for abbreviations; ln = natural log.
[b] %PE calculated for subset of immature individuals only.
[c] Adult sample sizes low, not all predictors recommended for use (see text).

Table 5
OLS body mass prediction equations from metaphyseal breadths.[a]

Sample	Predictor (ln)	*n*	R^2	Slope	Intercept	%SEE	%PE	QMLE
Total sample	FDMETML	60	0.96	2.61	−6.95	30.8	22.21578	1.039
	HDMETML	51	0.97	2.84	−7.96	24.1	15.54445	1.024
African apes	FDMETML	29	0.96	2.56	−6.90	23.8	14.63428	1.025
	HDMETML[b]	30	0.93	2.84	−7.99	29.6	18.78334	1.035
Asian apes	FDMETML	31	0.97	2.90	−7.75	26.5	18.8	1.028
	HDMETML	21	0.99	2.84	−7.98	15.5	11.4	1.010

[a] See text and Table 2 for abbreviations; ln = natural log.
[b] Equation for gorillas alone: $\ln(\text{mass}) = \ln(\text{HDMETML})*2.94-8.44$, $n = 28$, QMLE = 1.009, $R^2 = 0.98$.

However, prediction errors for distal femoral and humeral metaphyseal breadths are generally, although not always, similar to or lower than prediction errors generated from the ontogenetic equations for corresponding articular dimensions within taxonomic groups, sometimes substantially so. In these cases, metaphyseal breadths are preferable to articular breadths for estimating immature body masses. In some cases, proximal articular breadth-based equations from the ontogenetic sample perform better in immatures than metaphyseal equations (e.g., the femoral head versus the distal femoral metaphysis in the total sample and Asian apes). If multiple dimensions are available, we recommend use of the equation with the lowest prediction error for the appropriate reference group, which in some cases may be an epiphyseal articular measurement rather than a metaphyseal breadth.

3.2.3. Choice of reference sample: taxon When taxonomic and/or locomotor affiliations are known, these should be used to determine the appropriate reference sample (see Ruff, 2003). In most cases, sample sizes here are large enough ($n \geq 15$) that genus specific equations are feasible for use, if desired; adult gorillas are the exception to this ($n = 9$). However, in some situations, a specimen will be too fragmentary or intermediate in morphology to determine an appropriate single reference group. In these instances, body masses estimated from a broader sample may be appropriate. Choosing between these options depends on the scaling patterns between taxa (Ruff, 2002, 2003).

In most cases in the current study, the actual differences between mean body masses estimated using the total reference sample and the taxonomic subsets are quite small (between 1.5 and

3%, but see below), so on average, for most predictors, choice of reference sample will make a relatively small difference to actual estimated body masses. However, to maximize predictive accuracy and precision, we recommend following slightly different protocols for different predictors, as outlined previously (Ruff, 2003). The total sample equations can be used for FHDSI and HDMETML, as all groups are very similar and there are no significant slope or elevation differences. Regression lines for elbow and knee joint articular surface breadths are parallel in African and Asian apes, with the total sample line running between them, so it is most appropriate here to use the average of the body masses produced from the two equations. Regression lines for distal femoral metaphyseal breadth are not parallel between African and Asian apes, but as the total regression line falls between them, the total sample reference group should be used in cases of uncertainty. Last, while there are no significant slope or elevation differences between African and Asian ape adults in humeral head SI diameter, this measurement has some of the highest percent differences between body masses estimated in different reference groups (slightly higher than 3% in adults, and over 5% in ontogenetic samples). Because the total sample line is not intermediate between the African and Asian apes, we do not recommend using this as a predictor if other measurements are available.

4. Discussion

4.1. Locomotor effects on joint mobility and scaling

The current study provides evidence of scaling differences in some joints within hominoids that subtly impact body mass estimation. There is no evidence for differences within genera in joint size relative to body size, suggesting that the same equations can be used to generate body mass estimates for different species within the same genus. However, there is evidence for differences between genera and broader groupings, i.e., African and Asian apes. Most results for adult scaling patterns are broadly consistent with previous work, with slight differences between these results and previous studies of scaling in hominoids (Jungers and Susman, 1984; Jungers, 1991) probably related to sample composition and inclusion of different taxa. In general, the relative size of the more proximal joints tends to be more similar between different taxonomic groups than that of the more distal joints. This is especially pronounced for the femur.

