AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 134:412–423 (2007)

Which Measures of Diaphyseal Robusticity Are Robust? A Comparison of External Methods of Quantifying the Strength of Long Bone Diaphyses to Cross-Sectional Geometric Properties

Jay T. Stock* and Colin N. Shaw

Leverhulme Centre for Human Evolutionary Studies, Department of Biological Anthropology, University of Cambridge, Cambridge CB2 1QH, UK

KEY WORDS osteometrics; residual strength; long bones; biomechanics

ABSTRACT Measures of diaphyseal robusticity have commonly been used to investigate differences in bone strength related to body size, behavior, climate, and other factors. The most common methods of quantifying robusticity involve external diameters, or cross-sectional geometry. The data derived from these different methods are often used to address similar research questions, yet the compatibility of the resulting data has not been thoroughly tested. This study provides the first systematic comparison of externally derived measures of postcranial robusticity, with those based upon cross-sectional geometry. It includes sections taken throughout the skeleton, comparisons of prediction errors associated with different measurements, and analysis of the implications of different methods of body size standardization on the prediction of relative bone strength. While the results show reasonable correlations between diaphyseal diameters and strengths derived from cross-sectional geometry, considerable prediction errors are found in many cases. A new approach to externally based quantification of diaphyseal robusticity based upon moulding of sub-periosteal contours is proposed. This method maximizes correlation with cross-sectional geometry ($r^2 = .998$) and minimizes prediction errors in all cases. The results underscore the importance of accurate periosteal measurement in the quantification of bone strength, and suggest that, regardless of theoretical scaling predictions, external area based robusticity estimates involving the product of diaphyseal diameters are most directly comparable to cross-sectional geometric properties when they are standardized using the product of body mass and bone length. Am J Phys Anthropol 134:412–423, 2007. ©2007 Wiley-Liss, Inc.

Skeletal robusticity, in the most general sense, refers to the strength of a bone as reflected by its size and shape. There is considerable evidence for a relationship between mechanical loading and functional adaptation in the human skeleton, resulting in differences in skeletal robusticity (see Ruff et al., 2006 for review). On this basis, studies of skeletal robusticity have a long history of application in palaeontological and bioarchaeological research. In practice, the term robusticity has been used to refer to a variety of different methods of quantifying variation in skeletal size and shape. Initially the term was used to refer to diaphyseal thicknesses standardized to bone length (Martin and Saller, 1957; Bräuer, 1988). This approach to the study of skeletal robusticity has been used in numerous studies (Collier, 1989; Pearson, 2000a; Stock et al., 2005; Wescott, 2006). Other studies have adopted more detailed means of quantifying diaphyseal robusticity, the most common of which involves the application of beam theory, in which the cross-sectional geometry of long bone diaphyses is quantified in order to estimate the mechanical competence of a bone (Lovejoy et al., 1976; Lovejoy and Trinkaus, 1980; Ruff and Hayes, 1983; Ruff et al., 1984, 1993; Bridges, 1989, 1995; Trinkaus et al., 1994; Churchill, 1996; Larsen, 1997; Trinkaus, 1997; Trinkaus and Churchill, 1999; Ruff, 2000b; Stock and Pfeiffer 2001, 2004; Stock, 2006). Using this method, the calculation of biomechanical properties of cross-sections of long bone diaphyses is dependent upon the accurate determination of periosteal and endosteal contours of the diaphysis. To avoid direct sectioning of diaphyses, non-invasive method of contour determination are commonly used, including computed tomography (Jungers and Minns, 1979; Ruff and Leo, 1986) and a method which uses a combination of silicone moulds and biplanar radiographs (e.g. Trinkaus and Ruff, 1989; Stock, 2002). The latter method has been shown to provide an accurate means of estimating cross-section contours without destruction of the sample (Stock, 2002; O'Neill and Ruff, 2004). Despite the accuracy of these methods, there are several drawbacks that restrict their widespread application: a) computed tomographic and radiographic imaging facilities are often unavailable in remote research locations, or the transport of specimens to imaging facilities is impractical; b) the cost of these methods of imaging can be highly variable depending on research context, and is sometimes prohibitive, particularly in research involving

Grant sponsor: Leverhulme Trust, Natural Environment Research Council, U.K.

*Correspondence to: Jay T. Stock, Leverhulme Centre for Human Evolutionary Studies, Department of Biological Anthropology, University of Cambridge, Fitzwilliam St., Cambridge CB2 1QH, UK. E-mail: j.stock@human-evol.cam.ac.uk

Received 20 March 2007; accepted 1 June 2007

DOI 10.1002/ajpa.20686
Published online 13 July 2007 in Wiley InterScience (www.interscience.wiley.com).

TABLE 1. Variables used to quantify postcranial robusticity

Symbol	Definition	Mechanical relevance
Circ	Diaphyseal circumference	External quantification of long bone robusticity
Robusticity Index	(Maximum + Minimum diaphyseal breadth/bone length) * 100	External quantification of long bone robusticity
Dprod	Product of the maximum and minimum diaphysis diameters	Provides the unstandardized component of the robusticity index
TA	Total subperiosteal area	External quantification of combined cortical bone and medullary area
$I_{\max}$	Maximum second moment of area	Correlate of maximum bending strength
$I_{\min}$	Minimum second moment of area	Correlate of minimum bending strength
I_x	Second moment of area, x axis	Correlate of bending strength about x-axis
I_y	Second moment of area, y axis	Correlate of bending strength about y-axis
J	Polar second moment of area	Sum of any perpendicular second moments of area, correlate of torsional strength

large sample sizes; and c) the quality of images derived from CT scanners can be inconsistent, depending upon research location, machine calibration, and the experience level of the radiographer in imaging dry bone.

In this context, the use of traditional measures of robusticity based upon external dimensions of the diaphysis may be attractive as a research option if they are shown to correspondence closely with cross-sectional geometric properties. Despite the frequent use of external morphometric methods for quantifying robusticity in the literature, their accuracy has not been systematically tested with bones of different sizes and shapes, and with a full analysis of prediction errors associated with the methods. A few studies have provided preliminary tests. Where human samples have been used, studies have compared data from the femoral midshaft only. Pearson (2000a) found a correlation of $r^2 = 0.898$ between predicted log J and log J of 137 human femora. Other studies have investigated the relationship between shape indices derived from external dimensions and those of cross-sectional geometric properties. Jungers and Minns (1979) found a strong relationship ($r^2 = 0.986$) between I_x/I_y ratios and A-P/M-L diameter ratios among femora and tibiae of seven specimens representing three species. Although high correlations such as this are common in interspecific comparisons (Smith, 1984), in intraspecific comparisons, others have found somewhat lower correlations between I_x/I_y ratios and external dimensions of the diaphyses. Two unpublished dissertations have reported correlations of $r^2 = 0.762$ (Rockhold, 1998) and $r^2 = 0.829$ (Wescott, 2001) for the relationship between I_x/I_y ratios and A-P/M-L diameter ratios (both cited in Wescott, 2006).

In addition to testing the reliability of methods, there are a number of theoretical issues which make testing of externally based methods of quantifying robusticity important. If we consider the theory of beam biomechanics further, the strength of a bone is a function of the amount of cortical bone present, and its distribution about the centroid of a diaphysis. The further away from the section centroid that skeletal mass is situated, the greater its importance in resisting bending and torsional loading (Bertram and Swartz, 1991). It follows that the periosteal contour of a bone is the most relevant to a bones mechanical competence, with the endosteal contour having less influence. While this biomechanical principle is well known, the importance of the endosteal contour relative to the periosteal contour has not been adequately investigated. From the theoretical prediction of the importance of periosteal contours, it follows that external dimensions should provide relatively accurate means of estimating overall mechanical performance. However, the accuracy will depend upon how precisely subperiosteal distribution of cortical bone can be captured using various measurement techniques.

A variety of measurements are relevant to the comparison of methods of quantifying robusticity based upon external (referring to subperiosteal dimensions of the bone shaft measurable without reference to the endosteal contour) versus internal (referring to measures of robusticity based upon cross-sectional geometry of the subperiosteal and subendosteal contours) dimensions (Table 1). The size and shape of the periosteal contour can be quantified using maximum and minimum diameters of the shaft (Larsen, 1981; Ruff, 1987; Pearson, 2000a; Wescott, 2006), shaft circumference, and the total subperiosteal area (TA) of the cross section (Saringhaus et al., 2005). The mechanical performance of a diaphysis can also be quantified by calculating maximum ($I_{\max}$) and minimum ($I_{\min}$) second moments of area, which estimate the maximum and minimum bending strengths, respectively. Second moments are also commonly calculated about the x (I_x) and y (I_y) axes of a cross-section. Polar second moments of area (J) are calculated as the sum of any perpendicular second moments of area (such as $I_{\max}$ and $I_{\min}$, or I_x and I_y) and provide an estimate of the torsional strength of a long bone diaphysis, which may be the most relevant indicator of a bones' mechanical performance (Ruff et al., 1993).

