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Long Bone Articular and Diaphyseal Structure in Old World Monkeys and Apes. II: Estimation of Body Mass

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ABSTRACT Body mass estimation equations are generated from long bone cross-sectional diaphyseal and articular surface dimensions in 176 individuals and 12 species of hominoids and cercopithecoids. A series of comparisons is carried out to determine the best body mass predictors for each of several taxonomic/locomotor groupings. Articular breadths are better predictors than articular surface areas, while cross-sectional shaft strengths are better predictors than shaft external breadths. Percent standard errors of estimate (%SEEs) and percent prediction errors for most of the better predictors range between 10–20%. Confidence intervals of equations using sex/species means are fairly representative of those calculated using individual data, except for sex/species means equations with very low %SEEs (under about 10%), where confidence intervals (CIs) based on individuals are likely to be larger. Given individual variability, or biological "error," this may represent a lower limit of precision in estimating individual body masses. In general, it is much more preferable to determine at least broad locomotor affinities, and thus appropriate modern reference groups, before applying body mass estimation equations. However, some structural dimensions are less sensitive to locomotor distinctions than others; for example, proximal tibial articular M-L breadth is apparently "locomotor blind" regarding body mass estimation within the present study sample. In other cases where locomotor affiliation is uncertain, mean estimates from different reference groups can be used, while for some dimensions no estimation should be attempted. The techniques are illustrated by estimating the body masses of four fossil anthropoid specimens of *Proconsul nyanzae*, *Proconsul heseloni*, *Morotopithecus bishopi*, and *Theropithecus oswaldi*. Am J Phys Anthropol 120:16–37, 2003. © 2003 Wiley-Liss, Inc.

Although estimation of body mass from fragmentary skeletal remains will always carry some degree of error (Smith, 1996), such estimations will continue to play an important role in paleontological analyses, for a number of reasons (Ruff, 2000). Tooth dimensions have been most commonly employed to estimate the body mass of fossil primates (e.g., Gingerich et al., 1982; Conroy, 1987), in part because teeth are the most often preserved elements of the skeleton, and also because craniodental characteristics are generally the most taxonomically informative parts of the skeleton (thus, taxon-specific body mass estimates can be more easily derived than from unassociated postcrania). However, it is well-recognized that the physiological relationship between craniodental size and body mass is much less direct than that between the size of weight-bearing postcranial elements and body mass; therefore, dental estimates of body mass typically have much larger standard errors of estimate (SEEs) than those from postcrania (Ruff et al., 1989). Not surprisingly, given their role in supporting body weight, limb bone cross-sectional diaphyseal and articular properties have been found to be good predictors of body mass in a variety of mammalian taxa (Scott, 1990; Anyonge, 1993; Egi, 2001).

Several previous studies developed body mass prediction equations for nonhuman primates based on postcranial dimensions (Aiello, 1981; Jungers, 1987, 1990; Ruff, 1987, 1988, 1990; Ruff et al., 1989; Dagosto and Terranova, 1992; Rafferty et al., 1995; Delson et al., 2000). Most of these studies were limited in one or more ways, however, to particular areas of the skeleton or types of dimensions (e.g., either articulations or diaphyses, only external breadths), and/or a narrow taxonomic/locomotor range (e.g., only hominoids, only cercopithecoids). The present study is the first to include a broad representation of Old World anthropoids and both cross-sectional diaphyseal and articular surface

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TABLE 1. Mean sex/species body masses

	Males		Females		
Species	n[1]	Body mass (kg)	n	Body mass (kg)	Source for unassociated BM[2]
Pan troglodytes	1/10	56.0	1/10	43.6	Smith and Jungers, 1997
Gorilla gorilla	0/10	166.4	0/10	84.5	Smith and Jungers, 1997
Pongo pygmaeus	5/10	80.25	8/10	36.12	Smith and Jungers, 1997
Hylobates syndactylus	3/3	11.33	4/5	11.28	Regression on associated
Hylobates lar	5/5	5.90	5/5	5.50	
Papio cynocephalus	10/10	23.66	10/10	12.18	
Macaca nemestrina	2/3	10.31	4/6	5.92	Regression on associated
Macaca fascicularis	10/10	4.96	10/10	3.30	
Nasalis larvatus	6/6	20.95	5/5	10.56	
Colobus guereza	9/9	9.49	9/9	7.93	
Trachypithecus cristata	5/5	7.08	5/5	5.84	
Presbytis rubicunda	5/5	6.16	5/5	6.12	

[1] Number of specimens with associated body mass/total number of specimens.
[2] See text for explanation.

area properties of all major long bones. The study sample and structural properties are the same (with slight modifications) as those used in the preceding paper on locomotor reconstruction (Ruff, 2002). The choice of body mass predictors and reference samples, and the effects of using sex/species means vs. individuals in prediction, are evaluated. Sample applications to four fossil anthropoid specimens included in the previous paper (Ruff, 2002) are also given.

MATERIALS AND METHODS

The previous study (Ruff, 2002) included 179 individuals distributed between 13 species. The present study sample is identical, except that the 3 (2 male and 1 female) *Pan paniscus* specimens are not included (Table 1). None of these individuals has an associated body mass, and the use of sex/species mean literature values to estimate body mass when sample sizes are so small is dangerous due to the heightened probability of nonrandom sampling.

Almost three-quarters of the specimens (n = 127) in the study sample have individually associated body masses (Table 1). However, all but two of the African apes do not have associated body masses. Therefore, in analyses that included African apes, sex/species means were used to derive body mass estimation equations. Six of the 7 Old World monkey species are all of known body mass, along with *Hylobates lar*. In two other species (*Macaca nemestrina* and *Hylobates syndactylus*), two-thirds or more of the specimens are of known body mass. For sex/species means analyses, the body masses of the remaining specimens in these species were estimated using species-specific regressions of body mass on femoral length. Although in larger taxonomic groupings long bone length is not well-correlated with body mass (see below), it generally is well-correlated within species. In *Macaca nemestrina* (n = 6), the correlation of body mass with femoral length is 0.970, with an SEE of 0.71 kg (9.2% of the mean). In *Hylobates syndactylus* (n = 7), the correlation is 0.752, with an SEE of 0.85 kg (7.5% of the mean).[1] In the three great ape species, missing body masses were estimated using sex/subspecies mean body masses from Smith and Jungers (1997).

In all species, estimated body masses were averaged with known body masses, with each weighted according to number of specimens, to derive sex/species means, as given in Table 1. These values were only included in analyses using sex/species means; no estimated body masses were included in analyses using individuals. The *Colobus guereza* sample included only 1 male and 2 females with distal limb elements (i.e, a tibia, radius, and ulna) (Table 1 in Ruff, 2002). Even though these individuals had associated body masses, they were not included in sex/species means analyses, since the extremely small sample sizes within sex greatly increase the possibility of sampling error. Thus, sex/species means analyses including cercopithecoids have two fewer data points for the tibia, radius, and ulna than for the femur and humerus. Three other species had an individual missing the forelimb (Table 1 in Ruff, 2002); in each case, the sex/species mean body masses for the samples with or without these individuals were almost identical. In a few other cases, an individual surface area measurement was not available. All results tables provide n (or degrees of freedom) for each regression equation.

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[1] It may seem circular to use bone lengths to estimate body masses, which are then incorporated into predictive equations. However, bone length is relatively uncorrelated with the structural parameters used here to develop predictive equations, and as noted in the text, these estimated values were only used in sex-species means analyses, where most individuals in the sex-species group had an associated body mass. This technique, when possible, is preferable to using literature mean values, since it allows for nonrandom sampling with respect to body size. For example, the one *H. syndactylus* without an associated body mass happened to be the largest (i.e., had the longest femur) of any female siamang in the sample. This technique was not possible with *Pongo* because bone length does not predict body mass well in this species (%SEE = 28.5%).

TABLE 2. Abbreviations and definitions[1]

Lengths (mm)	
Femoral length′	Distance from superior surface of neck to average distal projection of condyles
Tibial length′	Distance from average proximal position of midpoints of medial and lateral plateau surfaces to center of tibiotalar surface
Humeral length′	Distance from most proximal point on humeral head to most distal point on lateral lip of trochlea
Radius length′	Distance from center of radial head to center of radiocarpal surface
Ulna length′	Same as radial length, measured from proximal edge of radial notch to distal edge of ulnar head
Articular surface areas (mm^2)	
FHSA	Femoral head surface area
FCSA	Femoral condyle surface area (medial + lateral)
TPSA	Tibial plateau surface area (medial + lateral)
TTSA	Tibiotalar surface area
HHSA	Humeral head surface area
HDSA	Humeral distal surface area (trochlear + capitular)
RHSA	Radial head surface area
RCSA	Radiocarpal surface area
UTSA	Ulnar trochlear surface area
UCSA	Ulnar “carpal” (distal) surface area
Articular surface breadths (mm)	
FHSI	Femoral head superoinferior breadth
FCML	Femoral total condyle mediolateral breadth
TPML	Tibial proximal mediolateral breadth
HHSI	Humeral head superoinferior breadth
HDML	Humeral distal mediolateral breadth
Section moduli (mm^3)[2]	
F50ZX	Femoral midshaft anteroposterior bending strength
F50ZP	Femoral midshaft torsional, or (twice) average bending strength
F80ZX	Femoral subtrochanteric (80% length′) anteroposterior bending strength
F80ZP	Femoral subtrochanteric (80% length′) torsional, or (twice) average bending strength
T50ZX	Tibial midshaft anteroposterior bending strength
T50ZP	Tibial midshaft torsional, or (twice) average bending strength
H40ZP	Humeral mid-distal (40% length′) shaft torsional, or (twice) average bending strength
R50ZP	Radial midshaft torsional, or (twice) average bending strength
U50ZP	Ulnar midshaft torsional, or (twice) average bending strength
Diaphyseal breadths (mm)[2]	
F50AP	Femoral midshaft anteroposterior breadth
F50AB	Femoral midshaft average anteroposterior and mediolateral breadths
T50AP	Tibial midshaft anteroposterior breadth
T50AB	Tibial midshaft average anteroposterior and mediolateral breadths
H40AB	Humeral mid-distal (40% length′) shaft average anteroposterior and mediolateral breadths
R50AB	Radial midshaft average anteroposterior and mediolateral breadths
U50AB	Ulnar midshaft average anteroposterior and mediolateral breadths

[1] See Ruff (2002) for illustrations and detailed descriptions.

[2] All locations for section moduli and diaphyseal breadths were determined using length′.

A list of all bone structural properties and their abbreviations is given in Table 2. Detailed descriptions and illustrations of these properties were given in the preceding paper (Ruff, 2002). They include bone lengths, articular surface areas and breadths, diaphyseal section moduli (measures of bending/torsional strength), and external breadths. Note that external breadths of the femoral subtrochanteric (“80%”) location were not available for most specimens, as explained in the previous paper, and so are not included here. Also, while only A-P breadths and section moduli of hindlimb diaphyses were used in the previous paper, both A-P and combined or average A-P/M-L properties for these locations were examined here (Table 2). While A-P bending strength of the hindlimb bones is most appropriate in locomotor analyses (see discussion in previous paper), this is not necessarily true for body mass estimation, as shown below. Section moduli were derived using computed tomography, and articular surface areas through linear measurements and geometric modeling (Ruff, 2002). Articular surface breadths are also reported for the proximal and distal femur and humerus, and the proximal tibia. Sex/species means for all properties are given in Tables 1A (hindlimb) and 1B (forelimb) in the Appendix. Individual values are given in a tab-delimited text file available online at the following address: http://www.hopkinsmedicine.org/FAE/primate_structural_properties.txt, which can be imported into spreadsheet programs, e.g., Excel.

Several different groups were used to generate body mass prediction equations. Sex/species means analyses were carried out for the total pooled sample ($n = 24$ or 22) and for hominoids ($n = 10$). Individual data analyses were carried out for cercopithecoids ($n = 78–95$), Asian apes ($n = 29–30$), cercopithecines ($n = 43–44$), and colobines ($n = 31–47$). These groups were chosen on both taxonomic grounds and on the basis of shared similarities in locomotor-positional behavior (Ruff, 2002). Because of the possibility of lesser apes largely determining the form of hominoid regression equations (because of their much smaller body size than other hominoids), a reference group consisting of only great apes was also considered. However, in most cases, hominoid regressions with and without lesser apes yielded similar results, so only the full hominoid sample results are shown here. Due to the small number of data points available ($n = 4$), no African ape regression equations were calculated. However, interested readers may develop additional estimation equations for any grouping of species, using the data listed in the Appendix and in the on-line data file.

The issue of nonindependence of data points in such analyses because of phylogenetic relatedness was discussed in Ruff (2002). No comparisons of prediction errors between different taxonomic/locomotor subgroups (or subgroups and the total sample) are carried out here; rather, comparisons are carried out between different structural properties within the same groups. Thus, this issue should not be an important factor in chosing between prediction equations based on different structural characteristics. The broader issues of variation in heritability of these traits and developmental constraints in both juveniles and adults are also interesting and potentially could affect body mass estimation (e.g., Ruff et al., 1991), but are beyond the scope of the present investigation.

