Allometry and Apparent Paradoxes in Human Limb Proportions: Implications for Scaling Factors

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ABSTRACT   It has been consistently demonstrated that human proximal limb elements exhibit negative allometry, while distal elements scale with positive allometry. Such scaling implies that longer limbs will have higher intralimb indices, a phenomenon not borne out by empirical analyses. This, therefore, creates a paradox within the limb allometry literature. This study shows that these apparently conflicting results are the product of two separate phenomena. First, the use of the geometric mean of limb elements produces allometry coefficients that are not independent, and that when using ordinary least squares regression must yield an average slope of one. This phenomenon argues against using the geometric mean as a size variable when examining limb allometry. While the employment of relevant dimensions independent of those under analysis to calculate the geometric mean—as suggested by Coleman (Am J Phys Anthropol 135 (2008) 404–415)—may be a partial method for resolving the problem, an empirically determined, independent and biologically relevant size variable is advocated. If stature is used instead of the geometric mean as an independent size variable, all major limb elements scale with positive allometry. Second, while limb allometry coefficients do indicate differential allometry in limb elements, and thus should lead to some intralimb index allometry, this pattern appears to be attenuated by other sources of limb element length variation. Am J Phys Anthropol 144:382–391, 2011.   ©2010 Wiley-Liss, Inc.

Researchers have argued that humans have significant limb segment length variance. Many studies of hominid limbs have implicated thermoregulation, nutrition, locomotion, and ancestry as influential factors on both intralimb proportions (i.e., brachial and crural indices) and relative limb length (e.g., cormic index). Following Allen's "rule" and the "thermoregulatory imperative" (Mayr, 1956; Ruff, 1991, 1993), studies of samples from a global distribution have demonstrated an empirical, clinal pattern in intralimb proportions among modern humans and other hominids (Trinkaus, 1981; Ruff, 1994; Holliday, 1997, 1999; Auerbach, 2007; Temple et al., 2008). Moreover, the majority of these studies implicate climatic factors—especially temperature—as an influential factor in the development of these clines. Additional studies have shown, however, that nutritional and stress factors likely affect total limb length, as well as the proportion of limb length to stature (Takamura et al., 1988; Jantz and Jantz, 1999; Bogin et al., 2002; Malina et al., 2004; cf. Auerbach, 2010a), though these may be partially dependent on individual genetics (Golden, 1994). In fact, recent studies strongly indicate a hereditary component to the development of intralimb indices during primary growth (Eleazer et al., 2010; Temple et al., in review), while the relative length of limbs to measures of body length (stature or torso length) vary throughout ontogeny (Humphrey, 1998; Bass et al., 1999; Ruff, 2007).

Allen's rule and thermoregulation, as currently conceived, argue that total surface area relative to volume—and therefore total extremity length—is the determinant factor in heat dissipation. That is, individuals with longer limbs relative to torso length or overall body size (i.e., mass, stature) dissipate heat more efficiently than individuals with shorter relative limb lengths. This relationship was demonstrated in morphological changes following migration of modern humans to Europe (Holliday, 1997), although this pattern has not been found as clearly in the Americas (Auerbach, 2007; Auerbach and Ruff, 2010). Intralimb indices also have moderately high correlations with latitude and climatic factors (Holliday, 1997; Auerbach, 2007). Although both limb lengths and limb indices exhibit relationships with climate and latitude, limb lengths and limb indices do not show a strong relationship with each other (Fig. 1 in Holliday, 1999), with the possible exception of crural indices among very tall individuals (see below).

While at first this relationship may appear paradoxical, as demonstrated by Holliday and Ruff (2001), the relative scaling and contribution of the proximal versus distal element in determining indices is obscured in the calculation of brachial or crural indices. Stated simply, a great amount of variation in the location of the division between proximal and distal elements within limbs (e.g., the elbow) occurs among individuals, even within a single population. Ironically, the Ruff and Holliday (2001)
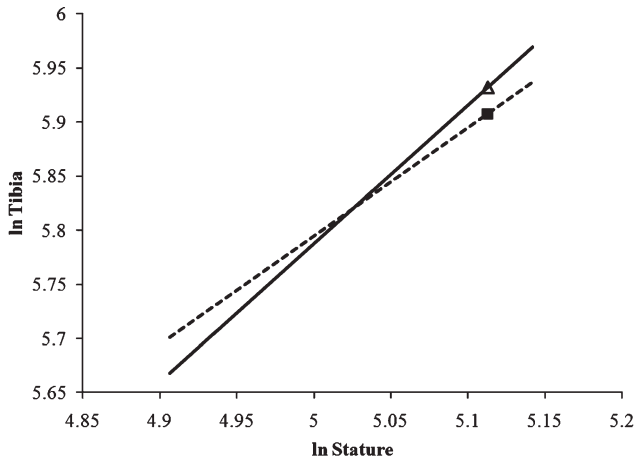
Fig. 1. Prediction of bone lengths for individuals following allometric and isometric trends. The solid line represents the empirically determined population allometric trend. The dashed line is the simulated isometric trend between tibial length and stature. The filled square is the predicted tibial length for an individual with a given stature given an isometric relationship, while the open triangle is the tibial length for the same individual predicted from the observed allometric trend.

paper and subsequent studies (Sylvester et al., 2008; Temple et al., 2008; Auerbach, 2010a) have introduced a paradox in documenting scaling within limbs: proximal elements have been shown to have negative allometry or isometry, while distal elements have positive allometry. Because of the different amounts of variance in proximal versus distal elements (Holliday and Ruff, 2001), the allometric patterns lead to a conclusion that longer limbs inherently have higher intralimb indices; the numerators in indices—distal elements—increase disproportionately relative to the denominator values, the proximal elements. A derivative paradox resulting from these studies, as well as previous allometric analysis (Jantz and Jantz, 1999), suggests that taller individuals should have higher crural indices due to positive allometry in the tibia, though this is not always the case (Auerbach, 2010b).