The issue of diaphyseal shape is of practical and theoretical importance in analyses of diaphyseal robusticity. A number of studies have either demonstrated a correlation between I_x/I_y ratios of the femoral midshaft and terrestrial mobility, or used variability in I_x/I_y ratios to interpret patterns of mobility in the past (Ruff, 1987, 1994; Larsen et al., 1995; Larsen, 1997; Holt, 2003; Stock and Pfeiffer, 2004). A relationship between terrestrial mobility and diaphyseal shape has also been demonstrated for $I_{\max}/I_{\min}$ ratios, which have been argued to be less sensitive to errors in diaphysis orientation prior during imaging or quantification of second moments of area (Stock and Pfeiffer, 2001). Diaphyseal shape indices have also been important in the interpretation of upper limb morphology. Neanderthal and early Upper Paleolithic hominins have higher I_x/I_y ratios of the mid-distal humerus than more recent European populations (Churchill et al., 1996), which has been interpreted as evidence for antero-posterior loading of the upper limbs (Schmitt et al., 2003). A similar pattern of humeral shape was found amongst Later Stone Age southern African women, which has been interpreted as a correlate of habitual antero-posterior loading related to the use of digging sticks and harvesting of shellfish (Stock and Pfeiffer, 2004). Several authors have estimated diaphyseal shape from maximum and minimum, or A-P and M-L shaft diameters to quantify diaphyseal shape (Bridges et al., 2000; Wescott, 2006).

Appropriate interpretation of measures of skeletal robusticity is dependent upon the accurate standardization of robusticity to body size, which is a primary influence on differences in skeletal mass. Traditional measures of robusticity based upon external dimensions are commonly standardized to bone length (Bräuer, 1988; Pearson, 2000a). While bone length can be used as a proxy for body size due to its correlation with stature, it correlates less strongly with body mass, which is a more significant influence on mechanical loading and long bone diaphyseal dimensions (Ruff et al., 1993; Ruff, 2000b). This has led to the general acceptance that measures of diaphysis cross-sectional area should be standardized to body mass, while second moments of area should be standardized to the product of body mass and bone (moment arm) length (Ruff, 2000a). Since external dimensions should be proportionate to area measures of cross-sectional geometry, Wescott (2006) standardized external dimensions of femoral diaphyses to femoral head diameter, an accepted proxy for body mass (Ruff, 1995; Ruff et al., 1997). These differences in methods of body size standardization may influence interpretations, and the compatibility of different analyses, yet their influence on interpretation has not been adequately explored. Does standardization of external metric data to bone length, body mass, or a combination of both produce data that is comparable to polar second moments of area standardized to body mass and bone length? If so, which method provides the best estimates?

The aim of this study is to test relationships between commonly used measures of robusticity, to determine the extent to which data derived from external metrics corresponds to internal cross-sectional geometric properties derived from periosteal and endosteal contours or computed tomography. The analysis also tests the importance of the endosteal contour in determining mechanical properties, by comparing cross-sectional geometric properties derived from standard cross-sectional dimensions using both a periosteal and endosteal contour, to those derived from a solid section based upon the periosteal contour only. The analyses focus on three particular questions: a) do external dimensions (maximum and minimum diameters, circumference, and total subperiosteal areas) provide accurate estimates of diaphyseal strength (polar second moments of area, J)?; b) do shape indices calculated on the basis of external dimensions provide a reasonable estimate of biomechanical shape indices (I_{max}/I_{min}, I_x/I_y)?; and c) does the standardization of external metrics to length, estimates of body mass, or the product of these body size estimate, or their product, provide a better prediction of diaphyseal strength (J)?

MATERIALS AND METHODS

This study uses external osteometric data and 1431 cross-sectional contours of claviculae, humeri, radii, ulnae, femora, and tibiae. All bones were measured and imaged at midshaft, while the humeri were additionally sectioned at the 35% location, femora at the subtrochanteric location, and tibiae at the nutrient foramen. The measurements are derived from the following populations: Andaman Islanders, Later Stone Age southern Africans, Yahgan of the Tierra del Fuego, Archaic foragers of the Great Lakes region, predynastic Egyptians, and mid dynastic Sudanese Nubians. Section locations were calculated from maximum lengths for all bones, with the exception of the ulna, which was measured without the styloid process. The maximum diameter of the femoral head was used as a proxy for body mass, and used directly in equations to estimate body mass. External dimensions of the diaphyses were quantified at the section locations using the following common measurements: maximum and minimum diameters (mm) for all diaphyseal section locations, circumference and total subperiosteal area. In addition, antero-posterior and medio-lateral diameters were measured at the femoral midshaft, as AP/ML strength ratios have commonly been used to evaluate diaphyseal morphology. In this case, ML and AP diameters were taken along, and perpendicular to, a plane defined by the alignment of the postero-distal extent of the femoral condyles. Cross-sectional geometric properties of long bone diaphyses were quantified using one of two methods: computed tomography (184 sections), or a combination of bi-planar radiographs and external moulds of periosteal contours (1242 sections) using a method previously described (e.g. Trinkaus and Ruff, 1989; Stock, 2002). Using the latter method, periosteal contours were moulded using Coltene President or Exaflex hydrophyllic polysiloxane, scanned, and endosteal boundaries estimated following the methods described in Stock (2002). Cross-sectional geometric properties were calculated using NIH Image on a Mac G4, using Moment Macro (Ruff, 2006). This process was used to calculate second moments of area (I_{max}, I_{min}, I_x, I_y) and polar second moment of area (J), which can be considered the most accurate and biomechanically meaningful estimation of bone strength, as suggested by experimental research (Lieberman et al., 2004). The product of maximum and minimum diameters (Dprod) was used to compare unstandardized shaft dimensions to unstandardized cross-sectional geometry. Where body mass standardization was used in analyses, diaphyseal second moments of area (J) were divided by the product of bone length and estimated body mass. Body mass was calculated using maximum femoral head diameter and the average of three regression equations cited in Ruff et al. (1997). This approach was used to provide greater compatibility between the results presented in this study, and those found in the literature.

The principal advantage of CT scanning or radiography is to model the endosteal contour of the section in the quantification of cortical bone distribution. Since the theory of beam biomechanics predicts that the influence of the endosteal contour will be minor relative to the periosteal dimensions, it would be useful to know whether the calculation of cross-sectional geometry based on the periosteal contour alone will generate reasonable estimates of sections quantified with a medullary cavity. If this were the case, does this method confer a significant advantage over other externally based methods? To address this question, the total subperiosteal area was measured from either CT scans or periosteal moulds taken at section locations, and an alternate set of cross-sectional geometric properties were calculated by digitizing sections without an estimated endosteal contour. In the following analysis, geometric properties calculated using both periosteal and endosteal contours will be referred to as “medullary” and properties derived from a periosteal contour only will be referred to as “solid” (Fig. 1).

Least-squares regression was used to determine the relationship between mechanical properties derived from

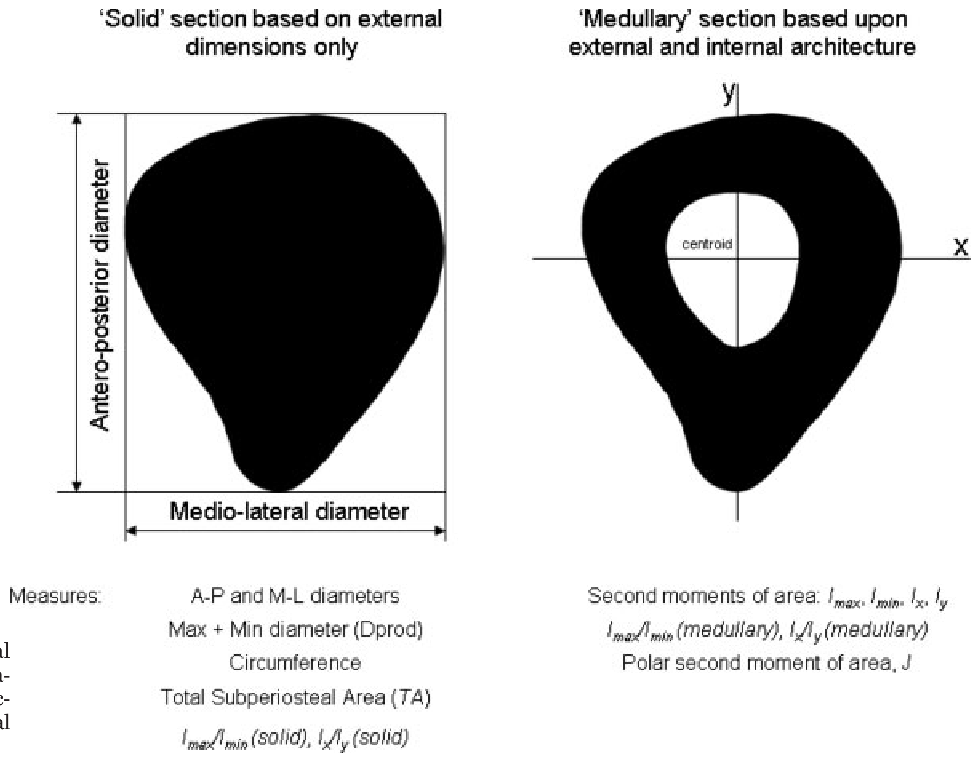

Fig. 1. Example of a femoral midshaft cross-section, with illustration of measures of skeletal robusticity based upon external and internal architecture.