Least squares regression analysis on natural log-transformed data was used to determine all prediction equations (sex/species mean data were log-transformed after calculation of the means). The relative prediction error of these equations is assessed primarily using the percent standard error of estimate (%SEE), a measure of predictive precision. For natural log-transformed data, the %SEE can be calculated as $\exp(\text{SEE} + 4.6052) - 100$. Transforming log body mass estimates back into original (kg) units creates detransformation bias, which can be corrected using several methods (Smith, 1993b). The simplest method is the so-called “quasimaximum likelihood estimator” (QMLE), which involves multiplying the detransformed (original units) value by $\exp(\text{SEE}^2/2)$ (this is equivalent to $\exp[(\text{residual mean square})/2]$). However, as discussed by Smith (1993b), this method itself may be inherently biased. To test for possible bias in use of QMLE, it was compared here with another correction factor, the “ratio estimator” (RE), which is calculated as (mean of observed y values)/(mean of detransformed predicted y values), for a variety of estimators and reference groups. Over 12 such comparisons, QMLE and RE correction factors differed by an average of less than 0.01%, with a maximum difference of 0.4%. (This trivial difference between results may be due to the very small correction factors here, i.e., less than 5% for all equations; see Smith, 1993a.) Therefore, because of its greater ease in application, the QMLE method was used here. Although QMLE correction factors may be easily calculated from SEEs (see above), for convenience they are given here for all regression equations. Confidence intervals (CIs) for body mass estimates can be calculated as $\pm \text{SEE} \times t_{(100 - \text{CI})(2),\, \text{d.f.}}$ (Zar, 1984), with $\text{d.f.} = n - 2$.[2] For example, the 50% CI for a sample of $n = 24$ is $\pm \text{SEE} \times 0.686$. Note that these confidence limits must themselves be multiplied by the same correction factors as the estimates after detransformation. The effects of using sex/species means equations to calculate CIs for individual specimens are addressed below.

In addition, percent prediction errors (%PEs) of body mass for different equations, i.e., measures of predictive accuracy, were calculated as [(actual-predicted)/predicted] × 100 (Smith, 1984), using a subset of individuals from the total sample with known body masses. One male and one female were randomly selected from each of the 11 species with available individual body masses (all species except gorillas; see Table 1). Although these individuals were used in deriving sex/species means, their relative influence on the group means was small in most cases (Table 1). Thus, for equations obtained using mean data, these individuals can be considered as effectively independent test cases. For this reason, %PEs were only calculated for the total sample sex/species mean data analyses. (The number of available individuals with body masses was considered too biased towards Asian apes (Table 1) to carry out similar analyses for hominoid sex/species means equations.) Following previous researchers (Dagosto and Terranova, 1992; Delson et al., 2000), the percents of estimates falling within 20% of actual body mass are also reported for each equation as another measure of predictive accuracy.

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[2] Confidence limits for individual specimens will actually be somewhat larger than this, depending on the reference sample size and the distance along the x axis from the specimen to the mean of the sample relative to the total dispersion of x (see Zar, 1984, equation 17.29, p. 275). However, in empirical tests it was found that this additional increment to CIs using the more exact equation was very small. For example, using FHSI to predict body mass in Old. 67 (*Theropithecus oswaldi*), and the cercopithecoid reference sample, the 50% CI using the exact equation is 47.1–58.7 kg, while the 50% CI using SEE × t is 47.4–58.4 kg. (This is actually somewhat of a “worst case scenario,” since the specimen is so far removed from the modern cercopithecoid mean.) The same analysis but using the total sample sex/species means equation gives 50% CIs of 53.4–67.0 kg and 53.6–66.6 kg, respectively, for the exact and approximate equations.

TABLE 3. Percent standard errors of estimate of body mass, using sex/species means

		% standard error of estimate		
Bone	Property[1]	Total sample (n = 22, 24)[2]	Hominoids (n = 10)	Cercopithecoids (n = 12, 14)[2]
Femur	Length′	54.8	51.3	25.0
	FHSA	20.0	12.9	15.4
	FHSI	17.4	12.0	11.1
	FCSA	14.0	19.8	10.0
	FCML	11.5	13.7	8.2
	F50ZX	15.8	21.5	5.3
	F50AP	22.1	31.6	9.1
	F50ZP	14.8	20.0	5.6
	F50AB	17.7	24.8	8.4
	F80ZX	12.8	18.7	6.1
	F80ZP	14.0	16.4	8.6
Tibia	Length′	61.8	30.4	28.7
	TPSA	16.4	15.6	12.0
	TPML	13.1	12.8	11.9
	TTSA	18.5	15.4	16.1
	T50ZX	33.0	29.0	14.1
	T50AP	35.8	35.6	16.3
	T50ZP	31.5	27.0	13.0
	T50AB	33.1	28.8	13.5
Humerus	Length′	68.5	54.8	15.9
	HHSA	34.7	21.9	25.5
	HHSI	26.5	12.0	17.7
	HDSA	23.7	14.0	22.0
	HDML	17.6	14.5	12.9
	H40ZP	14.2	12.7	13.2
	H40AB	15.8	16.6	14.6
Radius and ulna	Length′	106.6	189.6	18.8
	RHSA	24.1	9.8	11.9
	RCSA	17.9	20.8	16.5
	R50ZP	19.6	17.8	14.5
	R50AB	25.2	20.4	26.2
	UTSA	18.8	11.4	13.9
	UCSA	43.8	44.6	28.9
	U50ZP	19.0	13.8	13.1
	U50AB	25.9	22.9	14.5

[1] See Table 2 for property abbreviations.

[2] Total sample, n = 24 femur and humerus, and 22 tibia, radius, and ulna; cercopithecoids, n = 14 femur and humerus, and 12 tibia, radius, and ulna.

All statistical analyses and data plots were carried out using SYSTAT (1990).

RESULTS

Choice of structural properties

The %SEEs of body mass for the sex/species means analyses of the total sample and hominoids are given in Table 3, and for the individual analyses of cercopithecoids and Asian apes in Table 4. Although sex/species means were not used for body mass prediction in cercopithecoids, results based on cercopithecoid means are also given in Table 3, for comparison with the results for cercopithecoid individuals in Table 4 (see below). In addition to all articular and cross-sectional diaphyseal properties, results using bone lengths to estimate body mass are also given for comparison.

Several observations are apparent from examination of Tables 3 and 4. First, as expected, bone lengths are generally very poor predictors, with %SEEs above 50% for most total sample and hominoid sex/species means analyses. Only among cercopithecoid forelimb bones are lengths comparable in predictive precision to cross-sectional and articular properties. Second, articular breadths are always equal or superior to articular surface areas in precision. Thus, for estimating body mass, the more complex surface area reconstructions for the proximal and distal femur and humerus and proximal tibia are not necessary or even recommended (although some of these are valuable in determining locomotor behavior; Ruff, 2002).

In contrast, diaphyseal external breadths are always worse than section moduli in predictive precision. (Comparisons here should be made between comparable dimensions, i.e., A-P breadths with ZX section moduli, and average breadths with ZP section moduli; see Table 2.) The amount of difference in %SEEs varies, but is substantial in some cases. Breadths and section moduli based on average A-P and M-L dimensions (i.e., AB and ZP properties) have smaller %SEEs than those based on A-P dimensions (i.e., AP and ZX properties), except for the proximal femur in the total sample and in cercopithecoids, where F80ZX is superior to F80ZP.

In comparisons between bones, except for proximal tibial articular breadth, the tibia provides less precise body mass estimates than the femur (Tables

TABLE 4. Percent standard errors of estimate of body mass, using individuals

		% standard error of estimate	
Bone	Property[1]	Cercopithecoids (n = 78–95)[2]	Asian apes (n = 29, 30)[2]
Femur	Length′	25.4	64.8
	FHSA	20.3	17.9
	FHSI	16.6	14.0
	FCSA	15.7	26.1
	FCML	18.0	19.2
	F50ZX	14.2	18.0
	F50AP	17.1	29.8
	F50ZP	13.8	17.3
	F50AB	15.0	22.8
	F80ZX	12.6	21.9
	F80ZP	14.4	21.2
Tibia	Length′	26.9	43.5
	TPSA	17.3	23.4
	TPML	15.3	21.0
	TTSA	19.6	24.5
	T50ZX	16.7	33.4
	T50AP	18.2	36.5
	T50ZP	16.4	30.7
	T50AB	15.9	30.8
Humerus	Length′	18.7	24.7
	HHSA	25.9	16.6
	HHSI	19.9	18.8
	HDSA	24.1	21.0
	HDML	16.7	22.6
	H40ZP	16.5	18.8
	H40AB	18.8	24.5
Radius and ulna	Length′	20.5	36.2
	RHSA	15.9	21.0
	RCSA	18.7	22.1
	R50ZP	18.1	24.5
	R50AB	25.7	28.7
	UTSA	16.0	22.0
	UCSA	36.3	30.3
	U50ZP	17.6	16.6
	U50AB	19.3	22.9

[1] See Table 2 for property abbreviations.

[2] Asian apes, n = 30 hindlimb (except TTSA, 29), and 29 forelimb (except UTSA, 28); cercopithecoids, n = 95 femur (except FCML, 94), 80 tibia, 93 humerus, and 78 radius and ulna.

TABLE 5. Prediction errors in 22 individuals of known body mass, using total sample body mass prediction equations

Bone	Property[1]	Mean % PE[2]	% within 20%[3]
Femur	Length′	41.9	32
	FHSA	16.8	64
	FHSI	13.0	77
	FCSA	14.3	77
	FCML	9.2	91
	F50ZX	14.6	77
	F50AP	24.9	41
	F50ZP	12.0	77
	F50AB	14.1	73
	F80ZX	13.2	86
	F80ZP	23.5	41
Tibia	Length′	38.8	18
	TPSA	15.4	68
	TPML	12.1	86
	TTSA	17.3	68
	T50ZX	25.7	54
	T50AP	26.2	41
	T50ZP	23.0	54
	T50AB	22.5	59
Humerus	Length′	22.4	54
	HHSA	22.0	45
	HHSI	17.3	64
	HDSA	15.9	64
	HDML	12.8	73
	H40ZP	17.6	59
	H40AB	18.2	64
Radius and ulna	Length′	31.7	45
	RHSA	18.4	59
	RCSA	13.1	86
	R50ZP	12.6	82
	R50AB	18.1	59
	UTSA	16.3	54
	UCSA	28.3	54
	U50ZP	15.9	54
	U50AB	16.5	64

[1] See Table 2 for property abbreviations.

[2] %PE = absolute value of [(observed − predicted)/predicted] × 100.

[3] Percent of individuals falling within 20% of predicted value.

3 and 4). This is especially true for tibial cross-sectional diaphyseal dimensions in analyses that include hominoids, where %SEEs average 30% or more. As discussed below, this is most likely a result of the variable role of the fibula in supporting body mass. In comparisons of similar properties between the forelimb and hindlimb, the femur is generally slightly superior to the humerus in predictive precision (although not always, as in predictions using shaft strength among hominoids). The radius and ulna are generally worse than the humerus for shaft strength predictions, and comparable for articular predictions, except for distal ulnar surface area (UCSA), which is a uniformly very poor predictor. This last observation is perhaps not surprising, given the small size of this surface and its minor role in transmission of body weight (UCSA is useful, however, in locomotor reconstructions; see Ruff, 2002).

Table 5 lists %PEs of body mass in 22 individuals, using the total sample sex/species means equations. Results basically confirm those for %SEEs: lengths are generally poor estimators (of these, humeral length is the best), diaphyseal strengths are generally better predictors than breadths, articular breadths are better than surface areas, and distal ulnar surface area is very poor. The relative ordering of %PEs and %SEEs for different properties is similar (r = 0.75, both Pearson and rank-order correlations), with %PE equal to about 0.8 × %SEE on average. The main outlier in this regard is F80ZP, which has a much larger %PE than %SEE (compare with Table 3). This reinforces the superiority of F80ZX over F80ZP in the total sample regressions. These results also further justify use of %SEEs to evaluate different predictive equations in subgroups of the total sample, since they should be generally representative of %PEs as well. The percent of individual estimates falling within 20% of true body masses inversely parallels the %PE (r = −0.89). Several predictors are successful to this level of accuracy in more than 80% of all individuals, and many in over 60%, including all femoral predictors except length, midshaft A-P breadth, and F80ZP (Table 5).