The purpose of this study was to investigate and resolve this paradox of differential allometry within limbs that does not result in intralimb index allometry. This is an issue of body size allometry as defined by Smith (1993), even though it is intraspecific. In the case of all of the aforementioned studies that present the paradox, allometries were calculated using the geometric mean of the four limb lengths under consideration (following Mosimann, 1970; Mosimann and James, 1979) or using Jolicoeur's (1984) multivariate test. As demonstrated by Coleman (2008), however, the effects of dimensions used to calculate the geometric mean can create bias in studies of scaling. Indeed, the geometric mean may not be a biologically meaningful, independent morphological dimension (Jungers et al., 1995). The geometric mean depends on the biological relevance of the dimensions used in its calculation, and the allometric relationships of these variables to each other and body size, as will be explored in this article. That is, any interpretation about the allometry of dimensions is dependent on the variables used to calculate the geometric mean. We therefore hypothesize that the apparent paradox may, in part, be a product of using the geometric mean in investigating allometry. For these reasons, the allometry of limb element lengths is assessed against

stature as well as the geometric mean. The results of these two scaling analyses were then compared to elucidate the influence different scaling factors have on models of allometry within the limbs. Furthermore, limb allometries may be statistically significant but result in small morphological differences obscured by other sources of variation (e.g., stochasticity in limb dimensions arising from asymmetry). These other sources of variation may obscure allometric patterns between intralimb indices and limb lengths. Therefore, the morphological magnitude of any observed allometries will also be examined.

MATERIALS AND METHODS
Sample and measurements

A total of 1,007 adult indigenous American skeletons (560 males, 447 females) dating to before European colonization were measured for this study by one of us (BMA). The majority of these (967 skeletons) are identical to the sample used in Auerbach and Ruff (2010); see Table 1 in that paper for a list of sites sampled. The additional skeletons (25 males, 15 females) were added from the Huari necropolis located at Ancón, Peru, housed at the Field Museum of Natural History (Chicago, IL). Limb dimensions used in the calculation of brachial index (humerus maximum length and radius maximum length) and crural index (femoral bicondylar length and tibial maximum length) were taken on all skeletons, bilaterally where possible to minimize the effects of directional asymmetry (Auerbach and Ruff, 2006). As demonstrated by various authors in recent papers, humans in the Americas demonstrate the greatest range of human intralimb proportions, or at least ranges comparable with those observed in the Old World (Auerbach, 2007; Auerbach and Ruff, 2010; King, 2010); indigenous humans from the Americas are deemed sufficiently diverse to fully assess the allometry paradox. Sex and age were estimated using the methods described in Auerbach and Ruff (2010). All skeletons presented the necessary elements for the estimation of living stature using the revised Fully anatomical technique (Raxter et al., 2006, 2007), which were calculated for each.

Although body mass is generally considered to be the scaling factor of choice in size allometry (Jungers, 1985; Hens et al., 2000), stature is used herein. Stature was chosen as it is in the same dimensional space as the linear limb element dimensions. Body mass may be estimated from the femoral head (Auerbach and Ruff, 2004), and so the diameter femoral head could be used as an alternative to avoid taking the cube root of a dimension (body mass) that would itself need to be estimated. However, the femoral head has its own positive allometry in relation to body mass (Ruff et al., 1991), making it a poor choice as an independent scaling factor. In addition, as the Fully technique takes proportions into account in its calculation, its use as a stature estimate minimizes potential tautologies that would arise from mathematically (regression) derived size measurements, as well as preventing the use of a nonindependent scaling factor for intralimb indices.

Analyses

Effect of independent size variables on allometry coefficients. To explore the effect of using different size variables as independent variables in allometric regression

analyses, bone lengths (humerus, radius, femur, tibia) were regressed against both the geometric mean of the four bone lengths and statures in natural log space. We used ordinary least squares (OLS) regression, which is appropriate when one variable is unquestionably the criterion (Smith, 2009), and then compared the allometry coefficients using the two size variables. In all analyses, isometry is indicated by a slope of one. This and all other analyses were carried out separately for male and female samples.

Morphological comparison of allometric (empirical) and isometric (simulated) populations. Another goal was to assess the morphological consequences of allometric trends within our populations. To do this, we used two populations: one in which individuals followed the empirically determined population allometric trends; the other in which all individuals were created using simulated isometric trends.

Each bone length was regressed against stature in natural log space to determine the empirical allometric slopes. We then predicted logged bone lengths from the resulting regression equations and the logged statures from our samples (i.e., we calculated expected values) (Fig. 1). As noted earlier, OLS regression was utilized for this procedure as it has been shown that Model I regression techniques are preferable in cases of prediction (Hens et al., 2000; Smith, 2009). We then simulated an isometric population using the same logged statures, but under the requirement of isometry. To do this, we created isometric regression equations relating logged bone lengths to logged stature, which by definition had regression slopes of one. Then we established intercepts such that the regression lines passed through the population means, and then calculated isometric bone lengths from the simulated isometry slopes using logged statures (Fig. 1).

The result was two sample populations in which an individual (with the same stature in both populations) had two different simulated lengths for the same bone. One length was a natural log of the expected value for a given stature (i.e., falling on the regression line) as determined the empirical population allometric trends; the other length was predicted under the principle of isometry. As all predictions were calculated in natural log space, we took the antilog of predicted values to get actual bone lengths. We then followed procedures (smearing estimator, ratio estimate, and quasi-maximum likelihood estimator) advocated by Smith (1993) to estimate a correction factor for antilog bias, although these did not produce an appreciable difference in estimates (less than 0.5 mm in all cases).