periosteal and endosteal contours, versus those derived from traditional external metric data and mechanical variables estimated by periosteal contours alone. While these give a reasonable indication of the correspondence between measures of robusticity, even high correlation coefficients (r^2) often conceal considerable error in the predictive accuracy of regression equations (Smith, 1984). To investigate the relationships in more detail, the percent standard error of the estimate (%SEE) and the mean percent prediction error (%PE) were calculated for each regression (Smith, 1984), and the maximum % prediction errors reported. To investigate directional bias, average percentage bias was calculated by calculating percent prediction errors while maintaining information about the direction of errors. Calculation of these variables provides a better means of evaluating the accuracy of predictions based upon a regression formula than correlation coefficients. Raw data was $_{\log}10$ transformed prior to analysis, as the relationship between external dimensions and torsional strength is nonlinear as size increases. Log transformation was not necessary for shape indices, as there is a linear relationship between indices derived from different methods. Antilogs of predicted values were used to calculate %PE, in order for the error estimates to reflect actual differences in the prediction of bone strength. To provide a preliminary comparison of cross-sectional properties derived from CT scans versus biplanar radiographs and moulds, CT scan data was considered independently in an additional analysis.

RESULTS

The results of comparisons between unstandardized $_{\log}$external dimensions and $_{\log}$polar second moment of area are found in Table 2. These represent correlations between raw measurements of the diaphyseal size using different methods of quantification. Regressions of Dprod versus J show fairly strong correlations. When all sections are combined, the regression model produces a correlation of $r^2 = 0.979$ for the combined dataset, and $r^2 = 0.961$ for the subset of data derived from CT scans (Fig. 2). Individual correlations are lower, ranging from a high of $r^2 = 0.965$ for the mid-distal humerus (35% of length) to a low of $r^2 = 0.138$ for the tibial section at the nutrient foramen. The latter regression is likely influenced by variation in the morphology of the anterior border and interosseous crest of the lateral side of the tibial shaft at the nutrient foramen. This interpretation is supported by the somewhat lower correlations found for the comparison of data from the ulnar midshaft ($r^2 = 0.838$), which also has a highly variable interosseous crest.

When measures of $_{\log}$circumference are compared to $_{\log}J$, a similar trend is noted. While the overall correlation is slightly stronger ($r^2 = 0.983$; Fig. 3), the tibia nutrient foramen ($r^2 = 0.254$) and the ulna ($r^2 = 0.843$) have the lowest correspondence. Stronger correlations are found for regressions at the humerus midshaft and mid-distal locations, the radius midshaft, and both the subtrochanteric and midshaft locations of the femur, when compared with regressions against Dprod. In contrast to these results, the regressions of $_{\log}$TA and $_{\log}J$ produce very strong correlations of all sections, with the lowest value produced at the subtrochanteric femur ($r^2 = 0.959$). At the tibial nutrient foramen, the correlation of $r^2 = 0.974$ clearly illustrates the benefit of periosteal moulding when section contours depart significantly from approximate ellipses. The remaining correlation coefficients are all higher than $r^2 = 0.987$, leading to a very strong correspondence, ($r^2 = 0.998$, $r^2 = 0.996$ for CT derived data: Fig. 4) for the combined sample.

While these results suggest that external dimensions generally correlate strongly with cross-sectional geometry derived from internal architecture, we gain a more informed comparative perspective by investigating %SEE,

TABLE 2. Linear regression statistics[a], $_{log}$polar second moment of area (J) vs. $_{log}$external dimensions

	Model parameters and coefficients					Error					
	n	r^2	b_0	b_1	sig.	SEE	%SEE	%PE	Max %PE	BIAS %
$_{log}$ *J vs.* $_{log}$ (Dprod)										
All Sections	1287	0.979	−0.903	1.934	$P \leq 0.001$	0.09089	23.28	13.34	243.34	1.9060
All Sections (CT only)	152	0.961	−0.572	1.811	$P \leq 0.001$	0.09878	25.54	15.74	110.03	2.3918
Clavicle 50%	180	0.921	−0.862	1.921	$P \leq 0.001$	0.07951	20.09	14.82	71.31	1.6365
Humerus 50%	177	0.964	−0.738	1.888	$P \leq 0.001$	0.04916	11.99	9.02	41.70	0.4737
Humerus 35%	232	0.965	−0.857	1.915	$P \leq 0.001$	0.04241	10.26	7.71	29.99	−0.6390
Ulna 50%	127	.838	−0.773	1.849	$P \leq 0.001$	0.09883	25.55	14.33	159.96	0.0058
Radius 50%	125	0.912	−0.995	1.957	$P \leq 0.001$	0.06475	16.08	11.75	39.03	0.0002
Femur subtrochanteric	130	0.943	−0.820	1.907	$P \leq 0.001$	0.04555	11.06	8.11	43.56	−0.0002
Femur 50%	130	0.937	−0.707	1.867	$P \leq 0.001$	0.04424	10.72	7.80	37.66	−0.0001
Tibia nutrient foramen	90	0.138	2.350	0.756	$P \leq 0.001$	0.19520	56.75	37.64	192.42	−0.0002
Tibia 50%	96	0.952	−0.863	1.927	$P \leq 0.001$	0.04428	10.73	7.92	31.90	0.0002
$_{log}$ *J vs.* $_{log}$ circ										
All Sections	1199	0.983	−3.082	3.972	$P \leq 0.001$	0.08193	20.76	11.42	108.88	1.4463
All Sections (CT only)	151	0.963	−2.548	3.683	$P \leq 0.001$	0.09650	24.88	15.08	89.63	2.2312
Clavicle 50%	179	0.917	−3.275	4.108	$P \leq 0.001$	0.08134	20.60	14.85	74.70	1.7195
Humerus 50%	169	0.972	−2.721	3.773	$P \leq 0.001$	0.04369	10.58	7.64	42.88	0.3379
Humerus 35%	228	0.969	−3.108	3.998	$P \leq 0.001$	0.03921	9.45	6.85	39.27	−0.0003
Ulna 50%	127	0.843	−2.731	3.724	$P \leq 0.001$	0.09732	25.19	14.09	118.07	0.0050
Radius 50%	124	0.934	−3.303	4.100	$P \leq 0.001$	0.05616	13.80	9.87	46.15	−0.0005
Femur subtrochanteric	127	0.957	−2.959	3.917	$P \leq 0.001$	0.04011	9.68	7.15	35.01	−0.0002
Femur 50%	119	0.956	−2.584	3.703	$P \leq 0.001$	0.03773	9.08	6.43	54.25	0.0004
Tibia nutrient foramen	65	0.254	0.471	2.070	$P \leq 0.001$	0.18173	51.96	33.62	128.30	−0.0002
Tibia 50%	61	0.926	−2.566	3.709	$P \leq 0.001$	0.05155	12.60	7.18	85.51	−0.0003
$_{log}$ *J vs.* $_{log}$ *TA*										
All Sections	1431	0.998	−0.730	1.967	$P \leq 0.001$	0.03045	7.26	5.03	34.11	0.0865
All Sections (CT only)	184	0.997	−0.683	1.948	$P \leq 0.001$	0.02584	6.13	4.34	19.12	0.1746
Clavicle 50%	205	0.994	−0.670	1.930	$P \leq 0.001$	0.02108	4.97	3.76	16.40	−0.0019
Humerus 50%	217	0.992	−0.679	1.942	$P \leq 0.001$	0.02270	5.37	3.91	18.03	−0.0252
Humerus 35%	256	0.988	−0.666	1.933	$P \leq 0.001$	0.02461	5.83	4.16	23.56	−0.0001
Ulna 50%	145	0.994	−0.847	2.038	$P \leq 0.001$	0.01895	4.46	3.30	14.78	−0.0001
Radius 50%	129	0.996	−0.769	1.990	$P \leq 0.001$	0.01406	3.29	2.34	13.31	−0.0001
Femur subtrochanteric	134	0.959	−0.822	1.993	$P \leq 0.001$	0.03880	9.34	6.70	31.04	−0.0005
Femur 50%	136	0.989	−0.783	1.992	$P \leq 0.001$	0.01807	4.25	3.22	12.86	0.0000
Tibia nutrient foramen	108	0.974	−0.639	1.936	$P \leq 0.001$	0.03321	7.95	5.92	20.48	−0.0002
Tibia 50%	101	0.987	−0.826	2.023	$P \leq 0.001$	0.02290	5.41	3.99	15.38	0.0000

[a] Ordinary Least-Squares regression.

b_0, regression constant; b_1, regression coefficient (slope); SEE, standard error of the estimate; %SEE, percent standard error of the estimate; %PE, mean percent prediction error, absolute values; Max %PE, maximum percent prediction error for the estimate; Bias %, mean percent prediction error.