TABLE 6. Comparison of total sample with hominoid and cercopithecoid (individuals) body mass prediction regression lines, and recommendations for use of equations if locomotor affinities are unknown or intermediate

		Hominoid (H), cercopithecoid (C), and total (T) regression patterns			
Property[1]	Mean % dif.[2]	All very similar, use T	H and C parallel, T diag. between, use mean H and C	H and C not parallel, T intermediate, use T	H and C not parallel, T not intermediate, none recommended
TPML	0.7	X			
RCSA	3.4	X			
F80ZX	5.0	X			
H40AB	5.5	X			
FCML	5.6		X		
H40ZP	7.5			X	
F50AB	8.0		X		
F50ZP	8.2		X		
F50ZX	9.6		X		
TTSA	9.8		X		
F80ZP	9.9			X[3]	
R50AB	10.0			X	
HDML	11.9			X	
U50ZP	12.1			X	
R50ZP	12.3			X	
FHSI	13.6			X	
U50AB	14.2		X		
UTSA	18.8		X		
RHSA	20.0				X
T50ZP	20.3				X
T50ZX	20.8				X
T50AB	21.4				X
HHSI	21.6				X

[1] See Table 2 for property abbreviations.

[2] Mean percent difference between total sample body mass estimate and hominoid and cercopithecoid (individuals) sample body mass estimates (kg) over all sex/species data points, ranked from smallest to largest.

[3] F80ZX would be used in preference to F80ZP in total sample (also see Table 3).

Based on these findings, further analyses will include only articular surface breadths rather than areas (when there is a choice between the two), will eliminate distal ulnar surface area, and will use average breadths or section moduli except in the proximal femur in the total sample or cercopithecoids, where A-P dimensions will be used. Although section moduli have lower %SEEs and %PEs than external breadths, both kinds of data are retained, since in some studies it may not be possible to obtain section moduli in addition to breadths (in contrast, articular breadths will always be available when surface areas can be measured).

Choice of reference sample

Long bone structural properties will be influenced by both body mass and locomotor behavior. Thus, when locomotor affinities with specific modern reference samples can be established, using methods like those presented in Ruff (2002) or other methods, then those reference samples should be employed for body mass estimation. However, if a fossil anthropoid specimen is either intermediate or variable ("mosaic") in morphology compared to modern reference groups, or too incomplete to firmly assess locomotor behavior, then either equations based on a broader sampling of modern taxa or an average of estimates derived from different reference groups can be used. As shown later in the sample applications to fossil specimens, this is not an unusual situation. The choice of which of these options to employ depends on the particular patterns of distribution of structural properties relative to body mass in the different reference groups, as illustrated below.

The most common decision to be made in this regard will be whether to use the total sample equations or an average of hominoid and cercopithecoid equations. If all three equations give similar results, then the choice is relatively unimportant. One way to evaluate this potential "error" is to compute the average percentage difference (in real, i.e., kg units) between hominoid and cercopithecoid body mass estimates and total sample estimates over the total range of possible values. This has been done in Table 6 for all sex/species mean structural property values in the total sample (i.e., for $n = 24$ data points, or 22 for distal limb elements, without *Colobus*). Both AP and average (ZP) section moduli of the hindlimb are included here as a further test of their utility as body mass predictors, even though average section moduli generally have smaller %SEEs, as shown above. As another test of equivalence between hominoid and cercopithecoid equations, slopes and elevations were compared between the two, using ANCOVA (elevations only if slopes were nonsignificantly different; a conservative level of $P < 0.10$ was used here for slopes, but $P < 0.05$ for elevations). For these analyses, the sex/species mean data for cercopithecoids were used, to avoid mixing data derived from individuals (cercopithecoids) and means (hominoids). Examination of bivariate plots of mean and

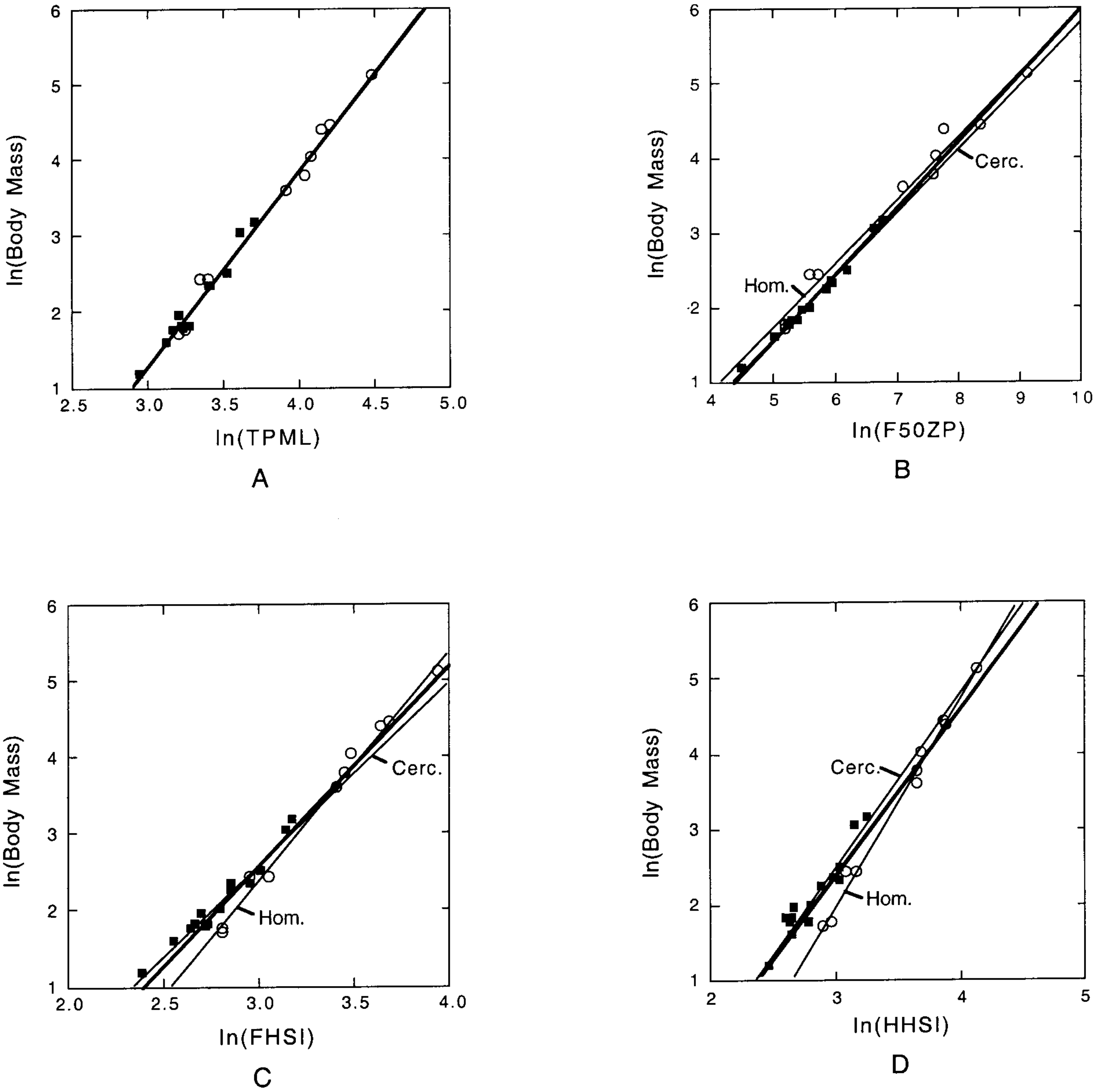

Fig. 1. Regressions of body mass on structural properties in total sample (heavy line), hominoids (open circles), and cercopithecoids (solid squares). Sex/species mean data points are shown, although cercopithecoid regression lines were determined using individual data (regressions through individuals and means are very close, as noted in text). All data were log-transformed. **A:** Tibial plateau M-L breadth (three regression lines completely overlap). **B:** Femoral midshaft (twice) average bending strength. **C:** Femoral head S-I breadth. **D:** Humeral head S-I breadth.

individual data for cercopithecoids indicated that the two yielded very similar results in terms of central tendencies, i.e., positions of regression lines. The positions of regression lines for the total combined sample relative to each subgroup were also visually evaluated, as detailed below.

Table 6 shows that of all structural properties evaluated, the M-L breadth of the proximal tibial articular surface (TPML) is the least affected by choice of prediction equation, with an average difference of only 0.7% between hominoid and cercopithecoid equations and the total sample equation. Another way to interpret this finding is that there is very little effect of locomotor difference on the relative M-L breadth of the proximal tibial surface. This is illustrated in Figure 1A, which shows a plot of body mass on TPML. Hominoids and cercopithecoids lie on almost precisely the same regression line (all three lines, including that for the total sample, fall on top of each other so that only a single line appears to be plotted; there is no difference in slope or elevation). Thus, when using this property in body mass estimation, identification of locomotor behavior is unimportant. The same is true, to a lesser extent, of the distal radial articular surface (RCSA), F80ZX, and H40AB, all of which have mean percent differences between estimates of less than 6% (Table 6) and no significant difference between groups in either slope or elevation. In these cases, the best option is to use the total sample regression if locomotor mode cannot be identified, although either of the subgroup equations will yield very similar results over most of the body size range represented in the total sample.

In a second kind of pattern, the hominoid and cercopithecoid regressions are parallel to each other (nonsignificantly different slopes but different elevations), and because all of the largest body mass values are hominoids (i.e., great apes), the total sample regression line tends to run diagonally between the two subsample lines. This pattern is illustrated in Figure 1B for F50ZP. It is also characteristic of F50ZX, F50AB, U50AB, and the tibiotalar (TTSA) and ulnar trochlear (UTSA) articular surfaces (Table 6). In these cases, the total sample equations should not be used, since they will be biased towards hominoids in their upper ends and towards cercopithecoids in their lower ends. Rather, as indicated in Table 6, the mean of hominoid and cercopithecoid predictions should be employed.

A third pattern is illustrated in Figure 1C. Here, the hominoid and cercopithecoid regressions are not parallel, crossing somewhere near the middle of the total data distribution, and the total sample regression lies between the two subsample regressions (occasionally falling slightly outside them at the crossing point). This pattern is characteristic of femoral head breadth (FHSI; shown in Fig. 1), all forelimb section moduli and breadths except H40AB, and distal humeral articular M-L breadth (HDML) (Table 6). Here the total sample equations should be used, since they should be relatively unbiased with respect to either subsample distribution.

Finally, for some properties, the hominoid and cercopithecoid regressions have widely different slopes, intersecting only near the edge of the total distribution, and the total sample regression does not bisect them. This is characteristic of humeral head S-I breadth (HHSI; shown in Fig. 1D), radial head surface area (RHSA), and all tibial diaphyseal dimensions. The mean percent difference in estimates between equations is 20% or more. In these cases, the use of either the total sample equation, or an average of hominoid and cercopithecoid equations, is not recommended. Unless locomotor mode can be identified, body mass estimation using these properties should not be carried out. All of these equations also have very high %SEEs in the total sample regressions (Table 3), as would be expected.

Also as expected, most properties with low mean percent differences between subgroups in Table 6 have relatively low total sample %SEEs and %PEs in Tables 3 and 5. However, the two measures are not perfectly correlated. For example, FCML has smaller prediction errors in the total sample regressions than TPML (Tables 3 and 5) but a larger average percent difference between subgroups (Table 6). This is because the index shown in Table 6 measures the variation between but not within subgroups, while those in Tables 3 and 5 include both. Thus, TPML relative to body mass is somewhat more variable within subgroups than FCML, but TPML relative to body mass is virtually constant between subgroups while FCML varies slightly. As another example, RCSA and UTSA have similar %SEEs and %PEs in the total sample regressions (Tables 3 and 5), but very different between-group values in Table 6. As shown in comparisons within hominoids and cercopithecoids (Tables 3 and 4), relative to body mass, RCSA is much more variable within subgroups than UTSA, yet between subgroups, RCSA is less variable. Thus, if locomotor mode can be identified, UTSA provides much better body mass estimates, and if not, RCSA is far preferable. Therefore, results of both kinds of comparisons must be considered in choosing the best prediction equations in any particular situation.

The comparisons of ZP and ZX results for the hindlimb in Table 6 support those in Tables 3 and 5: in each case except for the proximal femur (F80), the average (ZP) properties have smaller percent differences between subgroups than the A-P (ZX) properties. This is another reason for preferring the average strength properties in most body mass predictions.

True prediction errors for sex/species means equations

As noted by Radinsky (1982), confidence limits for individual predictions based on regression formulae derived from modern sample *means* are suspect. In fact, it might be expected that due to greater dispersion of individual values, SEEs of sample mean regressions would systematically greatly underestimate true confidence limits for individual predictions. The present study sample of cercopithecoids provides an opportunity to empirically test this idea, since almost all individuals in the sample are of known body mass. Thus, confidence limits for body mass estimations based on cercopithecoid sex/species means can be directly compared to those based on individuals from the same samples.