To determine the actual impact of the empirically determined allometry on bone lengths, we subtracted bone lengths of the isometrically created individual within a pair from the allometrically created individual. Summary statistics for both signed and absolute differences are reported.

The effect of increasing population variance on intralimb index correlations. The next goal was to determine if other unspecified sources of limb bone variation (e.g. random variation, fluctuating asymmetry, or measurement error) could obscure allometric signals when regressing intralimb indices (the quotient of distal and proximal elements) against limb lengths (the sum of distal and proximal elements). This was modeled starting with expected values for bone lengths for each individual based on the empirically determined allometric regression equations relating stature to bone lengths in natural log space (Fig. 2). We then artificially increased
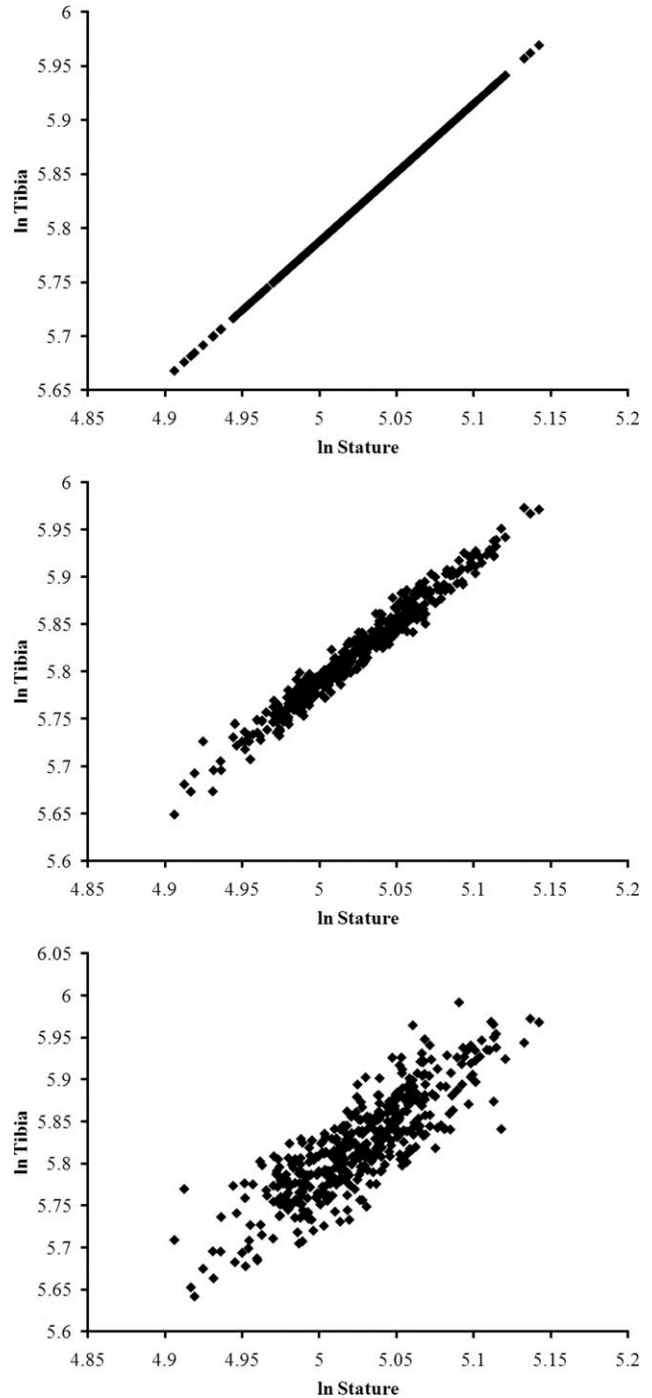

Fig. 2. Simulations of population variance with increasing residuals. Residuals are based on different proportions of the empirically determined standard deviation of the regression residuals: (**A**) a proportion of 0; (**B**) a proportion of 0.1 (i.e., 10% of the observed standard deviation); (C) a proportion of 1.1 (i.e., 110% of the observed standard deviation).

variation in bone length by adding modeled residuals to the expected bone length values. Simulated residual values were based on the standard deviation of the original data regression residuals and were generated in Matlab R2009b using pseudorandom number generator (Matlab v 7.9; Mathworks). These residuals were modeled such that they would have a simulated standard deviation

TABLE 1. *Female allometry coefficients*

Scaling factor	Humerus	Radius	Femur	Tibia
Stature	1.03	1.25	1.12	1.28
Geometric mean	0.89	1.12	0.90	1.08

TABLE 2. *Male allometry coefficients*

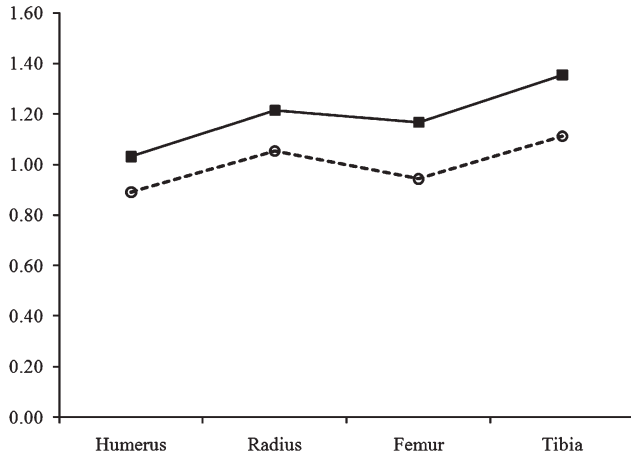| Scaling factor	Humerus	Radius	Femur	Tibia
Stature	1.03	1.21	1.17	1.35
Geometric mean	0.89	1.05	0.94	1.11

Fig. 4. Female allometry coefficients. The dashed line links the coefficients (open circles) of allometry coefficients calculated using the geometric mean. Allometry coefficients calculated using stature as the scaling factor (filled boxes) are connected using a solid line.