%PE and maximum %PE values. For the comparisons of $_{log}$Dprod and $_{log}J$, %SEE ranges from 10.3 to 56.7. The overall %SEE value of 23.28, means that 68% (or one standard deviation) of the actual values of J will fall within ±23.28% of the values of J predicted by the regression. Here, the average percent error of any estimate is 13.34, but errors range as high as 37.64% for the tibial nutrient foramen sections. Maximum percent areas for the analysis of all sections were as high as 243.3%, although the range for individual sections extended from 29.9% at the mid-distal humerus to 192.42% at the nutrient foramen of the tibia. The %SEE for the $_{log}$circumference regressions extended from 9.08% to 51.96%, with an overall value of 20.79%. The %PE for the $_{log}$circumference regression of all sections was 11.42, with a maximum %PE of 108.88. While the use of circumference appears to provide marginal improvement over Dprod when estimating bone strength, the errors of prediction are of a similar magnitude. The $_{log}$TA regressions, by comparison, are considerably lower, with an overall %SEE of 7.26, and %PE of 5.03. Percent prediction errors are under five for all bones except the subtrochanteric femur and the tibial nutrient foramen. The maximum %PE value for the entire dataset is 34.11, while individual values range form 12.86 to 31.04. Calculation of the mean percent bias of estimates demonstrates that on average, estimates of bone strength based upon diaphyseal diameters or circumferences tend to overestimate J values between 1 and 2% across all sections, however regressions for individual bones, and those based upon total subperiosteal area, converge around 0, showing negligible bias.

Table 3 presents regression statistics and error calculations for comparisons of diaphyseal shape indices, calculated at the mid-distal (35%) humerus, subtrochanteric femur, and femoral midshaft, three areas where shape indices have commonly been used. Maximum/minimum diameter ratios and I_{max}/I_{min} (solid) ratios based upon solid sections are compared to I_{max}/I_{min} (medullary) ratios calculated using both periosteal and endosteal contours. The results demonstrate that there is a reasonable correspondence between maximum/minimum diameter ratios and I_{max}/I_{min} (medullary) values, with r^2 values ranging from 0.624 to 0.786, and equaling 0.786 for the combined sample (Fig. 5). Error for these regressions was moderate, with %PE ranging from 5.86 to 6.73, and maximum %PE ranging from 24.73 to 33.49. The %SEE values ranged from 25.15 to 41.22, with a value for the combined regression of 33%. Regressions based upon periosteal moulding of a cross-section without a medullary cavity, I_{max}/I_{min} (solid), produced considerably stronger correlations and

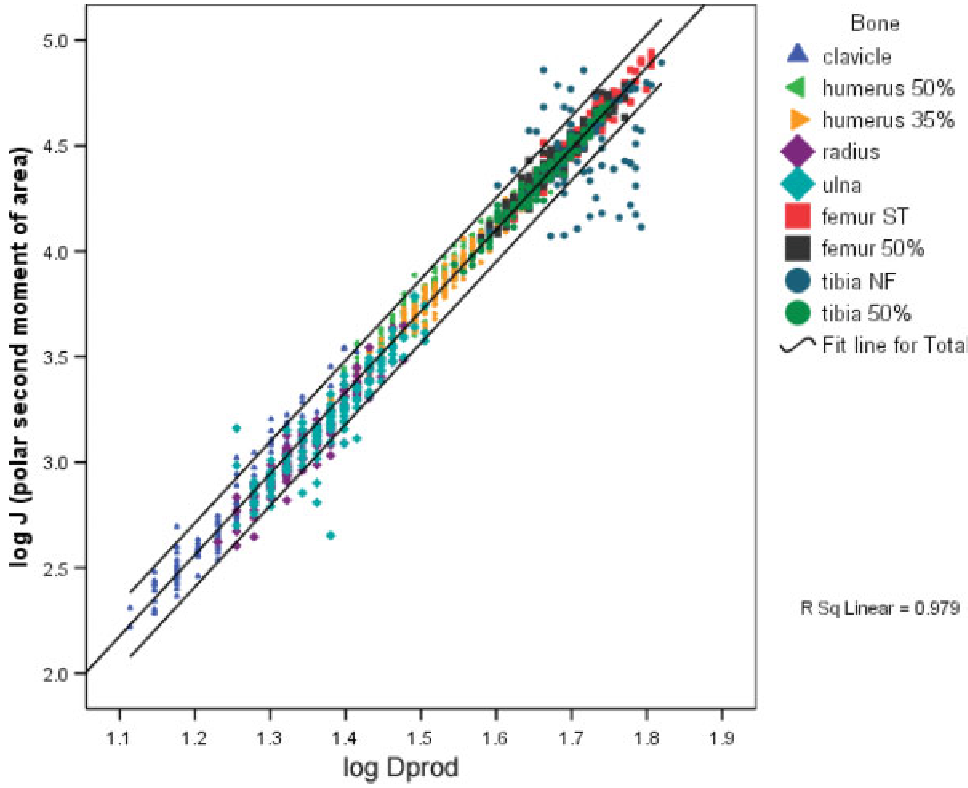

Fig. 2. Polar second moment of area versus the sum of maximum and minimum diameters. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

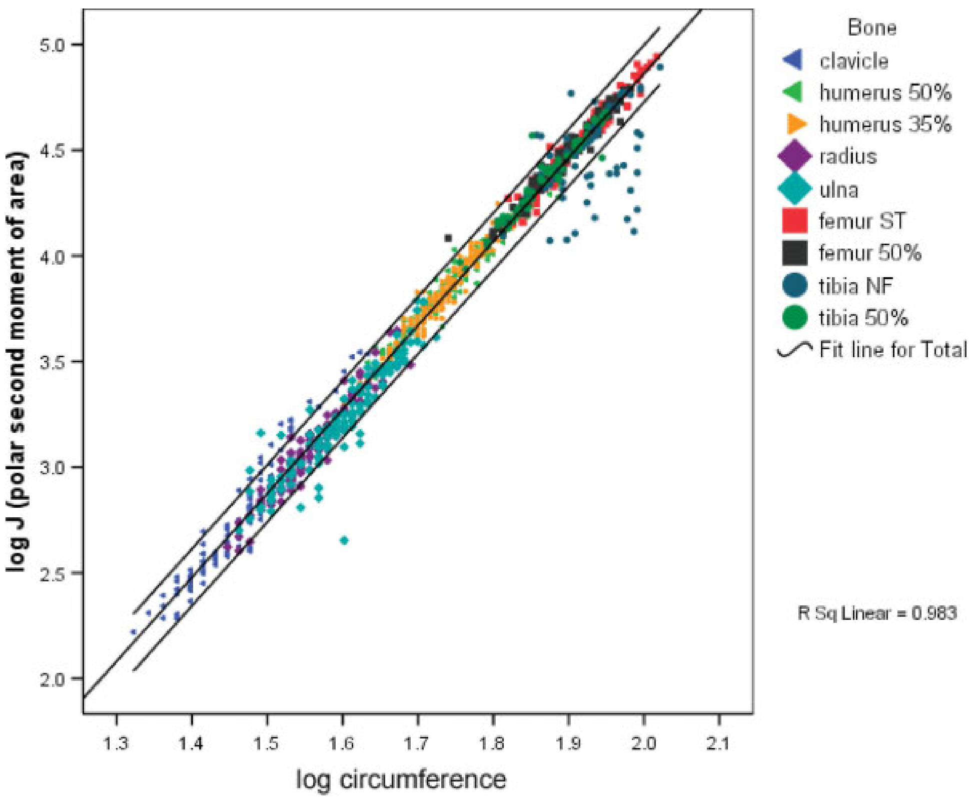

Fig. 3. Polar second moment of area *vs.* circumference. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

lower error estimates. The regression including all sections (r^2 = 0.969; Fig. 6) produced the following error estimates: %SEE = 8.67, %PE = 1.89, with a maximum %PE of 11.13, which suggest considerable improvement in biomechanical shape prediction accuracy when a periosteal mould is used to quantify external strength shape characteristics.