The above finding is not consistent with results from previous studies carried out across broader taxonomic groups. In primates, knee breadths, especially TPLML, were the least variable in proportion between Old World monkeys and apes, while femoral and humeral head SI diameters scaled differently between the two groups (Ruff, 2003). In studies of small bodied nonhuman primates and other mammals, relative tibial plateau width was also among the least variable proportions across taxonomic groups (Payseur et al., 1999). These results are in contrast to those of the current study, which shows relative similarity in proximal joints and greater variability in knee and elbow dimensions. This variation is not strictly taxonomic. In fact, orangutans and chimpanzees are very similar in knee and elbow scaling with mass, while gibbons and siamangs have relatively narrow knees, and gorillas have relatively wide knees. The relatively narrow knee in gibbons and siamangs has been noted before: in knee dimensions relative to diaphyseal cross-sectional properties, gibbons and siamangs group more closely with monkeys than with other apes, and generally tend to look more monkey-like in distal hindlimb joint surfaces and more like other hominoids in proximal joints (Ruff, 2002).

These patterns may be related to differences between more proximal and more distal joints in the relationships between body mass, joint loading, and joint mobility and stability. Within hominoids, orangutans, gibbons, and siamangs practice more forelimb-loading suspensory behavior than the more terrestrial, quadrupedal African apes (Fleagle, 1976; Doran, 1996), and tend to have higher available ranges of in vivo joint excursion than other primates, including African apes (Hammond, 2014). Articular dimensions, particularly those of ball-and-socket joints like the femoral and humeral head, are strongly influenced by joint mobility requirements: all else being equal, a larger surface area will permit relatively greater excursion at that joint (Ruff, 1988; Godfrey et al., 1991; Rafferty and Ruff, 1994; Egi, 2001). Consistent with this, within hominoids, orangutans and gibbons and siamangs have relatively large femoral and humeral head surface areas compared to their midshaft cross-sectional strength (Ruff, 2002). At these types of joints, at least in the hip, greater stability may be achieved through a deeper opposing articular surface, i.e., the acetabulum in the hip; within apes, orangutans and lesser apes have shallower acetabulae than African apes (Jenkins and Camazine, 1977; Ruff, 1988).

In contrast, knee and elbow breadths seem to be less directly related to joint mobility per se (Tardieu, 1983). Instead, increasing ML dimensions may serve to promote ML stability in these hinge joints (Currey, 2002). From this perspective, the relatively wide knees and elbows of gorillas are not a function of greater mobility at these joints, but rather greater stability, possibly related to their more terrestrial locomotor behavior (Doran, 1996) and/or large body size. Variation among hominoids in relative size of the femoral and humeral heads may be less marked because these dimensions are more directly related to joint excursion and are thus increased in orangutans and gibbons and siamangs, bringing them in line with those of chimpanzees and gorillas. Large proximal joints in all hominoids appear to be related to a common underlying adaptation to quadrumanous climbing involving more limb abduction (Fleagle, 1976). More generally, increasing joint size has different effects on mobility and stability in different types of joints—effects that are important to consider when interpreting and applying body mass estimation equations.

Within hominoids, therefore, proximal joints perform reasonably well in body mass estimation regardless of taxonomic affiliation, but as mentioned previously, in combined catarrhine samples, they work less well. Proximal joints may therefore not provide reliable body mass estimates in situations of greater uncertainty about locomotor and/or taxonomic relationships, such as is the case for some Miocene taxa. In these instances, it is preferable to use joint dimensions known to have more consistent relationships with body mass across catarrhines broadly, such as knee breadth. Thus, taxonomic level of analysis is critical in selecting parameters for use as body mass estimators, and it is important to consider the functional consequences of differences in relative joint size at multiple taxonomic levels to clarify the most appropriate body mass estimation method.