This has been done in Figure 2, which plots the ratios of CIs derived from cercopithecoid individuals to those derived from sex/species means, against the CIs from sex/species means, for all of the properties included as body mass estimators for cercopithecoids (i.e., all of the properties in Table 6 except for F50ZX, F80ZP, and T50ZX; see Table 8). *Colobus* was not included in the individual-based analyses for distal limb elements, to assure comparability with the sex/species means analyses for these elements. Results for two confidence intervals are shown: 50% CIs (Fig. 2A) and 95% CIs (Fig. 2B).

It is apparent from Figure 2 that the lowest confidence limits from sex/species means analyses are unrealistic compared to those derived from individuals. The four properties where CIs from individuals are more than about 40% greater than those from

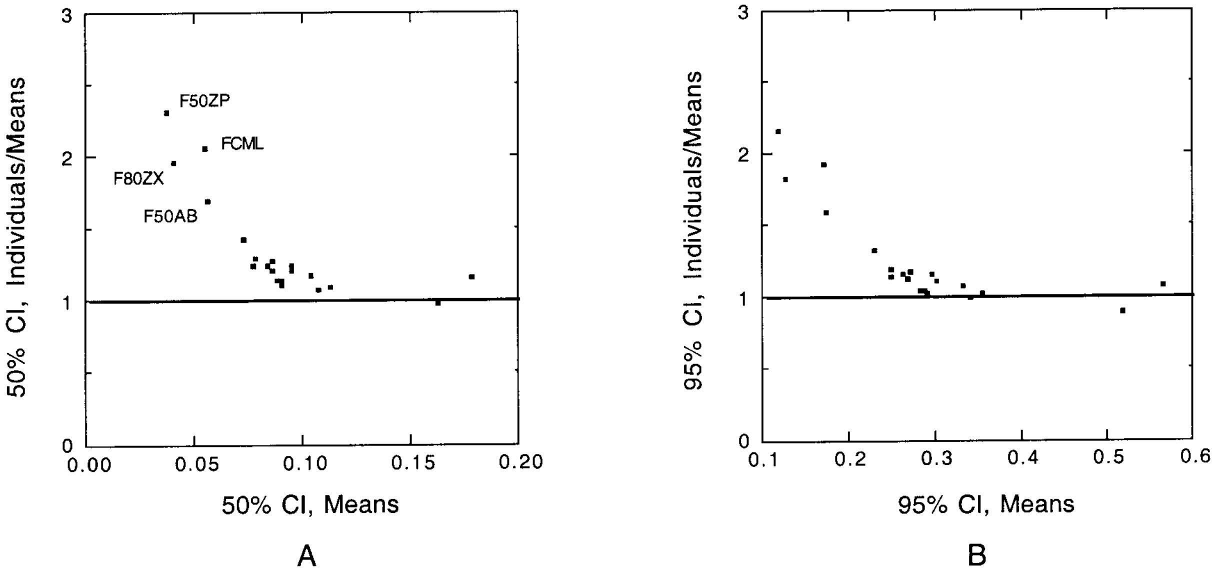

Fig. 2. Comparison of confidence intervals for estimation of body mass (log data) in cercopithecoids, using individuals and sex/species means. See Table 8 for list of all properties used in predictions. X axis, CIs using sex/species means; Y axis, ratio of CIs using sex/species means to those using individuals. **A:** 50% CIs. **B:** 95% CIs.

means are labeled in Figure 2A (the same four points are in an analogous position in Fig. 2B), and include the three cross-sectional measurements of the femoral shaft and the M-L breadth of the condyles. All of these parameters have extremely low %SEEs (less than 9%) in cercopithecoid sex/species means regressions (Table 3). In contrast, other properties that have higher %SEEs and CIs in sex/species mean analyses appear to have comparable CIs in analyses based on individuals: all are within about 40%, and in most cases within 20% of the means values (Fig. 2, Table 3). The mean ratio between individual and mean data CIs, not including the four properties with very low %SEEs, is 1.10 for 95% CIs and 1.18 for 50% CIs. Similar comparisons using SEEs instead of CIs (thus reducing the effects of different sample sizes in mean and individual-based analyses) yield almost identical results.

The same general pattern is illustrated in Figure 3, which shows the regression of body mass against two structural properties in cercopithecoid individuals and corresponding sex/species means. For F80ZX (Fig. 3A,B), a property with a very low %SEE and CIs in means analyses, confidence limits are about twice as great when using individuals. However, for TPML (Fig. 3C,D), which has moderately low %SEE and CIs using sex/species means, the CIs based on individuals are very similar to those from means. In fact, the data scatters and CIs for F80ZX and TPML using individuals are remarkably similar, despite the twofold difference in CIs in the means analyses. This suggests a certain minimum degree of individual variability in body mass relative to any structural parameter that must be expected in analyses of this kind, i.e., due to measurement and biological "error."

These results also suggest that in the great majority of cases, confidence limits based on sex/species means represent fairly accurate estimates of those based on individuals, but that extremely low CIs or SEEs based on means probably grossly underestimate those for individuals. Within the present cercopithecoid sample, the approximate threshold for this distinction is at about a 10%SEE for sex/species means analyses (Table 3). This is below the %SEE for any property used here in sex/species means analyses except for RCSA in hominoids (Table 3), indicating that the sex/species means confidence limits derived here are, on the whole, realistic. The same kinds of analyses were also carried out within Asian apes, with similar results, although the comparison is not quite as clean, since many orangutans do not have associated body masses (Table 1).

Body mass prediction equations

Body mass prediction equations, including SEEs and detransformation correction factors (see above), are given in Tables 7–9. Table 7 gives coefficients for total sample and hominoid sex/species means, Table 8 for cercopithecoid and Asian ape individuals, and Table 9 for cercopithecine and colobine individuals. Results are given for only the properties determined to provide the better estimates, when there is a choice between properties (e.g., articular breadths vs. areas), as discussed above. Equations for F80ZX are given for the total sample and cercopithecoids (including cercopithecoid subgroups[3]), and F80ZP for hominoids (all hominoids and Asian apes). For

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[3] Cercopithecoid subgroups show patterns of variation in %SEEs very similar to those of cercopithecoids as a whole (Table 4).

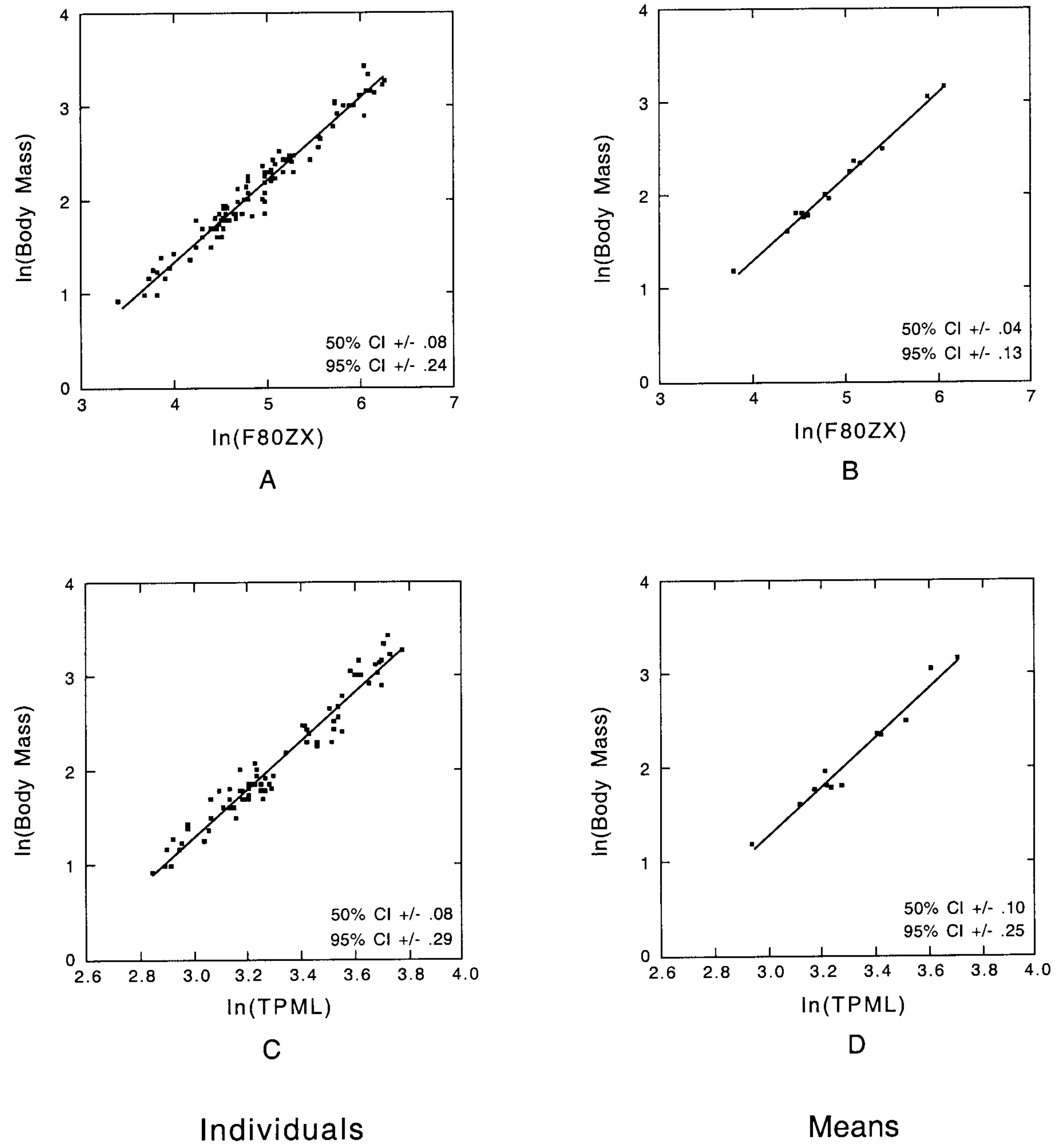

Fig. 3. Comparison of bivariate data scatters and confidence intervals for estimations of body mass in cercopithecoids using individuals (**A**, **C**) and sex/species means (**B**, **D**). Body mass predictors are femoral subtrochanteric shaft A-P bending strength (A, B) and tibial plateau M-L breadth (C, D).

the total sample sex/species means analyses (Table 7), all regression equations are given; however, half of these, indicated by brackets, are not recommended for use, following the analyses presented earlier. Rather, in these cases, when there is no information on locomotor behavior, or there is a "mosaic" of reconstructed locomotor behaviors relative to modern species, either the average of hominoid and cercopithecoid equations should be used, or body mass prediction using these particular properties should not be attempted, as indicated in Table 7 (see also Table 6).

Fossil applications

To illustrate the use of these equations, body mass estimates are calculated for four fossil anthropoid specimens also included in Ruff (2002) (Table 10). Detailed descriptions of these specimens and measurement techniques can be found there, as well as a discussion of locomotor affinities. Following the recommendations in Table 6, when there is evidence to suggest an intermediate morphology/function, the total sample equations are used for FHSI, FCML, HDML, and H40ZP, and the average of hominoid

TABLE 7. Body mass prediction equations using sex/species means (body mass in kg, natural log-transformed)

		Total sample					Hominoids				
Bone	Property[1]	d.f.[2]	Slope	Intercept	SEE[3]	CF[4]	d.f.[2]	Slope	Intercept	SEE[3]	CF[4]
Femur	FHSI	22	2.642	−5.338	0.1602	1.013	8	3.019	−6.668	0.1137	1.006
	FCML	[22	2.504	−6.055	0.1091	1.006][6]	8	2.584	−6.398	0.1286	1.008
	F50ZP	[22	0.8928	−2.887	0.1377	1.010][6]	8	0.8492	−2.518	0.1826	1.017
	F50AB	[22	2.651	−4.349	0.1625	1.013][6]	8	2.515	−3.890	0.2216	1.025
	F80ZX/ZP[5]	22	0.9031	−2.278	0.1204	1.007	8	0.7882	−2.080	0.1523	1.012
Tibia	TPML	20	2.589	−6.487	0.1227	1.008	8	2.591	−6.501	0.1476	1.011
	TTSA	[20	1.414	−4.670	0.1695	1.014][6]	8	1.347	−4.208	0.1432	1.010
	T50ZP	[20	0.9910	−3.081	0.2740	1.038][7]	8	0.9866	−2.887	0.2387	1.029
	T50AB	[20	2.944	−4.678	0.2861	1.042][7]	8	2.928	−4.456	0.2530	1.032
Humerus	HHSI	[22	2.228	−4.283	0.2354	1.028][7]	8	2.764	−6.291	0.1129	1.006
	HDML	[22	2.356	−4.904	0.1621	1.013	8	2.633	−5.966	0.1356	1.009
	H40ZP	22	0.8605	−2.406	0.1327	1.009	8	0.9171	−2.824	0.1197	1.007
	H40AB	22	2.498	−3.693	0.1470	1.011	8	2.635	−4.122	0.1536	1.012
Radius	RHSA	[20	1.405	−4.674	0.2160	1.024][7]	8	1.722	−6.556	0.0934	1.004
	RCSA	20	1.362	−4.254	0.1650	1.014	8	1.390	−4.410	0.1892	1.018
	R50ZP	20	0.9338	−1.807	0.1791	1.016	8	1.018	−2.277	0.1639	1.014
	R50AB	20	2.698	−3.210	0.2249	1.026	8	2.798	−3.416	0.1854	1.017
Ulna	UTSA	[20	1.194	−4.225	0.1723	1.015][6]	8	1.314	−5.101	0.1075	1.006
	U50ZP	20	0.8350	−1.282	0.1737	1.015	8	0.9450	−1.995	0.1289	1.008
	U50AB	[20	2.355	−2.367	0.2299	1.027][6]	8	2.764	−3.500	0.2065	1.022

[1] See Table 2 for property abbreviations and units of measurement. All properties natural log-transformed.
[2] Degrees of freedom used in calculating confidence intervals.
[3] Standard error of estimate (natural log units).
[4] Correction factor for detransformation bias (see text).
[5] F80ZX, total sample; F80ZP, hominoids.
[6] Use mean of hominoid and cercopithecoid equations rather than total sample equation (see Table 6).
[7] No estimation recommended without locomotor affiliation (see Table 6).