The calculation of I_x/I_y ratios is generally less accurate than I_{max}/I_{min}, because the orientation of the x and y axes is dependent upon the observer, rather than independent

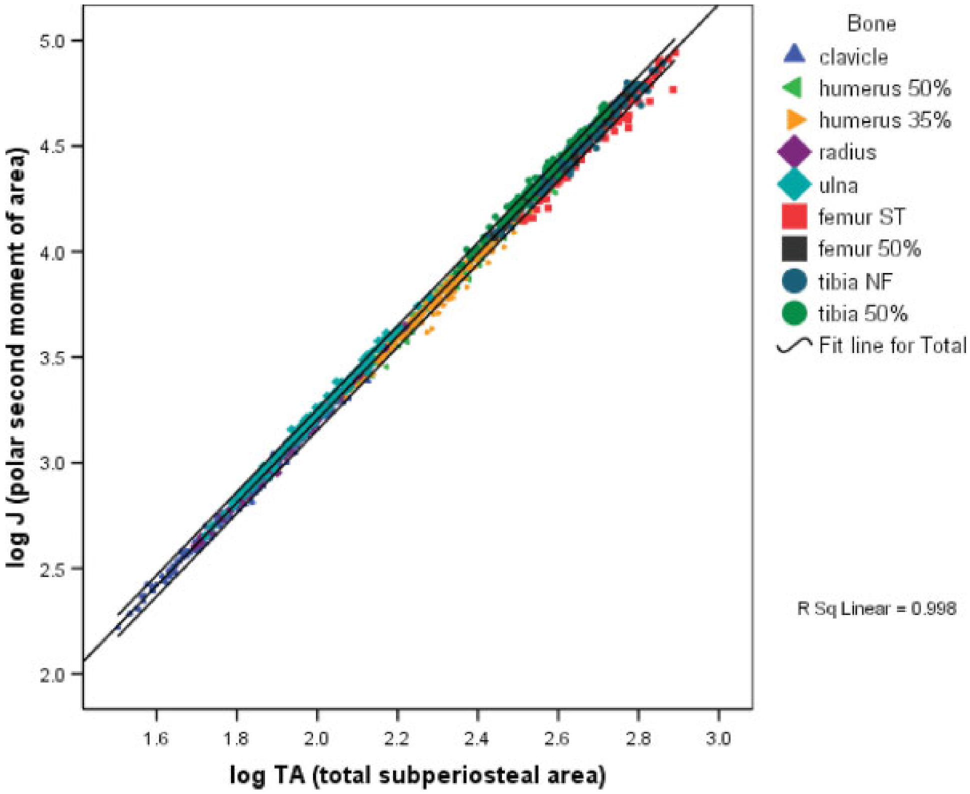

Fig. 4. Polar second moment of area *vs.* total subperiosteal area. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

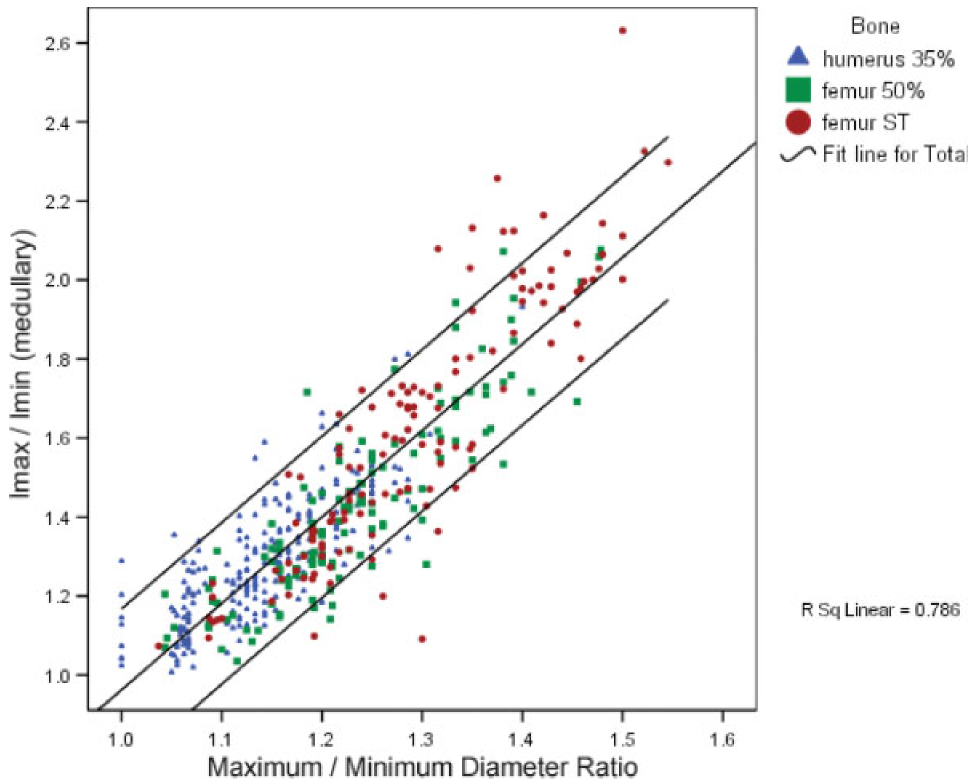

Fig. 5. Bending strength circularity index (I_{max}/I_{min} medullary) *vs.* external diaphysis shape (maximum/minimum diameter). [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

of section orientation. Since I_x/I_y ratios are commonly used to reflect anteroposterior/mediolateral dimensions of the midshaft of the femur, AP/ML diameter ratios and I_x/I_y (solid) ratios were compared to I_x/I_y (medullary) at this location. The regression of AP/ML diameter ratios against I_x/I_y (medullary) produced an r^2 value of 0.759, with mean and maximum %PE of 7.15 and 39.02%, respectively. In contrast, the regression using I_x/I_y (solid) resulted in a stronger correlation ($r^2 = 0.952$), with a considerably lower mean %PE of 2.34. While %SEE and %PE

TABLE 3. Linear regression statistics[a]*, diaphyseal shapes derived from cross-sectional geometry vs. externally based shape indices*

	Model parameters and coefficients					Error				
	n	r^2	b_0	b_1	sig.	SEE	%SEE	%PE	Max %PE	BIAS %
I_{max}/I_{min} (medullary) *vs.* max/min diam.										
All Sections	492	0.786	−1.226	2.189	$P \leq 0.001$	0.123848	33.00	6.54	33.93	0.0901
Humerus 35%	232	0.624	−0.761	1.795	$P \leq 0.001$	0.097447	25.15	5.86	24.73	0.0155
Femur ST	130	0.786	−1.753	2.611	$P \leq 0.001$	0.149900	41.22	6.73	33.49	0.0462
Femur 50%	130	0.766	−1.244	2.168	$P \leq 0.001$	0.114091	30.04	6.05	29.50	0.0466
I_{max}/I_{min} (medullary) *vs.* I_{max}/I_{min} (solid)										
All Sections	381	0.969	0.026	0.976	$P \leq 0.001$	0.036127	8.67	1.89	11.13	0.0051
Humerus 35%	231	0.940	0.036	0.968	$P \leq 0.001$	0.040061	9.66	2.06	11.24	0.0029
Femur ST	33	0.985	−0.017	1.016	$P \leq 0.001$	0.027188	6.46	1.50	5.97	0.0081
Femur 50%	117	0.986	0.031	0.973	$P \leq 0.001$	0.029121	6.94	1.62	8.12	0.0063
Femur 50% I_x/I_y (medullary)										
vs. AP/ML diameter	117	0.758	−0.998	2.016	$P \leq 0.001$	0.124745	33.27	7.15	39.02	0.0594
vs. I_x/I_y (solid)	117	0.952	0.036	0.956	$P \leq 0.001$	0.054461	13.36	2.34	19.19	−0.0157

[a] Ordinary Least-Squares regression
b_0, regression constant; b_1, regression coefficient (slope); SEE, standard error of the estimate; %SEE, percent standard error of the estimate; %PE, mean percent prediction error, absolute values; Max %PE, maximum percent prediction error for the estimate; Bias %, mean percent prediction error.