Fig. 3. Male allometry coefficients. The dashed line links the coefficients (open circles) of allometry coefficients calculated using the geometric mean. Allometry coefficients calculated using stature as the scaling factor (filled boxes) are connected using a solid line.

that was a specific proportion of the standard deviation of the original, empirically determined allometry residuals. This proportion was varied from 0 to 2 times the observed standard deviations at 0.1 increments. For instance, in the second modeling simulation, the modeled residuals had a standard deviation that was 0.1 (i.e. 10%) of the standard deviation of the original data residuals (Fig. 2). In the first simulation, when the proportion of zero was used (i.e., all bone lengths had residuals of zero, and so plotted on the regression slope), the allometric trend explained 100% of the variance in the simulated bone lengths. Increasing the magnitude of the residuals increased the variance in bone length not attributable to the allometric trend.

The modeled bone lengths (expected lengths plus modeled residuals) were regressed against statures in natural log space to ensure that simulated populations reflected the original population allometry. Simulated populations were discarded if the slope of the modeled data fell outside the 95% confidence interval of the original data regression slope. We took the antilog of the modeled limb lengths and of statures, and then calculated Spearman's rho correlation coefficients between proximal and distal limb element lengths (e.g., humerus and radius), each bone length and stature, and intralimb index and limb length (e.g., crural index and the sum of femoral and tibial length). For each of these comparisons, we averaged the correlation coefficient of 1,000 populations simulated at each of the standard deviation proportions. Thus, in total, 21,000 populations were
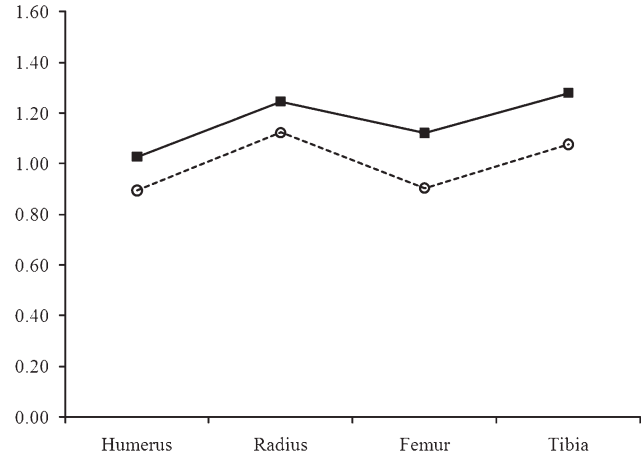
simulated, 1,000 at each of 21 different magnitudes of modeled residuals.

All statistics and simulations were conducted using Matlab R2009b (Matlab v 7.9; Mathworks).

RESULTS

Female and male allometry coefficients for all limb bone lengths regressed against the geometric mean of bone lengths and stature are provided in Tables 1 and 2 and in Figures 3 and 4. The allometric patterns for the limbs are similar using either stature or geometric mean as the size variable, although absolute values are quite different. For the male sample, the pattern of relative allometry among the limbs remains exactly the same independent of which size variable is used (Fig. 3). The male humerus coefficient is the lowest, followed increasingly by the femur, radius and tibia. In the female sample, the relative values of the coefficients change slightly between the size variables (Fig. 4). Using stature, the pattern follows the male pattern (humerus < femur < radius < tibia), but when using the geometric mean, the radius appears slightly more positively allometric than the tibia. In both the male and female sample, the use of the geometric mean as the size variable changes the absolute value of the allometry coefficients; utilizing the geometric mean translates the coefficients down from their values relative to stature. A consequence of this translation is that they have a mean of one, which has important implications for the use of the geometric mean (see the Discussion).

Summary statistics for the morphological difference between limb lengths predicted based on stature and either population allometric trends or isometric scaling are provided in Tables 3 and 4. Included are results for both directional (signed) and absolute differences. For both male and female samples the mean signed difference is small, less than 0.3 mm. Mean absolute differences, however, are larger and range from just above 0.3 mm up to approximately 4.5 mm. While mean values are all subcentimeter, maximum values indicate that in

TABLE 3. Summary statistics for morphological differences between allometrically and isometrically predicted limb lengths females (mm)

	Humerus		Radius		Femur		Tibia	
	ABS	SIGN	ABS	SIGN	ABS	SIGN	ABS	SIGN
Mean	0.26	0.01	1.77	0.10	1.60	0.09	3.08	0.18
Minimum	0.00	−0.84	0.00	−5.70	0.00	−5.17	0.01	−9.87
Maximum	1.03	1.03	7.21	7.21	6.44	6.44	12.53	12.53
Standard deviation	0.19	0.32	1.34	2.22	1.20	2.00	2.33	3.86

ABS, absolute differences; SIGN, signed differences. Signed differences = allometric predicted − isometric predicted.

TABLE 4. Summary statistics for morphological differences between allometrically and isometrically predicted limb lengths males (mm)

	Humerus		Radius		Femur		Tibia	
	ABS	SIGN	ABS	SIGN	ABS	SIGN	ABS	SIGN
Mean	0.33	0.02	1.75	0.10	2.42	0.14	4.35	0.27
Minimum	0.00	−1.17	0.00	−6.19	0.01	−8.60	0.01	−15.24
Maximum	1.41	1.41	7.66	7.66	10.57	10.57	19.22	19.22
Standard deviation	0.25	0.41	1.34	2.20	1.85	3.05	3.34	5.48

ABS, absolute differences; SIGN, signed differences.
Signed differences = allometric predicted − isometric predicted.

some cases the difference between allometrically and isometrically generated individuals is quiet large, close to 20 mm. This is, however, an extreme case, if the largest 1% of absolute differences are removed, then the largest value is approximately 13 mm.