TABLE 8. Body mass prediction equations using individuals, cercopithecoids and Asian apes (body mass in kg, natural log-transformed)

		Cercopithecoids					Asian apes				
Bone	Property[1]	d.f.[2]	Slope	Intercept	SEE[3]	CF[4]	d.f.[2]	Slope	Intercept	SEE[3]	CF[4]
Femur	FHSI	93	2.388	−4.560	0.1532	1.012	28	3.024	−6.718	0.1309	1.008
	FCML	92	2.523	−6.074	0.1656	1.014	28	2.697	−6.794	0.1754	1.016
	F50ZP	93	0.8523	−2.695	0.1293	1.008	28	0.9745	−3.258	0.1594	1.013
	F50AB	93	2.560	−4.162	0.1393	1.010	28	2.936	−4.968	0.2056	1.021
	F80ZX/ZP[5]	93	0.8763	−2.164	0.1183	1.007	28	0.8450	−2.414	0.1926	1.019
Tibia	TPML	78	2.574	−6.431	0.1420	1.010	28	2.690	−6.857	0.1910	1.018
	TTSA	78	1.299	−4.142	0.1791	1.016	27	1.282	−3.919	0.2195	1.024
	T50ZP	78	0.7250	−1.786	0.1517	1.012	28	1.148	−3.761	0.2674	1.036
	T50AB	78	2.140	−2.928	0.1479	1.011	28	3.420	−5.638	0.2688	1.037
Humerus	HHSI	91	2.322	−4.446	0.1816	1.017	27	2.675	−6.058	0.1719	1.015
	HDML	91	2.338	−4.779	0.1542	1.012	27	2.652	−6.074	0.2041	1.021
	H40ZP	91	0.7994	−2.056	0.1523	1.012	27	0.8832	−2.672	0.1726	1.015
	H40AB	91	2.438	−3.528	0.1720	1.015	27	2.582	−4.036	0.2194	1.024
Radius	RHSA	76	1.131	−3.308	0.1479	1.011	27	1.738	−6.639	0.1909	1.018
	RCSA	76	1.293	−3.907	0.1716	1.015	27	1.249	−3.771	0.1997	1.020
	R50ZP	76	0.7622	−1.101	0.1666	1.014	27	0.9754	−2.109	0.2193	1.024
	R50AB	76	2.198	−2.311	0.2284	1.026	27	2.712	−3.288	0.2526	1.032
Ulna	UTSA	76	1.351	−4.955	0.1481	1.011	26	1.220	−4.577	0.1992	1.020
	U50ZP	76	0.7997	−1.067	0.1617	1.013	27	0.8731	−1.696	0.1536	1.012
	U50AB	76	2.294	−2.191	0.1766	1.016	27	2.651	−3.366	0.2064	1.022

[1] See Table 2 for property abbreviations and units of measurement. All properties natural log-transformed.
[2] Degrees of freedom used in calculating confidence intervals.
[3] Standard error of estimate (natural log units).
[4] Correction factor for detransformation bias (see text).
[5] F80ZX, cercopithecoids; F80ZP, Asian apes.

and cercopithecoid equations for F50ZP (i.e., no "total sample" estimates were calculated using F50ZP). Fifty percent confidence intervals are also shown for each estimate. A mean of the "preferred" estimates for each specimen is given, along with the range of preferred estimates.

T. oswaldi (Old 67). Except for its humeral head size, *T. oswaldi* is well-characterized by cercopithecoid proportions (Ruff, 2002), and so results using cercopithecoid equations are given here. It was argued that its large humeral head (and long humerus) was most likely *not* a locomotor adaptation

TABLE 9. Body mass prediction equations using individuals, cercopithecines and colobines (body mass in kg, natural log-transformed)

		Cercopithecines					Colobines.				
Bone	Property[1]	d.f.[2]	Slope	Intercept	SEE[3]	CF[4]	d.f.[2]	Slope	Intercept	SEE[3]	CF[4]
Femur	FHSI	44	2.389	−4.541	0.1670	1.014	47	2.424	−4.684	0.1385	1.010
	FCML	44	2.493	−5.973	0.1771	1.016	46	2.662	−6.531	0.1561	1.012
	F50ZP	44	0.8468	−2.651	0.1251	1.008	47	0.8801	−2.866	0.1339	1.009
	F50AB	44	2.575	−4.161	0.1256	1.008	47	2.598	−4.295	0.1439	1.010
	F80ZX	44	0.8725	−2.158	0.1186	1.007	47	0.8869	−2.204	0.1193	1.007
Tibia	TPML	44	2.502	−6.210	0.1393	1.010	32	2.920	−7.560	0.1337	1.009
	TTSA	44	1.355	−4.358	0.1712	1.015	32	1.204	−3.744	0.1643	1.014
	T50ZP	44	0.6987	−1.636	0.1348	1.009	32	0.8857	−2.672	0.1516	1.012
	T50AB	44	2.064	−2.732	0.1337	1.009	32	2.623	−4.106	0.1387	1.010
Humerus	HHSI	43	2.461	−4.914	0.1603	1.013	46	2.030	−3.559	0.1638	1.013
	HDML	43	2.424	−5.071	0.1607	1.013	46	2.107	−4.063	0.1331	1.009
	H40ZP	43	0.8129	−2.202	0.1175	1.007	46	0.7889	−1.932	0.1490	1.011
	H40AB	43	2.563	−3.930	0.1386	1.010	46	2.315	−3.147	0.1299	1.008
Radius	RHSA	43	1.177	−3.568	0.1487	1.011	31	1.014	−2.700	0.1168	1.007
	RCSA	43	1.315	−4.067	0.1710	1.015	31	1.271	−3.726	0.1395	1.010
	R50ZP	43	0.7713	−1.228	0.1491	1.011	31	0.8181	−1.208	0.0993	1.005
	R50AB	43	2.394	−2.875	0.1273	1.008	31	2.442	−2.567	0.1160	1.007
Ulna	UTSA	43	1.373	−5.114	0.1400	1.010	31	1.301	−4.633	0.1397	1.010
	U50ZP	43	0.7922	−1.089	0.1621	1.013	31	0.8666	−1.258	0.1317	1.009
	U50AB	43	2.315	−2.316	0.1602	1.013	31	2.475	−2.406	0.1235	1.008

[1] See Table 2 for property abbreviations and units of measurement. All properties natural log-transformed.
[2] Degrees of freedom used in calculating confidence intervals.
[3] Standard error of estimate (natural log units).
[4] Correction factor for detransformation bias (see text).

TABLE 10. Body mass estimates (kg) for fossil specimens, with 50% confidence intervals[1]

Property[2]	Reference group	*T. oswaldi* (Old 67), Estimate (50% CI)	*P. nyanzae* (KNM-WT 13142A), Estimate (50% CI)	*P. heseloni* (KNM-RU 2036), Estimate (50% CI)	*Morotopithecus* (MUZM 80), Estimate (50% CI)
FHSI	Total		34.9 (31.3–38.9)		**29.5 (26.4–32.9)**
	Hominoids		**32.5 (30.0–35.2)**		
	Cercopithecoids	**52.6 (47.4–58.4)**			
FCML	Total				
	Hominoids				**37.3 (34.0–40.8)**
	Cercopithecoids	**55.8 (49.9–62.4)**			40.9 (37.0–46.4)
F50ZP	Hominoids		**40.4 (35.5–46.0)**	11.1 (9.7–12.6)	**41.3 (36.3–47.0)**[3]
	Cercopithecoids	**63.4 (58.1–69.2)**	34.3 (31.5–37.5)	**9.4 (8.6–10.2)**	**35.1 (31.1–38.3)**[3]
	Colobines			9.3 (8.5–10.6)	
HDML	Total			[16.9 (15.2–18.9)][4]	
	Hominoids			[14.5 (13.1–15.9)][4]	
	Cercopithecoids	**54.6 (49.2–60.6)**		[18.1 (16.3–20.1)][4]	
H40ZP	Total			8.8 (8.0–9.7)	
	Hominoids			7.8 (7.2–8.5)	
	Cercopithecoids	**55.8 (50.3–61.9)**		**9.1 (8.2–10.1)**	
	Colobines			9.6 (8.8–10.7)	
Mean (range)		**56.4 (52.6–63.4)**	**36.4 (32.5–40.4)**	**9.25 (9.1–9.4)**	**35.0 (29.5–41.3)**

[1] Bold, preferred estimate.
[2] See Ruff (2002) for property values for four specimens, except for F50ZP: 3,046, 1,484, 322.4, and 1,520 mm^3, respectively, in Old 67, KNM-WT 13142A, KNM-RU 2036, and MUZM 80.
[3] Use mean of Hominoid and Cercopithecoid estimates, 38.2 kg.
[4] See text.

per se, but rather related to unusual gelada-like feeding postures. Thus, humeral head size is not used in reconstructing body mass in this specimen.[4] The five body mass estimates for *T. oswaldi* average 56.4 kg, and range from 52.6–63.4 kg. Fifty percent CIs for each of these estimates are about ±5 kg. Cercopithecine equations (Table 9) give almost identical results (not shown), with a mean estimate of 56.3 kg and a range from 53.1–63.4 kg.

P. nyanzae (KNM-WT 13142A). This femur is best characterized as hominoid in proportion (Ruff, 2002), although somewhat intermediate between hominoids and cercopithecoids. Moreover, there are some other features of its postcranial skeleton that

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[4] This decision is actually justified on two grounds: both the probable nonlocomotor function of this feature (at least in terms of support of body mass), and the fact that HHSI is not recommended as a body mass predictor when locomotor mode is intermediate or "mosaic" (Table 6), as would be the case here if this feature were considered to be related to locomotion.

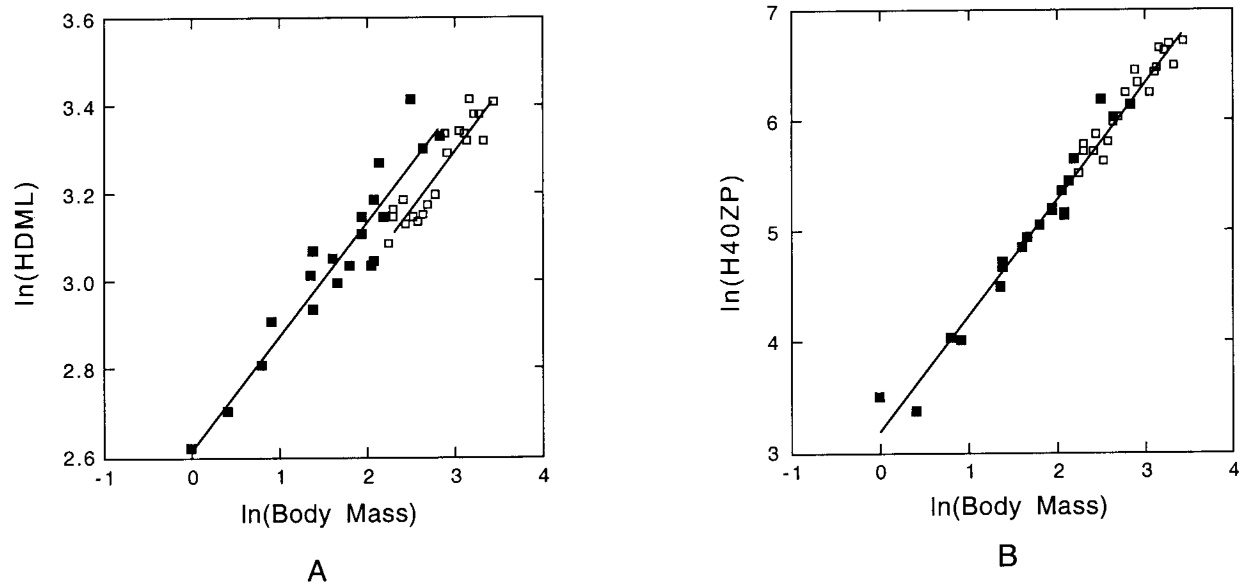

Fig. 4. Humeral distal articular M-L breadth (**A**) and mid-distal shaft (twice) average bending strength (**B**) relative to body mass in juvenile (solid squares) and adult (open squares) baboons. Least squares regression lines were plotted through juveniles and adults (lines completely overlap in B).

are distinctly nonhominoid-like (Ward et al., 1993). Thus, results from both hominoid and total sample (or cercopithecoid) equations are given, although those from hominoids are preferred. *P. nyanzae*'s two body mass estimates using the preferred hominoid equations are 32.4 and 40.4 kg, with a mean of 36.4 kg. Fifty percent CIs range from about ±3–±5kg. Interestingly, if this specimen were considered "intermediate" in morphology/function, and the total sample equation were used for FHSI and the average of hominoid and cercopithecoid equations were used for F50ZP, its overall mean body mass estimate would be almost identical, at 36.2 kg.