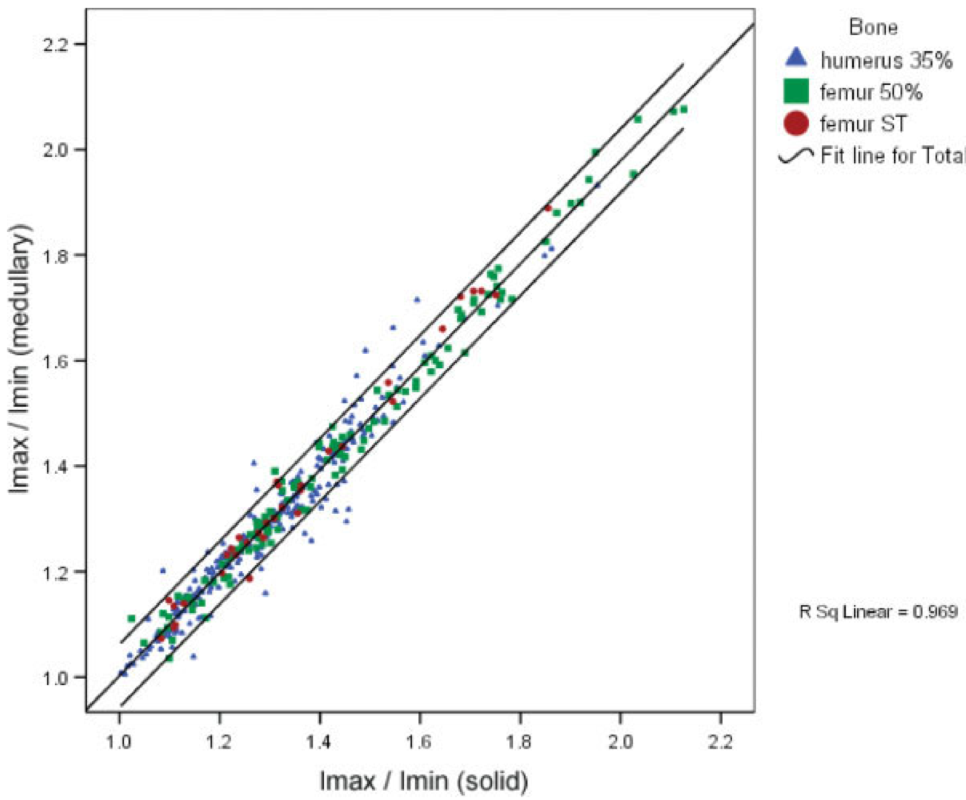

Fig. 6. Bending strength circularity index (I_{max}/I_{min} medullary) *vs.* strength circularity (I_{max}/I_{min} solid) without the medullary cavity. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

values were somewhat higher for these regressions than those involving maximum and minimum diameters and second moments of area, these differences likely reflect minor differences in section alignment during digitization. None of the methods of shape estimation appear to bias estimates to a significant degree.

The previous analyses demonstrate a consistent improvement upon prediction of diaphyseal strength and shape indices when complete periosteal contours are included in measurement protocol to quantify external morphology. An added level of complexity is incorporated when one considers that external dimensions are commonly standardized to body size using methods that differ from those commonly employed in studies of cross-sectional analyses. Table 4 compares Dprod values standardized length (cf. Pearson, 2000a), femoral head diameter (cf. Wescott, 2006), and the product of bone length and body mass, as well as total subperiosteal area (TA) standardized to the product of length and body mass, to standardized J values. It is common to standardize second moments of area such as J to the product of length and body mass, while area measurements such as TA, or Dprod, are most often standardized to body mass alone (Ruff, 2000b). Here, they have been standardized using length and body mass, in order to determine the extent to which external dimensions can be used to predict standar-

TABLE 4. Linear regression statistics[a], *$_{log}$body mass and moment arm (bone) length standardized polar second moments of area (J) vs. $_{log}$external dimensions (standardized using length, femoral head diameter, and length and body mass respectively)*

	Model parameters and coefficients					Error				
	n	r^2	b_0	b_1	sig.	SEE	%SEE	%PE	Max %PE	BIAS %
(Dprod/bone length)*100										
Clavicle 50%	151	0.334	−1.126	3.074	$P \leq 0.001$	0.23876	73.28	49.55	188.43	15.8595
Humerus 50%	161	0.678	−1.969	4.756	$P \leq 0.001$	0.16914	47.62	32.92	171.35	7.8466
Humerus 35%	209	0.513	−1.625	4.447	$P \leq 0.001$	0.18193	52.03	35.75	152.55	8.9557
Ulna 50%	102	0.496	−1.761	4.310	$P \leq 0.001$	0.19613	57.08	37.05	231.68	10.6406
Radius 50%	103	0.316	−0.769	3.240	$P \leq 0.001$	0.19069	55.13	36.29	186.68	10.0687
Femur subtrochanteric	130	0.403	−0.254	3.555	$P \leq 0.001$	0.17708	50.34	34.13	155.94	8.4653
Femur 50%	129	0.422	−0.855	4.100	$P \leq 0.001$	0.16111	44.91	31.49	167.56	7.0155
Tibia nutrient foramen	80	0.079	1.551	1.804	$P \leq 0.001$	0.21728	64.92	42.70	135.76	12.1983
Tibia 50%	92	0.488	−1.544	4.492	$P \leq 0.001$	0.16777	47.15	32.60	208.31	7.6689
(Dprod/fhd)*100										
Clavicle 50%	151	0.535	−5.175	4.570	$P \leq 0.001$	0.19960	58.34	40.40	188.79	11.1496
Humerus 50%	161	0.480	−6.608	5.061	$P \leq 0.001$	0.21490	64.02	44.78	293.61	13.4631
Humerus 35%	209	0.290	−5.062	4.259	$P \leq 0.001$	0.21958	65.80	44.81	237.02	13.4439
Ulna 50%	102	0.305	−5.164	4.336	$P \leq 0.001$	0.23029	69.94	44.99	213.68	14.5427
Radius 50%	103	0.108	−1.706	2.391	$P \leq 0.001$	0.21783	65.13	43.54	149.99	12.9126
Femur subtrochanteric	130	0.125	−1.677	2.530	$P \leq 0.001$	0.21450	63.87	42.72	203.29	12.7694
Femur 50%	129	0.068	−0.119	1.763	$P = 0.003$	0.20461	60.18	40.68	181.52	11.5174
Tibia nutrient foramen	80	0.007	4.909	−0.589	n.s.	0.22563	68.12	44.99	147.78	13.1791
Tibia 50%	92	0.180	−3.370	3.343	$P \leq 0.001$	0.21225	63.02	43.53	186.96	12.7725
(Dprod/length*BM)*100										
Clavicle 50%	151	0.852	−5.558	2.781	$P \leq 0.001$	0.11246	29.56	20.31	124.53	3.4541
Humerus 50%	161	0.935	−4.087	2.586	$P \leq 0.001$	0.07607	19.14	14.29	52.80	1.3971
Humerus 35%	209	0.936	−4.052	2.555	$P \leq 0.001$	0.06611	16.44	12.15	38.08	1.0092
Ulna 50%	102	0.863	−4.449	2.572	$P \leq 0.001$	0.10217	26.52	14.63	81.40	2.3159
Radius 50%	103	0.902	−4.496	2.555	$P \leq 0.001$	0.07231	18.12	13.07	38.89	1.2360
Femur subtrochanteric	130	0.929	−3.254	2.443	$P \leq 0.001$	0.06122	15.14	41.51	227.62	0.8175
Femur 50%	129	0.924	−3.023	2.354	$P \leq 0.001$	0.05841	14.40	10.85	49.91	0.7489
Tibia nutrient foramen	80	0.350	−0.763	1.529	$P \leq 0.001$	0.18249	52.23	34.60	194.04	8.6654
Tibia 50%	92	0.884	−3.130	2.339	$P \leq 0.001$	0.07980	20.17	15.02	64.62	1.5193
(TA/length*BM)*100										
Clavicle 50%	151	0.978	−0.066	1.763	$P \leq 0.001$	0.04293	10.39	7.68	27.89	0.3776
Humerus 50%	161	0.985	0.407	1.697	$P \leq 0.001$	0.03612	8.67	6.61	21.62	0.2107
Humerus 35%	209	0.981	0.428	1.671	$P \leq 0.001$	0.03553	8.53	6.45	20.66	0.2007
Ulna 50%	102	0.985	0.206	1.764	$P \leq 0.001$	0.03388	8.11	5.70	24.91	0.1940
Radius 50%	103	0.987	0.234	1.699	$P \leq 0.001$	0.02658	6.31	4.53	18.51	0.0819
Femur subtrochanteric	133	0.968	0.588	1.697	$P \leq 0.001$	0.04122	9.96	7.47	25.21	0.2860
Femur 50%	132	0.977	0.682	1.656	$P \leq 0.001$	0.03219	7.69	6.07	17.22	0.1227
Tibia nutrient foramen	83	0.954	0.569	1.693	$P \leq 0.001$	0.04802	11.69	8.42	28.85	0.4309
Tibia 50%	93	0.974	0.571	1.699	$P \leq 0.001$	0.03797	9.14	7.02	23.65	0.2291

[a] Ordinary Least-Squares regression.
b_0, regression constant; b_1, regression coefficient (slope); SEE, standard error of the estimate; %SEE, percent standard error of the estimate; %PE, mean percent prediction error, absolute values; Max %PE, maximum percent prediction error for the estimate; Bias %, mean percent prediction error.

dized J values, and to evaluate the impact of body size standardization on externally based metric data.