4.2. Joint growth and body mass in immature specimens

Juvenile hominoids show locomotor/taxonomic variation in relative articular and metaphyseal breadths that is similar to that of adults. This suggests that characteristic joint proportions are present from early in ontogeny and supports previous evidence that joint dimensions are not developmentally plastic (Lieberman et al., 2001), as behavior changes with age in several of these taxa (Doran, 1997).

The similarities found here between adult and juvenile relative joint sizes, within taxon, differ from patterns of joint growth in humans, in which joints are relatively large during childhood and adolescence (Ruff et al., 1994; Ruff, 2002, 2003). This apparent contradiction could be explained by the relatively small within-taxon sample sizes of the current study, which may not be large enough to detect these differences. It is notable that the statistically significant differences found are generally limited to groups with the largest immature sample size, and it may be that larger sample sizes would be more effective at detecting these differences. Alternatively, the ontogeny of relative joint size in humans may be impacted by potential differences in growth patterns and the presence or degree of adolescent growth spurt experienced between humans and nonhuman primates (Leigh and Shea, 1995; Leigh, 1996; Hamada and Udono, 2002). Body size changes during ontogeny could also explain why immatures seem to be somewhat more variable than adults in the relationship between joint size and body size (also see Ruff, 2007).

Despite general similarity in joint scaling between adults and older juveniles, comparisons of metaphyseal breadths to joint breadths indicate that the former are generally better immature body mass predictors than the latter. This could be because of measurement error for immature joints. Using joint breadths for immatures, at least in the manner of the current study, inherently assumes that the joint surface is sufficiently formed to be comparable to the adult state. This may be more or less clear for some joints than for others, leading to variably increased inaccuracy. Identification of appropriate developmental cutoffs for use of articular measurements based on other maturity markers is complicated by potentially weak correlations between rates of development between different body systems, both within and between taxa (Brimacombe and Kuykendall, 2015). For example, although we attempted to exclude individuals with incompletely formed joints by limiting our sample to those with erupted second molars, the two smallest tibial plateau measurements for the chimpanzees in this study are clearly substantially smaller relative to body mass than all others (this is likely also the reason for the slope difference between adults and immatures found in this group). This suggests that they were not fully formed, which could be because these individuals were small or skeletally immature for their dental maturity stage. However, other joint measurements from these same individuals appear to fall much closer to the overall regression lines for this taxon. Differences in formation time between joints, and potentially between taxa, mean that it is difficult to construct a general age or size cutoff beyond which articular surface measurements are no longer useful. Metaphyseal breadths are more straightforward and should not be as affected by these considerations.

Additionally, there could be taxon-specific differences in specific aspects of joint morphology that muddy results for joint breadths, but are not present for metaphyseal breadths. However, it is worth noting that results from corresponding metaphyseal and articular breadths are often fairly similar to one another, where they can be directly compared. In addition to these considerations, individuals with unfused epiphyses are more likely to have measurable metaphyseal breadths than epiphyses. For these reasons, we recommend generally using metaphyseal breadths to estimate immature body masses.

5. Conclusions

Limb bone joint breadths are good body mass estimators in both adult and immature hominoids, with percent prediction errors falling below 20%, and often below 15%. Scaling of joint size to body size is generally similar in different hominoid taxa, but there is more variation in the knee and elbow than in the hip and shoulder. This finding contrasts with previous studies at broader taxonomic levels, which found relative knee dimensions to be the most similar between disparate groups. It is likely that these patterns are due to a combination of locomotor effects resulting from general similarity in adaptations to quadrumanous climbing between all hominoids and from differences in the effect of increasing joint breadth on the mobility and stability of different types of joints. This highlights the importance of considering the functional impacts of joint size at several taxonomic levels when performing body mass estimations.

Metaphyseal breadths of the distal femur and humerus were also found to be good body mass predictors in non-adults. In most (although not all) cases, metaphyseal breadths perform better than articular surface dimensions in juveniles, potentially because of differences in details of joint morphology between taxa or because of measurement error in the joints of the younger individuals. Scaling relationships and variation between taxa in epiphyseal and metaphyseal breadths were similar to those for articular dimensions in adults, suggesting early ontogenetic establishment of relative joint size.

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