As described in the Materials and Methods, correlation coefficients were determined between various dimensions using simulations of different data dispersions around the allometric regression slope; these consist of regression residuals calculated from proportions of the standard deviation of the empirically determined residuals. The mean of these, calculated from 1,000 simulated populations, are presented in Tables 5 and 6, as well as Figures 5 through 8. Table 5 have the correlations for the female upper limb and lower limb simulations (visually demonstrated in Figs. 5 and 6), while Table 6 have the correlations for the male simulations (shown in Figs. 7 and 8). In all cases it is apparent that although proximal and distal limb elements can maintain relatively high correlations with stature (Spearman's $\rho = 0.6–0.8$), correlations between proximal and distal limb elements decline more rapidly as the modeled residuals become larger. Even more striking is the precipitous decline in correlations between intralimb index and limb length. When the simulated residuals are only 0.5 (50% of the standard deviation) of that observed in the empirical data, the correlations between intralimb index and limb length are already at or below 0.40. These correlations continue to decline rapidly approaching approximately $\rho = 0.15$. Even when the modeled residuals are of the same magnitude as the original data (proportion = 1, or the observed standard deviation), the correlation between intralimb index and total limb length is about 0.20.

DISCUSSION

Allometric coefficients calculated using the geometric mean corroborate the patterns shown by all of the previous studies of limb allometry discussed in the Introduction. The results also show that the choice of the scaling factor has an important effect on the concluded pattern of allometry within limbs. Allometry coefficients of scaling limb element lengths against stature and against the geometric mean yield similar patterns overall, though the actual coefficients differ notably. Importantly, when scaled against the geometric mean, the allometry coefficients yield positive (e.g., radius) and negative (e.g., humerus) values, while these same bones all demonstrate positive allometries when scaled against stature. As stature is at least partially independent of the lengths of limb bone elements, and therefore what we argue to be a better indicator of size, this discrepancy is striking. Yet, which pattern reflects biological reality?

While the geometric mean is regarded a good approximation of size in the absence of empirically measured dimensions, such as body mass (Mosimann, 1970; Falsetti et al., 1993), it is fundamentally a mathematical construct of the dimensions that are employed in its calculation. The results presented above indicate that scaling by the geometric mean of the dimensions of interest may generate allometric coefficient patterns that match those calculated using other scaling factors, though the values are transposed due to the nature of the geometric mean. That is, all of the coefficients calculated using the geometric mean as the size variable must average to one when using OLS regression; the mathematical proof for this phenomenon is provided in the Appendix at the end of this article. The general conclusion from this proof is that any positive slopes for dimensions calculated against the geometric mean *necessitate* negative slopes from other dimensions. This result would be true using other regression procedures (e.g. reduced major axis) or multivariate techniques (principal components analysis) although the mathematical relationship would be different. Coleman (2008) also demonstrated that the choice of dimensions could bias the results of analyses when using the geometric mean. His recommendation was to choose dimensions that are independent of dimensions under analysis (while remaining relevant to the representation of size) to calculate the geometric mean. While this offers a potential solution, the dimensions used to calculate the geometric mean may have their own allometric relationship relative to real biological size. As noted in the Materials and Methods, for example, femoral head—though a linear dimension—would be a poor scaling factor as it has a known (positive) allometry relative to body mass. In such a case, it would be difficult to determine which variable was driving any found allometry, the variables of interest or the variables used to calculate the geometric mean.

The implications of the proof and of the observed pattern argue against the use of the coefficient values generated using the geometric mean. Stature, which is used as an alternative dimension, provides an independent and biologically meaningful measurement against which linear dimensions may be scaled. Indeed, the resulting coefficients from scaling against stature are more easily interpreted: all limb

TABLE 5. Female simulation results for brachial index and crural index

Proportion of standard deviation	Correlation coefficient (ρ)			
	Between radius and humerus	Between humerus and stature	Between radius and stature	Between brachial index and upper limb length
0.0	1.00	1.00	1.00	1.00
0.1	0.99	1.00	1.00	0.88
0.2	0.98	0.99	0.99	0.68
0.3	0.95	0.98	0.97	0.53
0.4	0.92	0.96	0.96	0.43
0.5	0.88	0.94	0.93	0.36
0.6	0.84	0.92	0.91	0.32
0.7	0.79	0.90	0.88	0.28
0.8	0.74	0.87	0.85	0.25
0.9	0.69	0.84	0.82	0.24
1.0	0.65	0.82	0.79	0.22
1.1	0.60	0.79	0.76	0.21
1.2	0.56	0.76	0.74	0.20
1.3	0.52	0.74	0.71	0.19
1.4	0.48	0.71	0.68	0.18
1.5	0.45	0.69	0.66	0.18
1.6	0.42	0.66	0.63	0.17
1.7	0.39	0.64	0.61	0.17
1.8	0.36	0.62	0.59	0.17
1.9	0.34	0.60	0.57	0.17
	Correlation coefficient (ρ)			
	Between tibia and femur	Between femur and stature	Between tibia and stature	Between crural index and lower limb length
0.0	1.00	1.00	1.00	1.00
0.1	1.00	1.00	1.00	0.86
0.2	0.99	0.99	0.99	0.65
0.3	0.97	0.99	0.99	0.50
0.4	0.95	0.98	0.97	0.40
0.5	0.93	0.97	0.96	0.33
0.6	0.90	0.95	0.95	0.29
0.7	0.87	0.94	0.93	0.26
0.8	0.84	0.92	0.91	0.24
0.9	0.81	0.90	0.89	0.22
1.0	0.77	0.89	0.87	0.20
1.1	0.73	0.87	0.85	0.19
1.2	0.70	0.85	0.82	0.18
1.3	0.66	0.83	0.80	0.17
1.4	0.63	0.81	0.78	0.17
1.5	0.60	0.79	0.76	0.16
1.6	0.57	0.77	0.74	0.16
1.7	0.54	0.75	0.72	0.15
1.8	0.51	0.73	0.70	0.15
1.9	0.48	0.71	0.68	0.15

elements demonstrate some positive allometry, and thus taller individuals have proportionately longer limbs overall as shown in previous studies (e.g., Takamura et al., 1988; Jantz and Jantz, 1999; Auerbach, 2010b).