The results demonstrate that there is generally poor correlation between length standardized Dprod and standardized J values, with r^2 values ranging from 0.079 to 0.678. Average %PE values are consistently high, ranging from 31.49 to 73.28, with maximum % prediction errors consistently over 100%, and extending as high as 231% error of prediction. When Dprod is standardized to femoral head diameter correlations are considerably lower, with all r^2 values for the lower limb sections falling below 0.180, and the highest correlation at the clavicular midshaft ($r^2 = 0.535$). Mean %PE values were consistently above 40 for all sections, suggesting that most predictions of standardized J based upon FHD standardized Dprod values will be >40% different than actual values. Maximum %PE values ranged from 147 to 293, further underscoring the potential difference between predicted strength and measured strength using this approach. While the bulk of this variance is due to the different methods of standardization employed, the results underscore potential incompatibility in data published using different methods of quantification and size standardization.

When Dprod is standardized using bone length and estimated body mass, regressions show closer correspondence with standardized J values, with r^2 values ranging from 0.350 for the tibia nutrient foramen, to 0.936 for the mid-distal humerus. As found with earlier comparisons, the ulna showed the next lowest correlation ($r^2 = 0.863$), with the remainder of correlations higher than $r^2 = 0.884$. Error values associated with these regressions are considerably lower with most %PE values between 10 and 20, while the range of maximum %PE values from 38 to 227 demonstrates the potential for considerable error to be introduced in some estimates.

Comparisons of length and body mass standardized TA and standardized J values produced considerably stronger correlations. In these regressions, r^2 values were consistently high, ranging from 0.954 to 0.987. Associated with the higher correlations is a significant decrease in error associated with predicted values. Mean %PE values were consistently low, ranging from 4.5 to 8.4, with maximum %PE values ranging from 17.2 to 27.9. The consistency of these results and the relatively low prediction errors suggest that moulds of periosteal contours can be used to achieve reasonable estimates of diaphyseal strengths derived from internal architecture.

A further complication to methods of standardization is apparent when we consider the average bias of estimates. Methods based on external diameters standardized to bone length and femoral head diameter produced average positive biases of 15.9% and 11.1%, respectively, while standardization of Dprod to both length and estimated body mass reduced the positive bias to 3.5%. In contrast, the average bias of predicted J values using TA standardized to length and body mass was 0.4%.

DISCUSSION

The current study highlights the importance of accurate modeling of the periosteal contour in studies of bone strength. In all regressions, data derived from periosteal contours provided the highest correlations, greatest accuracy and minimal bias for prediction of strength derived from cross-sectional geometry. The analysis of unstandardized external metric data demonstrated that there is relatively strong correspondence between external diameters, circumference, and internal architecture. However, the range of error involved in these estimates was considerably larger than predictions derived from periosteal contours. The demonstration of an extremely high correlation between TA and J values ($r^2 = 0.998$) suggests that accurate quantification of the periosteal contour is of primary importance when estimating diaphyseal strength.

When considered collectively, the results presented here suggest that when direct sectioning, CT scanning, and radiography are unavailable to determine or estimate endosteal contours, measurement of TA provides the best externally based method of evaluating diaphyseal strength for all bones. While external diameters (Dprod) provide strong correlations and reasonable predictions of bone strength in many circumstances, diaphyseal circumference provides more accurate results when periosteal contours are irregular or feature a significant interosseous crest. Conversely, Dprod provides better estimates than circumference when diaphyses are elliptical or near circular. While percent prediction errors were quite high in some regressions involving Dprod and circumferences, those produced in the regressions between TA and J fall within the range of error generally accepted in modeling cross-sectional geometry from radiographic imaging and periosteal moulds (e.g. Trinkaus and Ruff, 1989; Stock, 2002), which underscores the quality of data derived from periosteal moulding of the diaphyses.

These results have methodological implications for the analysis of cross-sectional geometric properties of bone diaphyses. They underscore the importance of precise measurement of the subperiosteal contour in analyses of cross-sectional geometry, and suggest that a high level of accuracy can be achieved without radiographic imaging, in circumstances where scanners are unavailable. Apart from direct sectioning of diaphyses, CT scanning may still provide the best means of data collection, however, the similarities in regression coefficients for the CT and combined datasets suggest that periosteal contours are of greatest importance in determining cross-sectional properties, irrespective of whether endosteal boundaries were collected from CT scans, or estimated using biplanar radiographs. Whether using CT scans or periosteal moulds, it is necessary to ensure that the machine settings are optimized and calibrated, and high image resolution is used from scanning and moulding through to property quantification, in order to ensure the greatest accuracy in data. Further research should investigate the relationship between the accuracy of CT scanning and periosteal moulding against direct sectioning of the diaphyses in the quantification of the periosteal boundary.

The analysis of diaphyseal shape data also demonstrated reasonable correlations between ratios of diaphyseal diameters and $I_{\max}/I_{\min}$ and I_x/I_y ratios, however errors associated with these regressions were consistently more that 3× higher than shape indices derived from periosteal contours. This clearly illustrates that strength shape indices can be estimated with considerable accuracy using only external data, when the periosteal contour is accurately moulded. This underscores a further advantage of the use of periosteal moulds for external quantification of diaphyseal shape.

Size standardization is a crucial step in interpreting variation in skeletal robusticity (Ruff, 2000b). Previous studies suggest that differences in bone length between individuals and populations may cause traditional measures of robusticity (external diameters standardized to bone length), to differ from those based on estimates of bone strength standardized to body mass (Holliday, 2002). This interpretation is clearly supported by the comparison of methods of standardization here. While length standardization may be appropriate within a particular study, it may produce results that are incomparable to studies standardizing using the product of body mass and length. The combination of different methods of quantifying external dimensions of diaphyses, and different methods of body size standardization, could account for some of the variation noted in studies which utilize length standardized external dimensions (Pearson, 2000b; Wescott, 2006). Although different methods of quantifying robusticity and standardizing for body size should be sufficient to identify the most significant morphological trends, we recommend the standardization of external dimensions to both bone length and a proxy for body mass, whether femoral head diameter, or estimated body mass. This will achieve greater comparability across studies and minimize bias in reported data.

While the results presented here illustrate differences in the quality of data produced by different methods of quantification of diaphyseal size and shape, they still provide support for the use of these different methods. Of key importance is that the regression analyses did not identify significant bias in predictions based upon different methods. This suggests that while there may be considerable error about the mean in some predictions, when sample sizes are sufficiently large, observed trends in the means should be mechanically meaningful. However, the results suggest that when sample sizes are smaller, it is of key importance to minimize methodological error, in which case periosteal mould based analyses will provide better results than external metrics.

CONCLUSIONS

The current study demonstrates the importance of accurate measurement of periosteal dimensions in biomechanical analyses. The high correlations between TA and J found in this study suggest that endosteal contours have relatively minimal impact on bone strength, in circumstances where bone mass is not pathologically low. A methodological implication of these results is that the accurate modeling of the periosteal contour should be of primary importance over the modeling of the endosteal contour. When this is done through periosteal moulding, externally derived biomechanical variables provide extremely accurate estimates of those calculated from cross-sectional geometry.

ACKNOWLEDGMENTS

This research benefitted from funding from the Leverhulme Trust, and the Natural Environment Research Council, to JTS. We thank Clark Larsen and two reviewers for comments which improved this manuscript. We also thank the following individuals for access to skeletal collections under their care, or for their assistance during this research: Graham Avery, Maggie Bellatti, James Brink, Emiliano Bruner, Brunetto Chiarelli, Louise Humphrey, Robert Kruszynski, Giorgio Manzi, Jacopo Moggi-Cecchi, Alan Morris, Susan Pfeiffer, Jerry Rose, Judith Sealy, Ronald Singer, and Chris Stringer.