P. heseloni (KNM-RU 2036). The subadult *P. heseloni* femur and humerus are cercopithecoid in proportion (forelimb to hindlimb shaft strength comparison); in fact, they tend towards colobines in this respect (Ruff, 2002). However, in other respects, *P. heseloni* has been considered more hominoid-like or intermediate between hominoids and cercopithecoids in its postcranial morphology and inferred function (e.g., Walker and Pickford, 1983; Beard et al., 1986; Begun et al., 1994). Therefore, while body mass estimates using cercopithecoid equations are preferred, those from both hominoids and the total sample (when appropriate), along with colobines, are also given for comparison. In addition, some estimates based on the distal humeral articular surface of this specimen are also listed in Table 10. As shown previously (Ruff, 2002), KNM-RU 2036 has humeral articular-to-shaft proportions similar to juvenile baboons and relatively large compared to adults. The implications of the higher body mass estimates derived from this surface are discussed below.

The two cercopithecoid estimates for *P. heseloni* based on the femoral and humeral section moduli are very close: 9.4 and 9.1 kg, respectively, for a mean estimate of 9.25 kg. Estimates using the colobine equations are similar, at 9.3 and 9.6 kg. Hominoid equations yield more disparate results, as would be expected given its nonhominoid-like humeral-to-femoral strength proportions (Ruff, 2002), i.e., 11.1 and 8.8 kg. If it were considered intermediate in morphology/function, and the average of hominoid and cercopithecoid equations were used for F50ZP and total sample equation were used for H40ZP, its mean body mass estimate would be 9.5 kg, similar to that using the cercopithecoid equations. Fifty percent CIs for the preferred estimates are about ±1 kg.

The body mass estimates derived from distal humeral articular breadth in KNM-RU 2036, using any of the available equations, are much larger than those using shaft strengths (Table 10), ranging from 14.5–18.1 kg. This follows from its highly unusual (for an adult) articular-to-shaft strength proportions, which are a result of its juvenile age status (Ruff, 2002). A previous study of human juveniles (Ruff et al., 1994) indicated that shaft cross sections may track body mass more directly during development (also see Moro et al., 1996), with articulations growing ahead of body mass, on a growth curve more similar to that of stature. This hypothesis was further tested here by comparing age changes in distal humeral articular breadth and humeral shaft strength against body mass in a sample of 20 juvenile baboons drawn from the same population as the adult baboons in this study (see Ruff, 2002).

Figure 4A shows that articular size is indeed larger relative to body mass in juvenile baboons than in adult baboons. In contrast, shaft strength shows a remarkably tight and constant relationship to body mass throughout growth and into adulthood (Fig. 4B). This means that equations based on articular size in adults will overestimate body mass in juveniles, but the same equations based on shaft strength should not. In fact, this is true in baboons: adult distal humeral articular breadth (HDML) overpredicts body mass in juveniles by an average of 68.4% ± 8.8% (SE), but percent prediction error using humeral shaft strength (H40ZP) is nonsignificantly different from 0 (2.5% ± 3.6%). If the same is done for only older juvenile baboons, more developmentally similar to KNM-RU 2036 (3.8–6.7 years in females [n = 4] and 4.8–7.5 years in males [n = 4]), average %PE using HDML is 50.8% ± 16.5%, but using H40ZP, only 4.9% ± 6.2%. Thus, it seems likely that the body mass estimates for KNM-RU 2036 derived from shaft strengths are accurate with regard to its *current* (i.e., at time of death) body mass. However, the size of its fused distal humeral articular breadth strongly suggests that its *ultimate* adult body mass would have been significantly larger. The results in Table 10 indicate that body mass for this specimen may have increased anywhere from 50% to almost 100%, depending on which adult prediction equation is used (the lower value if hominoids are used). The size of the distal humeral articulation relative to shaft strength in KNM-RU 2036 is somewhat large compared to older juvenile baboons, suggesting a possibly more hominoid-like articular to shaft proportion (Fig. 10B in Ruff, 2002). More data for juvenile hominoids are necessary to fully test this possibility, which if true would also indicate a “mosaic” pattern of structural/functional proportions, since forelimb-to-hindlimb shaft strength proportions ally it with cercopithecoids (Ruff, 2002). However, the HDML hominoid-based “adult” body mass estimate for this specimen of 14.5 kg in Table 10 may also be reasonable on other grounds. The two individuals in the juvenile baboon sample best matched developmentally (dentally) with KNM-RU 2036, with erupted canines but nonerupted M3s (Walker et al., 1986), are a female weighing 9.0 kg and a male weighing 14.0 kg. Using the average adult body masses shown in Table 1, these individuals would have increased 35% and 69%, respectively, into adulthood, which if applied to KNM-RU 2036 yield estimated adult body masses of 12.5 and 15.2 kg, i.e., bracketing the 14.5-kg hominoid-based estimate.

Morotopithecus (MUZM 80). The *Morotopithecus* femur was found to be intermediate between hominoids and cercopithecoids in relative femoral head size, but hominoid-like in relative femoral condyle size (Ruff, 2002). Results using both hominoid and cercopithecoid (or total, as appropriate) equations are given for this specimen, although the hominoid equation is preferred for the femoral condyle estimate. Preferred body mass estimates range from 29.5–38.2 kg (the latter the mean of hominoid and cercopithecoid estimates from F50ZP), for a mean of 35.0 kg. Fifty percent CIs range from about ±3–±5 kg. Note that the difference in hominoid and cercopithecoid estimates from femoral condyle breadth (3.6 kg) is smaller than that from F50ZP (5.2 kg), as would be expected given earlier results (Table 6).

DISCUSSION

Factors influencing prediction error

The precision and accuracy of body mass prediction equations using long bone cross-sectional and articular properties are relatively good compared to more typically employed equations based on dental size. For example, in the comprehensive study of primates by Conroy (1987), %SEE of body mass based on M_1 occusal area was 20% within hominoids and 39% within anthropoids (analyses carried out using species means for males). This compares to %SEEs of about 10–15% for the best estimators here (Tables 3 and 4), with %PEs in the same general range (Table 5). The best predictors vary depending on the bone and the reference sample (i.e., the taxonomic/locomotor analogy used). Articular surface breadths are better predictors than articular surface areas, probably because surface areas are more closely related to joint excursion and thus joint position rather than mechanical loading per se (Ruff, 2002). Cross-sectional section moduli are better body mass predictors than shaft external breadths. This is not surprising, since external breadths, while highly correlated with section moduli, still do not reflect the total distribution of bone within a section, i.e., they do not completely represent adaptation to mechanical stimuli, including variation in medullary cavity dimensions (for further discussion, see Ruff, 2002). Thus, the extra effort involved in obtaining true diaphyseal cross-sectional parameters is justified for the purpose of body mass estimation.

Tibial cross-sectional diaphyseal dimensions are particularly poor body mass predictors except within cercopithecoids. This is very likely a result of a variable mechanical role for the fibula within anthropoids, bearing more or less of the weight (and muscular) loads, and thus affecting relative tibial shaft strength. Variation in fibular form and function among different groups of mammals is well-documented (Barnett and Napier, 1953). Anthropoids all have a “mobile” fibula (Barnett and Napier, 1953), but the robustness of the fibula relative to the tibia varies. Using data provided by Schultz (1953, his Table 1), the ratio of fibular to tibial circumference can be calculated for a number of species. Among cercopithecoids it varies from 0.446–0.500 (mean, 0.468; n = 13 sex/species means), and in hominoids from 0.520–0.624 (mean, 0.558; n = 10 sex/species means). Thus, hominoids have a relatively more robust fibula and are also somewhat more variable in this index, both of which accord with the results shown here.

The precision and accuracy of body mass estimates, as assessed by %SEE and %PE, are not the only measures of the usefulness of specific prediction equations. Another consideration is the likelihood of error when locomotor mode is misinterpreted (or cannot be assessed), or when there is no good modern locomotor analogue for a particular fossil specimen. In this case, the specificity of a prediction result to a particular locomotor group comes into play. For example, if a fossil specimen can be determined to have used its forelimb in a hominoid-like manner, then the equation based on humeral head breadth (HHSI) provides an excellent body mass prediction (Table 3). However, if locomotor affinities are uncertain, then this same structural parameter is a very poor estimator, and in fact is not recommended for use at all in this circumstance (Table 6). While this characteristic of a prediction equation can be judged in part by the size of its associated prediction errors, other considerations illustrated above also affect the degree of sensitivity to locomotor affiliations. Of the structural properties examined here, the M-L breadth of the proximal tibial articular surface is the most "locomotor blind" and also has among the smallest %SEE and %PE in the total combined sample. The M-L breadth of the distal femur has even smaller prediction errors and is almost as "locomotor blind." Other properties that demonstrate these characteristics to varying degrees include radiocarpal surface area and some cross-sectional dimensions of the femoral and humeral shafts. The choice of which properties to employ in body mass estimation, when there is a choice, will therefore depend on preliminary analyses of locomotor affinities.

Confidence intervals for individual predictions calculated from sample mean data appear to be relatively accurate, significantly underestimating true confidence limits only when sample mean equations have very small %SEEs (less than about 10%). This is based mainly on comparisons within cercopithecoids, although it is supported by additional comparisons within Asian apes. The apparent similarity in the lower limit of error when predicting individual body masses from different structural properties suggests a kind of minimum threshold of individual variability relative to body mass below which it may not be possible to extend. Thus, given biological "error," a %SEE (and %PE) of about 10–15% may be the best attainable from any skeletal parameter.

Previous studies

The results shown here are in broad agreement with those reported recently by Delson et al. (2000) for a large sample of cercopithecoids. For postcranial predictors of body mass, they included midshaft breadths and total lengths of the humerus and femur. Within all cercopithecoids and within cercopithecines and colobines separately, femoral midshaft breadths and humeral lengths were the best predictors. Mean %PE for the total cercopithecoid sample for these parameters ranged from 10–13%. Mean %PE for femoral length was 19%, and for humeral midshaft breadths 14–20%. These %PEs were calculated based on test cases consisting of mean values for sex/species (or subspecies) groups rather than individuals, as was the case here. Results shown in Figure 2 indicate that estimation errors for individuals would have been slightly larger; also, %SEEs average slightly higher than %PEs (see above). Thus, the %PEs reported in Delson et al. (2000) are comparable to the %SEEs found here for the same properties in cercopithecoids (Table 4: femoral midshaft breadths and humeral length, 15–19%; femoral length, 25%; humeral midshaft breadths, 19%).

Three other studies included cross-sectional diaphyseal measures of strength, as well as some other long bone dimensions, for body mass prediction in other orders of mammals. Anyonge (1993) measured bone lengths and cross-sectional properties of the femur and humerus in 28 species of large carnivores; femoral condyle surface area was also calculated. Percent standard errors of estimates of body mass (species mean data) using cross-sectional properties generally varied between about 10–35%, depending on property and reference group (total, felids, canids, or ursids), with the great majority over 20%. This is slightly worse than the sex/species mean results here (Table 3): the average %SEE for the total sample and hominoid femoral and humeral shaft strength equations is 16.1%; if cercopithecoid mean analyses are included, this falls to 13.7%. The generally higher %SEEs in Anyonge (1993) may be due to a variety of factors: less precise estimation of cross-sectional properties (radiographically determined rather than through CT), less precise body mass estimates (none were associated; midranges of maximum and minimum recorded weights were used in some cases), or more variability in locomotor behavior within reference groups. Bone lengths in this study, as in the present study, provided much less precise body mass estimates. Interestingly, within the total pooled carnivore sample (but not necessarily in subgroups of this sample), femoral condyle articular surface area had the lowest %SEE of body mass (below that of cross-sectional parameters), similar to results here for femoral condyle M-L breadth. This suggests that size of the knee joint articular surface in carnivores, as in anthropoid primates, may be less sensitive to locomotor differences than other structural properties.