Although a partial explanation of the paradox has been shown to be a consequence of the mathematics behind the geometric mean, the use of stature as a scaling factor continues to demonstrate more positive allometry in distal elements compared to proximal elements. This differential allometry would still lead to changes in intralimb indices with changes in limb length. As such, the question remains whether the morphological manifestations of the allometry in bone dimensions are sufficient to create observable allometry in intralimb indices?

Comparisons of observed deviations from isometry (Tables 3 and 4) indicate that mean absolute differences are generally below 0.5 cm (matching the results of Sylvester et al., 2008). In specific cases, however, the limb length deviations are as great as 2 cm, a difference much larger than that found by Sylvester et al. (2008). Even excluding the largest 1% of differences, those found here are higher than those reported by Sylvester et al. (2008), who report values from ±3 standard deviations of size, and thus should be comparable to the maximum values presented here. There are three possibilities that may contribute to these different results. First, Sylvester et al. (2008) used principal components analysis to create their isometric and allometric individuals, and so used the geometric mean as the size-scaling variable, whereas stature estimates were used as the size-scaling variable here. Although the use of the different size variables produces similar relative allometry coefficients, their precise values change slightly; coefficients calculated using stature may be slightly greater. Second, Sylvester et al. (2008) created individuals that represent up to three standard deviations of size. The analysis in this article includes individuals that are beyond three standard deviations, as they were modeled from the total sample and thus provided extreme cases. Finally, and likely the most important con-

TABLE 6. Male simulation results for brachial index and crural index

	Correlation coefficient (ρ)			
Proportion of standard deviation	Between radius and humerus	Between humerus and stature	Between radius and stature	Between brachial index and upper limb length
0.0	1.00	1.00	1.00	1.00
0.1	1.00	1.00	1.00	0.87
0.2	0.98	0.99	0.99	0.66
0.3	0.96	0.98	0.98	0.51
0.4	0.94	0.97	0.97	0.41
0.5	0.90	0.95	0.95	0.34
0.6	0.87	0.93	0.93	0.29
0.7	0.83	0.91	0.91	0.26
0.8	0.79	0.89	0.88	0.23
0.9	0.74	0.87	0.86	0.21
1.0	0.70	0.84	0.83	0.19
1.1	0.66	0.82	0.80	0.18
1.2	0.62	0.79	0.78	0.17
1.3	0.58	0.77	0.75	0.16
1.4	0.55	0.75	0.73	0.15
1.5	0.51	0.72	0.71	0.14
1.6	0.48	0.70	0.68	0.14
1.7	0.45	0.68	0.66	0.14
1.8	0.42	0.66	0.64	0.13
1.9	0.39	0.64	0.62	0.13

	Correlation coefficient (ρ)			
	Between tibia and femur	Between femur and stature	Between tibia and stature	Between crural index and lower limb length
0.0	1.00	1.00	1.00	1.00
0.1	1.00	1.00	1.00	0.91
0.2	0.99	1.00	1.00	0.75
0.3	0.98	0.99	0.99	0.60
0.4	0.97	0.98	0.98	0.49
0.5	0.95	0.97	0.97	0.41
0.6	0.93	0.96	0.96	0.36
0.7	0.90	0.95	0.95	0.31
0.8	0.88	0.94	0.94	0.28
0.9	0.85	0.92	0.92	0.25
1.0	0.82	0.90	0.90	0.23
1.1	0.79	0.89	0.89	0.21
1.2	0.76	0.87	0.87	0.19
1.3	0.73	0.85	0.85	0.18
1.4	0.70	0.83	0.83	0.17
1.5	0.67	0.82	0.82	0.16
1.6	0.64	0.80	0.80	0.15
1.7	0.61	0.78	0.78	0.15
1.8	0.58	0.76	0.76	0.14
1.9	0.55	0.75	0.74	0.13

tributing factor, is that Sylvester et al. (2008) created individuals using sex-combined samples whereas this paper's analyses were conducted by sex. Sylvester et al. (2008) demonstrate that while males and females often share common allometry coefficients, they have different intercepts in multivariate space. Allometry coefficients for sex-combined samples where males and females have different intercepts (despite common allometry coefficients) will produce a sex-combined allometry coefficient that differs from each of the sex-specific samples.

The reason interlimb indices do not exhibit strong allometric patterns is demonstrated by the effect that the variance around the slopes have on intralimb correlations. In all simulations (Tables 5 and 6), as variance increases, the correlation coefficient between stature and individual limb elements does not decrease below 0.57, even with twice the standard deviation observed in the actual data. Importantly, when the modeled residuals reach the magnitude of the original em-

pirical data, the simulated data have correlations that mirror those of the empirical data. We conclude, then, that the paradox is fully resolved by these simulations.