LITERATURE CITED

Bertram JE, Swartz SM. 1991. The "law of bone transformation": a case of crying Wolff? Biol Rev Camb Philos Soc 66:245–273.

Bräuer G. 1988. Osteometrie. In: Knussman R, editor. Anthropologie. Stuttgart: Gustav Fischer Verlag. p 160–231.

Bridges PS. 1989. Changes in activities with the shift to agriculture in the Southeastern United States. Curr Anthropol 30:385–394.

Bridges PS. 1995. Skeletal biology and behavior in ancient humans. Evol Anthropol 4:112–120.

Bridges PS, Blitz JH, Solano MC. 2000. Changes in long bone diaphyseal strength with horticultural intensification in West-Central Illinois. Am J Phys Anthropol 112:217–238.

Churchill SE. 1996. Particulate versus integrated evolution of the upper body in late pleistocene humans: a test of two models. Am J Phys Anthropol 100:559–583.

Churchill SE, Weaver AH, Niewoehner WA. 1996. Late Pleistocene human technological and subsistence behavior: functional interpretation of upper limb morphology. Quatern Nova 6:413–447.

Collier S. 1989. The influence of economic behaviour and environment upon robusticity of the post-cranial skeleton: a comparison of Australian Aborigines and other populations. Archaeol Oceania 24:17–30.

Holliday TW. 2002. Body size and postcranial robusticity of European upper paleolithic hominins. J Hum Evol 43:513–528.

Holt BM. 2003. Mobility in upper Paleolithic and Mesolithic Europe: evidence from the lower limb. Am J Phys Anthropol 122:200–215.

Jungers WL, Minns RJ. 1979. Computed tomography and biomechanical analysis of fossil long bones. Am J Phys Anthropol 50:285–290.

Larsen CS. 1981. Functional implications of postcranial size reduction on the prehistoric Georgia coast, USA. J Hum Evol 10:489–502.

Larsen CS. 1997. Bioarchaeology: interpreting behavior from the human skeleton. Cambridge: Cambridge University Press. p 1–461.

Larsen CS, Ruff CB, Kelly RL. 1995. Structural analysis of the stillwater postcranial human remains: behavioural implications of articular joint pathology and long bone diaphyseal morphology. In: Larsen CS, Kelly RL, editors. Bioarchaeology of the stillwater marsh: prehistoric human adaptation in the Western Great Basin: anthropological papers of the American Museum of Natural History. p 107–133.

Lieberman DE, Polk JD, Demes B. 2004. Predicting long bone loading from cross-sectional geometry. Am J Phys Anthropol 123:156–171.

Lovejoy CO, Burstein AH, Heiple KG. 1976. The biomechanical analysis of bone strength: a method and its application to Platycnemia. Am J Phys Anthropol 44:489–506.

Lovejoy CO, Trinkaus E. 1980. Strength and robusticity of the Neandertal tibia. Am J Phys Anthropol 53:465–470.

Martin R, Saller K. 1957. Lehrbuch der Antropologie. Stuttgart: Gustav Fischer Verlag.

O'Neill MC, Ruff CB. 2004. Estimating human long bone cross-sectional geometric properties: a comparison of noninvasive methods. J Hum Evol 47:221–235.

Pearson OM. 2000a. Activity, climate, and postcranial robusticity: implications for modern human origins and scenarios of adaptive change. Curr Anthropol 41:569–607.

Pearson OM. 2000b. Postcranial remains and the origin of modern humans. Evol Anthropol 9:229–247.

Rockhold LA. 1998. Secular change in external femoral measures from 1840 to 1970: a biomechanical interpretation, M.A. thesis. University of Tennessee, Knoxville.

Ruff C, Holt B, Trinkaus E. 2006. Who's afraid of the big bad Wolff? "Wolff's law" and bone functional adaptation. Am J Phys Anthropol 129:484–498.

Ruff CB. 1987. Sexual dimorphism in human lower limb bone structure: relationship to subsistence strategy and sexual division of labour. J Hum Evol 16:391–416.

Ruff CB. 1994. Biomechanical analysis of northern and southern Plains femora: behavioural implications. In: Owsley DW, Jantz RL, editors. Skeletal biology of the great plains: migration, warfare, health and subsistence. Washington, DC: Smithsonian Institution Press. p 235–246.

Ruff CB. 1995. Biomechanics of the hip and birth in early Homo. Am J Phys Anthropol 98:527–547.

Ruff CB. 2000a. Biomechanical analyses of archaeological human skeletons. In: Katzenberg MA, Saunders SR, editors. Biological anthropology of the human skeleton. Toronto: Wiley-Liss. p 71–102.

Ruff CB. 2000b. Body size, body shape, and long bone strength in modern humans. J Hum Evol 38:269–290.

Ruff CB. 2006. Moment macro for NIH Image and Image J. Available at http://www.hopkinsmedicine.org/FAE/mmacro.htm.

Ruff CB, Hayes WC. 1983. Cross-sectional geometry of pecos pueblo femora and tibiae—a biomechanical investigation. I. Method and general patterns of variation. Am J Phys Anthropol 60:359–381.

Ruff CB, Larsen CS, Hayes WC. 1984. Structural changes in the femur with the transition to agriculture on the Georgia coast. Am J Phys Anthropol 64:125–136.

Ruff CB, Leo FP. 1986. Use of computed tomography in skeletal structure research. Yrbk Phys Anthropol 29:181–196.

Ruff CB, Trinkaus E, Holliday TW. 1997. Body mass and encephalization in Pleistocene Homo. Nature 387:173–176.

Ruff CB, Trinkaus E, Walker A, Larsen CS. 1993. Postcranial robusticity in homo. I. Temporal trends and mechanical interpretation. Am J Phys Anthropol 91:21–53.

Saringhaus LA, Stock JT, Marchant LF, McGrew WC. 2005. Bilateral asymmetry in the limb bones of the chimpanzee (*Pan troglodytes*). Am J Phys Anthropol 128:840–845.

Schmitt D, Churchill SE, Hylander WL. 2003. Experimental evidence concerning spear use in Neandertals and early modern humans. J Archaeol Sci 30:103–114.

Smith RJ. 1984. Allometric scaling in comparative biology: problems of concept and method. Am J Physiol Regul Integr Comp Physiol 246:R152–R160.

Stock J. 2002. A test of two methods of radiographically deriving long bone cross-sectional properties compared to direct sectioning of the diaphysis. Int J Osteoarchaeol 12: 335–342.

Stock J, Pfeiffer S. 2001. Linking structural variability in long bone diaphyses to habitual behaviors: foragers from the southern African Later Stone Age and the Andaman islands. Am J Phys Anthropol 115:337–348.

Stock JT. 2006. Hunter-gatherer postcranial robusticity relative to patterns of mobility, climatic adaptation, and selection for tissue economy. Am J Phys Anthropol 131:194–204.

Stock JT, Pfeiffer S, Chazan M, Janetski J. 2005. F-81 skeleton from Wadi Mataha, and its bearing on human variability in the Epipalaeolithic of the Levant. Am J Phys Anthropol 128: 453–465.

Stock JT, Pfeiffer SK. 2004. Long bone robusticity and subsistence behaviour among Later Stone Age foragers of the forest and fynbos biomes of South Africa. J Archaeol Sci 31:999–1013.

Trinkaus E. 1997. Appendicular robusticity and the paleobiology of modern human emergence. Proc Natl Acad Sci 94:13367–13373.

Trinkaus E, Churchill SE. 1999. Diaphyseal cross-sectional geometry of near eastern Middle Paleolithic humans: the humerus. J Archaeol Sci 26:173–184.

Trinkaus E, Churchill SE, Ruff CB. 1994. Postcranial robusticity in homo. II. Humeral bilateral asymmetry and bone plasticity. Am J Phys Anthropol 93:1–34.

Trinkaus E, Ruff C. 1989. Diaphyseal cross-sectional morphology and biomechanics of the Fond-de-Foret 1 femur and the Spy 2 femur and tibia. Bulletin de la Société Royale Belge d'Anthropologie et de Préhistoire 100:33–42.

Wescott DJ. 2001. Structural variation in the humerus and femur in the American Great Plains and adjacent regions: differences in subsistence strategy and physical terrain, Ph.D. dissertation. University of Tennessee, Knoxville.

Wescott DJ. 2006. Effect of mobility on femur midshaft external shape and robusticity. Am J Phys Anthropol 130:201–213.