Egi (2001) derived body mass estimation equations for 47 species of small to medium-sized eutherian carnivores and carnivorous marsupials. Bone lengths, cross-sectional diaphyseal properties, and articular surface areas and volumes were evaluated as predictors. Percent standard errors of estimates for cross-sectional and articular properties were generally 8–10%, with larger prediction errors for bone lengths, especially in combined locomotor groups. Distal femoral articular properties were again better predictors than femoral head properties, as in Anyonge (1993) and the present study. Tibial shaft properties were worse than those of the femur or humerus, again mirroring the present results, except, interestingly, in cursors, where the fibula is much reduced and ostensibly contributes little to variation in tibial loading.

Biknevicius (1999) calculated body mass prediction equations from cross-sectional geometric properties of the femur in armadillos and caviomorph rodents. Ninety-two individuals distributed among 32 species (26 caviomorph rodent species) were included. All individuals had associated body masses, although species means were used to generate equations. External breadths as well as bone lengths were also used for estimation. Percent standard errors of estimates using cross-sectional parameters ranged from 12–28%, with higher %SEEs among the more taxonomically (and presumably behaviorally) more diverse caviomorph rodents. Cross-sectional properties were considerably better estimators than external shaft breadths (28–43%SEE), and femoral length was even worse (37–49%SEE), similar to results of the present study. Including bone length as an additional predictor in multivariate equations slightly improved predictive precision from shaft breadths, but did not improve prediction from section properties. When these equations were applied to five species from another taxonomic group (pangolins), most equations produced large percent prediction errors of body mass. However, the equations from section properties in caviomorph rodents gave average %PEs of less than 15%. Biknevicius (1999) pointed out the importance of accounting for differences in locomotor and other behavioral uses of the limbs in analyses of this kind.

Other considerations

The use of multivariate rather than single-variable regression equations to predict body mass was not addressed in the present study, although such equations could easily be generated from the sex/species mean data (Appendix Tables 1A,B) and individual data (on-line data file). In several trial comparisons, it appeared that including more than one structural variable in prediction equations did not usually significantly improve prediction precision, at least over the better predictors. For example, including both FCML and F50ZP in multivariate equations results in %SEEs of 10.7%, 14.1%, and 13.3% in the total sample, hominoids, and cercopithecoids, respectively, which compares with %SEEs of 11.5%, 13.7%, and 13.8% for univariate equations using the better predictor of these two in the same samples (Tables 3 and 4). Including FCML, F50ZP, and femoral length in cercopithecoids results in a %SEE of 13.4%, only marginally better than that for F50ZP alone (13.8%). Similarly, Jungers (1987) reported that a single variable (femoral head breadth) had an SEE of body mass in a hominoid sample that was actually better than that for a multivariate equation combining this and three other articular breadths. However, in some cases, multiple variables may increase predictive precisison: including femoral length with F50ZP in hominoids results in a %SEE of 15.2%, significantly better than that for F50ZP alone in this group (20.0%). Thus, for the less precise predictors in particular, the inclusion of additional variables, if available, may be advisable.

There is one caveat to this recommendation, however: there are potential pitfalls in using multiple regression equations derived from a more behaviorally heterogeneous sample, i.e., the total combined sample here. For example, multivariate equations using FHSI, FCML, and F50ZP for *Morotopithecus* (its three predictors) give the paradoxical result of the highest body mass estimate being obtained from the total sample equation, with lower body mass estimates from both hominoid and cercopithecoid equations. This is very likely due to the same general factors observed in univariate comparisons (Table 6 and Fig. 1), caused in some cases by nonrandom association of locomotor behavior with body size. These factors are very difficult to assess in multivariate analyses. Thus, it may be best to avoid multivariate prediction equations unless locomotor behavior can be assessed and a more behaviorally homogeneous modern reference group identified.

If more than one univariate prediction equation is used, there is a question of whether the results should be averaged or whether one should be chosen or "weighted" more than the other(s). As Smith (1985, p. 447) noted, "There is little value in averaging the results of a few contradictory estimates in the hope that their average will be more accurate. When predicted values differ widely, one or more of them is wrong." One example that he gives is the estimations of body mass by Aiello (1981) in the Miocene hominoid *Dendropithecus* from humeral length and femoral midshaft diameter, which gave results differing by more than a factor of two. Of course, it seems clear from the analyses presented here, as well as elsewhere (e.g., see studies above), that the bone length estimate here is the "wrong" one and should not be used (this was recognized in the original analysis by Aiello, 1981). But there are cases where it is not clear why different estimators produce somewhat different results, e.g., for *Theropithecus oswaldi* in the present study (Table 10), where F50ZP produces an estimate of 63.4 kg, while the other four properties give estimates of 52.6–55.8 kg. The "best" estimator here in terms of %SEE (in cercopithecoids) is F50ZP, so perhaps the higher estimate should be given more weight. However, although *T. oswaldi* is most similar in proportions and probably locomotion to modern cercopithecoids, it is certainly possible, and even probable, that the mechanical loading of its limbs varied somewhat from that of any modern species. Thus, it could be argued that the most "locomotor blind" estimator available (in this case, FCML; Table 6) should be given more weight. Interestingly, this predictor gives a body mass estimate of 55.8 kg, close to the average of the five estimates (56.4 kg).

There is also a question of which confidence limits are appropriate in analyses of this kind, when more than one predictor is used. The most conservative approach would be to combine the confidence intervals for all prediction equations. However, this is inherently biased against more complete specimens, which will have more estimation parameters and thus likely a larger total range of CIs. The average body mass estimate should actually be *more* certain in these cases, assuming that all parameters are "good" estimators, since potential bias from a single estimator is reduced. Combining all estimators into a single multivariate equation (with a single CI) is one solution. However, this approach can be problematic with behaviorally intermediate or indeterminate specimens, as noted above, which is exactly where different univariate equations are likely to produce the most disparate results (e.g., see *Morotopithecus* in Table 10). Perhaps the best advice is simply to report all confidence limits for specific equations, and to use biological (as opposed to strictly statistical) judgment in interpreting these results and the likely accuracy of any prediction (see Delson et al., 2000).

Of course, there is also the issue of which confidence limits (e.g., 50%, 95%) to report. Again, if the appropriate statistics are included in results tabulations (including SEE and degrees of freedom for each equation), readers may use their own judgment and calculate any particular limits using standard t tables. Compared to the 50% CIs shown in Table 10, 95% CIs are naturally much larger (on the order of three times larger), depending on sample size of the reference group. Using this more stringent criterion, even the best estimators have wide error ranges. For example, the 95% CI of body mass for *T. oswaldi* using F50ZP is 49.1–82.0 kg. The total range of 95% CIs for this specimen using the five estimators shown in Table 10 is 38.8–82.0 kg, covering more than a twofold difference in body mass. As discussed earlier, it is possible that the better estimators here are near the limit of prediction precision for any skeletal parameter. One legitimate reaction to this information would be to simply discontinue body mass prediction in fossils. However, for several reasons discussed elsewhere (Ruff, 2000), body mass prediction is important and will continue to be so. The significance to be attached to single body mass estimates is, again, not just a statistical issue, but also a biological issue. Obtaining estimates for multiple specimens of a particular taxon will increase confidence in both statistical and biological interpretations.

Fossil specimens

The sample applications to fossil specimens were included here primarily as methodological demonstrations. However, it is of interest to compare the estimates obtained to those previously reported for the same taxa and/or specimens.

The body mass estimate of 56 kg for the *T. oswaldi* specimen (a male) obtained here is similar to previous estimates for this individual or taxon. Delson et al. (2000, their Table 16) reported mean estimates for this specific specimen of 64 kg from femoral and humeral lengths and midshaft diameters, and 55 kg from dental dimensions. Jolly (1972) gave an estimate based on combined femoral and humeral shaft breadths of 65 kg for a male from Olduvai IV and 63 kg for a male from Olorgasailie, using a modern reference sample of four sex/species means for *Papio anubis* and *Mandrillus sphinx*. Leakey (1993) gave a mean estimate of about 52 kg for three specimens from Olduvai II (presumably combined sex), including an estimate of 65 kg for the same specimen that was examined here, with estimates derived from femoral head dimensions and a modern sample of male baboons. Krentz (1993) used the method of Jolly (1972) and an equation based on femoral circumference and a diverse reference sample of Old and New World anthropoids, and obtained a mean estimate of 53.7 kg for male *T. oswaldi* from Olduvai.

The body mass estimates for the *P. nyanzae* and *P. heseloni* specimens are very similar to those obtained previously, using a similar approach but a more limited number of structural properties and/or modern taxa (Ruff et al., 1989; Rafferty et al., 1995). Because the latter specimen has figured strongly in a number of allometric comparisons (e.g., Aiello, 1981; Walker et al., 1983; Rafferty et al., 1995), and because it illustrates the complexities involved in body mass estimation in juvenile specimens, it is of interest to examine both its current (at time of death) and ultimate (adult) body mass estimates in somewhat more detail.

The body mass of KNM-RU 2036 was previously estimated on the basis of dental size as anywhere from 13–27 kg, depending on the particular dental dimension and reference group (Gingerich, 1977; Gingerich et al., 1982; Conroy, 1987). An estimate based on the M-L breadth of the tibiotalar articular surface, femoral shaft cross-sectional properties, and humeral shaft breadth, using a combined catarrhine sample (identical to the present "total sample"), was 9.8 kg (Rafferty et al., 1995). This is slightly higher than but close to that obtained here using femoral and humeral shaft strengths and cercopithecoid equations (Table 10). It is interesting that the previous estimate (Rafferty et al., 1995) of 10.6 kg from tibiotalar M-L breadth was higher than that from shaft breadths (9.3–9.4 kg).[5] However,

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[5] The distal tibial articular surface area for this specimen is 137 mm^2. Cercopithecoid and hominoid equations (Tables 7 and 8) yield body mass estimates of 9.6 and 11.3 kg, respectively, with a mean of 10.4 kg, almost identical to that obtained by Rafferty et al. (1995), using a combined reference sample.

this estimate is still well below those based on distal humeral articular breadth (Table 10). Unlike the distal humerus, the distal tibial epiphysis of this specimen was not fused (Walker and Pickford, 1983), and so was still growing (i.e., was not adult size yet), consistent with epiphyseal fusion sequences of both baboons (Bramblett, 1969) and humans (Krogman, 1962). The evidence from the distal humerus given here indicates that previous suggestions that body mass would not have increased substantially into adulthood in this specimen were probably wrong (Walker and Pickford, 1983; Walker et al., 1986; Ruff et al., 1989). A higher body mass estimate is actually more consistent with dentally based estimates (see above; the permanent dentition is also adult-sized, of course), and may indicate that *P. heseloni* was less megadont than previously suspected (Rafferty et al., 1995). (However, even with an adult body mass estimate of 14–18 kg, it is still more megadont than *P. nyanzae* and *P. major*; see Fig. 6 in Rafferty et al., 1995.) Its relative encephalization with an adult body mass of 14.5 kg (using the hominoid equation for HDML and assuming that brain growth was complete in the specimen) would be somewhat reduced from previous estimates, but still at the upper end of the range of values for modern monkeys of a similar body size range (Walker et al., 1983). Although KNM-RU 2036 has traditionally been considered a female, its craniodental morphology in this regard is ambiguous (Napier and Davis, 1959), and its M_1 occlusal area is above the mean for *P. heseloni* from Rusinga/Mfangano (62.2 mm^2; mean of 12 specimens = 56.8 mm^2; M.F. Teaford, personal communication). It is possible, then, that it was a subadult male, which perhaps would have grown to be similar in body mass to adult specimens such as KPS I (estimated body mass = 13.9 kg; Rafferty et al., 1995). Further possible ramifications of this new adult body mass estimate are beyond the scope of this paper. However, in any event, the analysis of this specimen clearly demonstrates the importance of considering factors other than locomotion per se (in this case, age-related changes in proportions; see Fig. 4; see also Ruff, 2002) in applying and interpreting body mass prediction equations.

The mean body mass estimate for *Morotopithecus* of 35 kg is within the range of values calculated by MacLatchy and Pilbeam (1999) using many of the same skeletal features. Their estimates from femoral head and bicondylar breadths are particularly close to those of the present study: using reference samples comparable to the “preferred” estimates here (Table 10), they obtained estimates of 29 kg from the femoral head and 37 kg from the condyles. Their estimates from femoral cross-sectional properties are based on equations reported in an earlier, less comprehensive study (Ruff, 1987), and are significantly higher than those obtained here, i.e., 51–54 kg. Part of this difference in results is due to their use of cortical area rather than shaft strength (section modulus) to predict body mass: the *Morotopithecus* femoral shaft has particularly thick cortices relative to its outer dimensions (Gebo et al., 1997; MacLatchy et al., 2000), resulting in a large cortical area relative to section moduli, i.e., axial compressive strength relative to bending/torsional strength. In fact, this feature of its shaft cross-sectional morphology has been interpreted as evidence in support of cautious climbing behavior, through analogy with living species exhibiting the same morphology (orangutans and lorisines; Gebo et al., 1997; MacLatchy et al., 2000). As discussed earlier (Ruff, 2002), this would be consistent with other indications from its postcranial skeleton. Shaft cortical areas were not specifically investigated in the present study, in part because they are much less useful in overall biomechanical analyses (Ruff, 2002). (Over all reference groups, they are about equivalent in predictive precision of body mass to section moduli.) The present body mass estimates for *Morotopithecus* are more internally consistent between articulations and shaft, although the total range of values, including CIs, is still relatively large. This specimen presents a good example of the problems sometimes imposed by “mosaic” morphologies relative to those of living species, which in turn may represent a good argument for preferring results from more “locomotor blind” estimators such as FCML (Table 6). This parameter gives a body mass estimate of 37 kg (Table 10), close to the average of 35 kg obtained from all three structural parameters.