It is not surprising that the relationship between proximal and distal elements decrease more precipitously, as increasing the standard deviation results in more independent variation between element lengths. Longer humeri may necessitate longer radii, for example, but there is considerable autonomy in the relationship between these lengths. Indeed, the slightly lower correlations between distal elements and stature than the correlations between proximal elements and stature may be a consequence of greater variance in distal elements, as shown by Holliday and Ruff (2001). This also likely contributes to some of the greater independence in the lengths of elements within the same limb, assuming the higher variance in distal element lengths decreases the covariance of these with proximal element lengths.
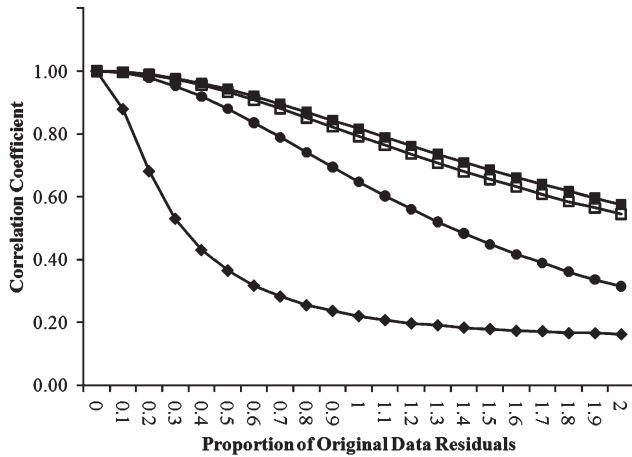
Fig. 5. Correlations for female upper limb relationships with simulated proportions of the observed standard deviation (Table 5): closed boxes, humerus length and stature; open boxes, radius length and stature; closed circles, humerus length and radius length; closed diamonds, brachial index and upper limb length.
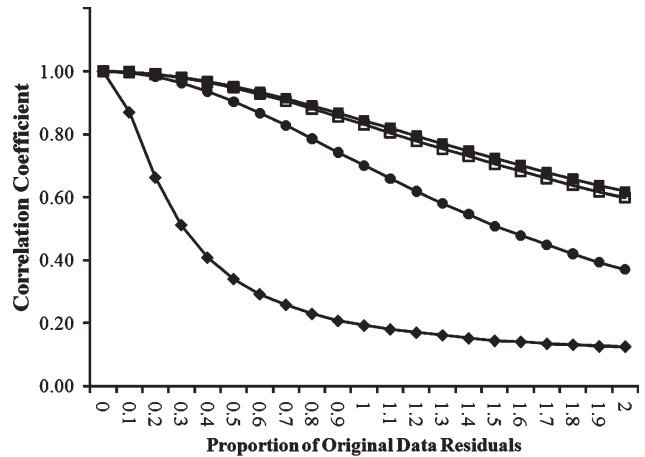

Fig. 7. Correlations for male upper limb relationships with simulated proportions of the observed standard deviation (Table 5): closed boxes, humerus length and stature; open boxes, radius length and stature; closed circles, humerus length and radius length; closed diamonds, brachial index and upper limb length.
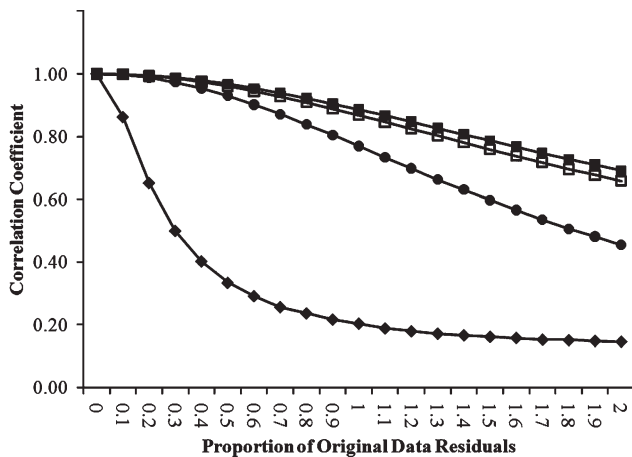

Fig. 6. Correlations for female lower limb relationships with simulated proportions of the observed standard deviation (Table 5): closed boxes, femur length and stature; open boxes, tibia length and stature; closed circles, femur length and tibia length; closed diamonds, crural index and upper limb length.

Fig. 8. Correlations for male lower limb relationships with simulated proportions of the observed standard deviation (Table 5): closed boxes, femur length and stature; open boxes, tibia length and stature; closed circles, femur length and tibia length; closed diamonds, crural index and upper limb length.
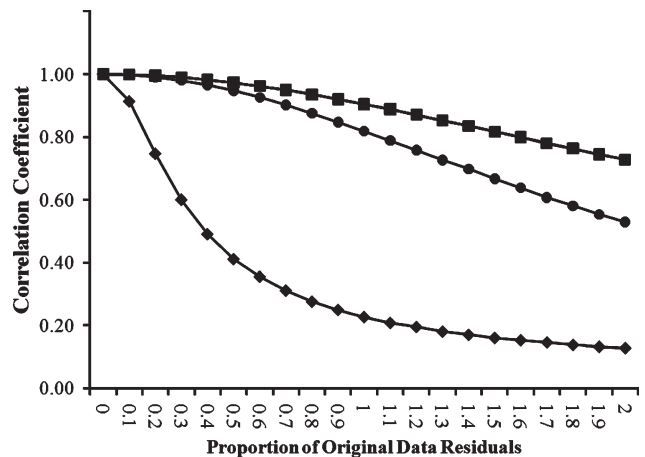
The relationship between intralimb indices and total limb length in the simulations provide the most crucial evidence to explain Holliday's low correlations (Figure 1 in Holliday, 1999). The results of this study present correlations between intralimb indices and total limb length nearly identical to those reported by Holliday, with correlations at or below 0.2. At only half the observed variance (a proportion of 0.5), the correlation between intralimb indices and total limb length are already below 0.5. Therefore, although relationships between limb elements and among elements and stature are higher than 0.6 in the observed data, and therefore indicate only moderate dispersion around the regression slope, there is only a weak relationship between intralimb indices and total limb length due to high variance in intralimb indices relative to total limb length.