CONCLUSIONS

Body mass estimation in Old World anthropoids from most long bone articular and cross-sectional dimensions is relatively precise and accurate compared to other available methods. Two general types of criteria are used to judge the usefulness of prediction equations: their prediction errors (%SEE and %PE), and the degree to which reference group assignment affects predictions. The latter criterion is most important when locomotor affliation with modern species is not clear. The most precise and “locomotor blind” estimator is M-L breadth of the proximal tibial articular surface. In general, articular breadths are preferable to articular surface areas, and section moduli to shaft breadths. Unless locomotor mode can be determined with some confidence, some parameters such as humeral head breadth are not recommended at all for body mass estimation. Tibial diaphyseal cross-sectional dimensions are poor estimators in the total sample and among hominoids, probably due to the variable biomechanical role of the fibula. Long bone lengths are generally very poor body mass estimators.

Confidence intervals calculated from sex/species means regressions appear to be relatively reasonable approximations of CIs using individuals from the same taxa, except for sex/species means equations with very low %SEEs (less than about 10%), in which case true individual CIs are likely to be considerably higher. Since the great majority of prediction equations based on means are not this precise, CIs from these equations can reasonably be applied to individual fossil specimens. It may be that there is a certain lower limit of uncertainty in individual body mass prediction from any skeletal parameter, given inherent measurement and biological "error."

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APPENDIX TABLE 1A. Sex/species means, hindlimb (see Table 2 for abbreviations, Table 1 for sample sizes).

Genus	Species	Sex	Body mass (kg)	Femur length′ (mm)	FHSA (mm^2)	FHSI (mm)	FCSA (mm^2)	FCML (mm)	F50ZX (mm^3)	F50ZP (mm^3)	F50AP (mm)	F50AB (mm)	F80ZX (mm^3)	F80ZP (mm^3)	Tibia, length′ (mm)	TPSA (mm^2)	TPML (mm)	TTSA (mm^2)	T50ZX (mm^3)	T50ZP (mm^3)	T50AP (mm)	T50AB (mm)
Pan	*troglodytes*	M	56.0	269.6	2,354	32.6	2,095	55.9	956.5	2,067.3	22.0	23.2	1,037.1	2,223.9	220.5	1,029	58.9	468	679.9	1,201.1	21.5	18.6
Pan	*troglodytes*	F	43.6	268.9	2,268	31.7	1,849	55.2	887.9	1,968.4	21.2	22.7	918.3	2,065.2	217.5	980	56.6	417	593.5	1,041.1	21.1	18.1
Gorilla	*gorilla*	M	166.4	350.2	5,851	51.3	5,558	87.0	3694.9	9,072.5	32.4	37.2	4,020.8	9,200.4	272.5	2,243	88.4	964	2,083.0	3,699.7	31.6	27.4
Gorilla	*gorilla*	F	84.5	295.6	3,619	39.7	3,168	66.4	1824.0	4,294.1	26.1	29.4	1,905.3	4,550.5	228.4	1,331	67.4	574	933.1	1,660.7	24.0	21.0
Pongo	*pygmaeus*	M	80.2	262.7	3,439	38.3	2,589	60.9	962.6	2,319.3	20.3	23.3	1,120.6	2,691.9	237.5	1,126	63.2	570	667.5	1,209.5	21.0	18.4
Pongo	*pygmaeus*	F	36.1	227.2	2,292	30.3	1,669	48.2	510.9	1,192.7	16.5	18.5	602.5	1,392.7	207.3	723	50.1	360	327.9	591.7	16.6	14.5
Hylobates	*syndactylus*	M	11.33	196.0	994	21.1	579	29.5	153.6	312.0	11.8	11.8	158.7	271.2	173.7	300	30.1	126	107.9	187.5	11.9	9.9
Hylobates	*syndactylus*	F	11.28	191.6	832	19.1	500	28.2	132.1	268.5	11.1	11.2	130.6	231.6	164.0	271	28.3	114	87.6	153.9	11.2	9.5
Hylobates	*lar*	M	5.90	199.2	579	16.5	460	24.7	91.1	182.9	10.2	10.2	94.7	155.7	168.0	222	25.9	95	87.9	148.4	11.6	9.3
Hylobates	*lar*	F	5.50	193.6	517	16.5	431	23.9	89.0	181.5	10.4	10.3	88.7	143.3	164.6	193	24.8	86	83.2	141.0	11.0	9.1
Papio	*cynocephalus*	M	23.66	253.2	1,183	23.8	1,076	37.8	429.2	873.1	16.7	16.7	424.1	686.1	220.1	629	40.8	237	488.0	850.6	19.2	16.6
Papio	*cynocephalus*	F	12.18	210.1	889	20.2	730	30.5	227.7	482.5	13.1	13.7	219.2	373.5	180.7	432	33.7	160	257.1	443.6	15.6	13.3
Macaca	*nemestrina*	M	10.31	193.0	578	17.4	608	28.2	187.4	384.9	12.9	12.7	171.3	288.0	171.7	341	30.6	153	147.8	264.8	12.8	11.3
Macaca	*nemestrina*	F	5.92	165.3	445	15.2	403	23.3	97.1	195.6	10.5	10.4	99.2	166.8	152.2	219	25.4	114	81.7	145.3	10.6	9.2
Macaca	*fascicularis*	M	4.96	135.6	377	12.9	342	20.6	75.4	155.4	9.2	9.3	79.6	162.9	123.5	172	22.6	83	60.0	103.8	9.4	8.1
Macaca	*fascicularis*	F	3.30	117.6	276	10.9	223	17.9	43.0	90.3	7.8	8.0	45.0	92.5	107.6	115	19.0	58	32.8	55.2	7.7	6.6
Nasalis	*larvatus*	M	20.95	239.8	1,054	23.2	1,003	35.1	379.0	761.3	16.3	16.2	361.7	568.5	214.7	497	36.8	253	347.9	588.2	17.5	14.9
Nasalis	*larvatus*	F	10.56	209.0	698	19.1	697	28.9	180.4	378.0	12.1	13.1	160.9	275.1	183.2	344	30.1	180	153.9	263.0	13.4	11.5
Colobus	*guereza*	M	9.49	191.3	656	17.4	524	26.6	174.2	348.6	12.6	12.5	154.9	252.1								
Colobus	*guereza*	F	7.93	183.0	628	16.4	452	25.4	132.1	272.1	11.5	11.7	117.1	197.6								
Trachypithecus	*cristata*	M	7.08	174.8	411	14.9	416	23.5	116.4	237.5	10.4	10.7	124.8	191.5	155.8	221	24.8	103	107.1	183.1	11.4	10.1
Trachypithecus	*cristata*	F	5.84	167.0	389	14.1	349	22.5	92.9	188.5	9.9	10.1	95.4	152.3	145.4	197	23.8	94	73.4	129.8	9.7	8.9
Presbytis	*rubicunda*	M	6.16	193.6	434	15.3	448	24.5	102.9	219.0	10.5	10.9	92.1	151.4	176.2	239	26.5	118	123.5	208.5	12.4	10.5
Presbytis	*rubicunda*	F	6.12	188.8	407	14.3	383	22.8	96.0	201.1	10.2	10.5	86.4	146.8	168.4	221	25.0	109	97.7	167.0	11.5	9.7

APPENDIX TABLE 1B. Sex/species means, forelimb (see Table 2 for abbreviations, Table 1 for sample sizes).

Genus	Species	Sex	Body mass (kg)	Humerus length′ (mm)	HHSA (mm^2)	HHSI (mm)	HDSA (mm^2)	HDML (mm)	H40ZP (mm^3)	H40AB (mm)	Rad/ulna length′ (mm)	RHSA (mm^2)	RCSA (mm^2)	R50ZP (mm^3)	R50AB (mm)	UTSA (mm^2)	UCSA (mm^2)	U50ZP (mm^3)	U50AB (mm)
Pan	*troglodytes*	M	56.0	289.1	1,881	39.9	1,595	44.2	1,655.9	21.4	252.4	477	446	528.4	14.7	970	106.6	566.5	14.1
Pan	*troglodytes*	F	43.6	286.7	1,891	38.4	1,421	41.3	1,491.6	20.6	250.8	424	383	441.9	13.7	806	99.2	438.1	13.1
Gorilla	*gorilla*	M	166.4	434.9	5,088	61.8	4,175	67.8	5,373.8	32.3	332.4	893	830	1,279.8	20.0	2,363	269.0	1,696.0	22.5
Gorilla	*gorilla*	F	84.5	363.2	3,157	47.8	2,278	52.3	2,671.0	26.9	283.2	562	467	617.7	16.2	1,351	181.3	790.2	17.9
Pongo	*pygmaeus*	M	80.2	371.2	3,565	48.0	2,461	48.8	2,592.7	24.9	363.9	562	617	755.5	16.6	1,351	254.9	1,029.6	18.1
Pongo	*pygmaeus*	F	36.1	321.7	2,193	38.1	1,555	39.4	1,281.3	19.5	313.0	354	399	351.0	12.6	904	166.7	435.0	13.6
Hylobates	*syndactylus*	M	11.33	270.7	918	23.6	561	23.2	272.9	11.3	299.7	193	139	96.2	7.8	311	58.7	104.0	9.0
Hylobates	*syndactylus*	F	11.28	257.5	792	21.8	530	22.1	243.4	10.9	280.0	167	121	75.0	7.3	308	50.9	87.1	8.0
Hylobates	*lar*	M	5.90	235.4	545	19.3	386	19.9	165.1	9.9	251.6	123	85	59.2	6.8	193	22.9	57.6	7.1
Hylobates	*lar*	F	5.50	226.0	485	18.1	362	19.5	157.7	9.8	249.2	130	83	57.6	6.7	168	22.0	55.5	7.0
Papio	*cynocephalus*	M	23.66	217.6	819	25.8	1,072	28.6	681.3	15.5	233.2	285	233	266.2	12.1	397	29.1	186.9	10.2
Papio	*cynocephalus*	F	12.18	181.2	536	20.8	671	23.4	346.8	12.5	192.3	184	149	138.9	9.7	257	23.4	104.0	8.2
Macaca	*nemestrina*	M	10.31	174.5	707	20.7	540	22.5	283.1	11.7	170.5	156	158	96.4	8.4	255	29.0	79.4	7.4
Macaca	*nemestrina*	F	5.92	152.0	405	16.1	376	18.5	157.8	9.6	151.3	104	100	52.7	7.1	172	17.6	41.8	6.1
Macaca	*fascicularis*	M	4.96	124.8	303	14.1	276	15.5	112.7	8.8	120.8	81	73	43.3	6.6	141	12.7	33.5	5.6
Macaca	*fascicularis*	F	3.30	110.4	202	11.9	188	13.0	60.9	7.3	104.1	56	54	21.3	5.4	94	8.5	16.4	4.5
Nasalis	*larvatus*	M	20.95	215.6	869	23.2	726	27.8	470.9	14.0	222.6	263	191	172.9	9.8	340	41.5	136.4	8.9
Nasalis	*larvatus*	F	10.56	184.8	623	19.8	456	21.8	228.2	10.9	189.6	168	131	77.2	7.3	223	28.9	56.9	6.5
Colobus	*guereza*	M	9.49	151.1	491	17.9	351	19.8	220.3	10.3									
Colobus	*guereza*	F	7.93	141.8	388	16.5	310	18.6	152.4	9.5									
Trachypithecus	*cristata*	M	7.08	141.2	276	14.5	310	17.6	157.7	9.3	133.4	97	89	48.8	6.5	167	21.0	46.2	6.1
Trachypithecus	*cristata*	F	5.84	132.8	278	14.0	283	16.4	126.3	8.7	127.2	84	81	40.0	6.1	146	17.9	34.6	5.4
Presbytis	*rubicunda*	M	6.16	132.4	276	14.1	247	16.5	107.9	8.4	152.6	90	79	39.7	5.9	139	16.3	35.7	5.6
Presbytis	*rubicunda*	F	6.12	130.0	244	13.4	214	15.2	99.9	8.2	148.2	77	73	38.3	5.9	130	14.3	32.6	5.4