These results, then, demonstrate the independence of intralimb proportions and *absolute* limb lengths. This is due to some independence in the lengths of proximal and distal elements. Population differences in intralimb proportions arising from ancestral or developmental sources also contribute to the pattern. Two individuals may have equal total upper limb length, for example, but the radius may be proportionally longer in one. What makes the results reported in Tables 5 and 6 interesting in this light is that variance in the intralimb indices compared to total limb length would need to be nearly zero to maintain correlations as high as those observed between element lengths and among elements and stature.

The specific implications for this relationship when applying Allen's rule to total limb length versus intralimb indices among hominids is beyond the scope of this study. However, it does suggest that the relationships between intralimb proportions and relative limb length with climatic factors are not necessarily equivalent. High correlations between intralimb indices and climate, or between relative limb length and climate do not

necessitate high correlations between intralimb indices and relative limb length. One important caveat that this study reinforces from previous studies (Jantz and Jantz, 1999; Sylvester et al., 2008; Auerbach, 2010b) is that taller individuals will have proportionately longer distal limb elements. This, in turn, may mean that higher limb proportions observed in some especially tall human groups (e.g., the Arikara) are the result of allometric and not thermoregulatory effects, especially as stature has not been indicated to directly covary with climatic factors (Ruff, 1994; Auerbach, 2007; King, 2010).

CONCLUSIONS

In conclusion, this study supports the hypothesis that the apparent paradox introduced in the Introduction is a mathematical consequence of the use of the geometric mean as a scaling factor. In addition, the results show that overall variation in limb lengths among individuals is sufficient to mask allometric trends between intralimb indices and limb lengths. More generally, however, this article demonstrates the following broad reaching results:

- Using the geometric mean as a scaling factor may obscure real allometric coefficients, at least for linear dimensions, as all coefficients must average to one (OLS regression). Although it is possible that using dimensions that are independent of those utilized in analyses while remaining biologically relevant to size to calculate the geometric mean (following Coleman, 2008) may in part resolve this problem, it is suggested that an appropriate, empirical biological dimension (e.g., stature or body mass) be used as a scaling factor whenever practical.
- *All* limb elements demonstrate positive scaling relative to stature in humans. Distal elements have higher allometric coefficients than proximal elements. These allometries may result in deviations as great as 2 cm from isometry, though they are on average less than 0.5 cm. In addition, distal elements have higher variance, as shown previously in other studies (e.g., Holliday and Ruff, 2001).
- Intralimb indices do not correlate with total limb length due to the independent variance of element lengths within limbs. However, there is a general trend for proximal and distal limb elements to have positive allometry, although at different magnitudes. This is in part a consequence of populations with similar variance in total limb lengths having dissimilar variance in intralimb proportions.
- Higher intralimb indices may be the result of allometric effects in especially tall human populations.

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APPENDIX

This proof demonstrates algebraically why the use of the geometric mean as a scaling factor automatically yields positive and negative allometries, even when all allometries may be negative or positive when scaled against an independent biological factor. Given the nature of all calculations made from the geometric mean (see below), the slopes of scaling trends will equal a mean slope of 1.

Definitions:

B_n = the slope of the nth variable against the geometric mean

X = vector of deviations of x_i from the mean of x (independent variable)

y_n = vector of deviations of nth variable y from its mean (dependent variable)

n = number of variables

$^{-1}$ = inverse

^{T} = transpose

PROOF: Mean $B = 1$ (The mean slope of allometries calculated using the geometric mean equals 1).

1. The matrix definition of an OLS slope is:

$$B_n = (X^T \cdot X)^{-1} \cdot X^T \cdot y_n$$

2. X is the average of the y_n variables [as the log(geometric mean) equals the mean of the logged data]

$$X = (y_1 + y_2 + y_3 + \ldots + y_n) \div n$$

3. This can be rearranged to:

$$y_n = X \cdot n - y_1 - y_2 - y_3 - \ldots - y_{n-1}$$

4. Substitute the equation for y_n into the matrix definition of the OLS slope

$$B_n = (X^T \cdot X)^{-1} \cdot X^T \cdot (X \cdot n - y_1 - y_2 - y_3 - \ldots - y_{n-1})$$

5. Distributive Law:

$$B_n = (X^T \cdot X)^{-1} \cdot X^T \cdot X \cdot n - (X^T \cdot X)^{-1} \cdot X^T \cdot y_1$$
$$- (X^T \cdot X)^{-1} \cdot X^T \cdot y_2 - \ldots (X^T \cdot X)^{-1} \cdot X^T \cdot y_{n-1}$$

6. Simplifying the first part of the equation (up to n) using linear algebra, using the principle that $(X^T \cdot X)^{-1} \cdot X^T \cdot X = I$ (the 1×1 identity matrix), yields:

$$B_n = 1n - (X^T \cdot X)^{-1} \cdot X^T \cdot y_1 - (X^T \cdot X)^{-1} \cdot X^T \cdot y_2$$
$$- \ldots (X^T \cdot X)^{-1} \cdot X^T \cdot y_{n-1}$$

7. Substitute the matrix definition of the OLS slope (step one, above):

$$B_n = n + B_1 - B_2 - B_3 - \ldots - B_n - 1$$

8. Rearranging this equation yields:

$$n = B_1 + B_2 + B_3 + \ldots + B_n - 1 + B_n$$

9. Dividing though by n yields:

$$1 = (B_1 + B_2 + B_3 + \ldots + B_n - 1 + B_n) \div n$$