Mass Prediction in Theropod Dinosaurs

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Body size is a crucial life history parameter for an organism. Therefore, mass estimation for fossil species is important for many kinds of analyses. Several attempts have been made to yield equations applicable to dinosaurs. In this paper, we offer bi- and multivariate equations based on log transformed appendicular skeleton data from a sample of 16 theropods which were known from reasonably complete skeletal remains, and spanning a wide size range. Body masses of the included taxa had been found by displacement methods of scale models, based on measurements taken directly on the mounted skeletons. Seven of the bivariate regression analyses resulted in correlation coefficients equal to or above 0.975 and femoral length was the best available measurement ($r = 0.995$; standard error of the estimate (%SEE) = 19.26; percent prediction error (%PE) = 13.81). Also, 32 multivariate analyses yielded equations with high correlation coefficients ($r > 0.990$) and low standard errors.

Keywords: Body mass; Bivariate analyses; Multivariate analyses; *Tyrannosaurus*

INTRODUCTION

Many biological variables show an intimate relationship with body size. Body size can be defined by a number of parameters, for instance overall height or length, but the variable of primary importance is body mass (e.g. Jerison, 1973; Eisenberg, 1981; McMahon and Bonner, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Damuth and MacFadden, 1990). Thus, it is often of considerable significance to obtain a reliable mass estimate for dinosaurs and other extinct animals.

In cases where most of the skeleton is recovered and in largely undistorted condition, a skeletal mount may be assembled, and double graphic integration methods may be employed to find the volume of the animal, and, thus, its mass by multiplying by a pre-selected overall tissue density (e.g. Mazzetta *et al.*, 1998; Henderson, 1999; Hurlburt, 1999; Christiansen, 2001). This appears to be the most accurate method currently available, since it deals with complete specimens and reconstructed body outlines based on the outline of the skeleton. Accordingly, it is possible to restore soft tissue proportions with some accuracy.

In many cases, however, skeletons are fragmentary, and the above procedure is not feasible. If an osteometric variable can be shown to covary significantly with body mass in extant taxa, it may be employed in computing masses of extinct taxa (e.g. Kurtén, 1967; Gingerich, 1990; Janis, 1990; Ruff, 1990; Scott, 1990; Van Valkenburg, 1990; Anyonge, 1993; Hartwig-Scherer, 1993; Richards and Turnbull, 1995; Fariña *et al.*, 1998; Biknevicius, 1999; Christiansen, 1999a).

The physical proportions of non-avian theropods differed markedly from those of extant animals, even their sistertaxon, the Avialae. Accordingly, the notion that an adult *Tyrannosaurus rex* was around 11 meters in overall length will reveal little relevant information for the purpose of reconstructing ecological and physical parameters, such as the strength of its bones, inferred locomotory potential, possible territorial size, number of eggs produced per clutch or potential modal prey size. Thus, one cannot simply compare overall dimensions of non-avian theropods to those of mammals or reptiles, or even avialean theropods. The nature of the reference data sample is important (Hartwig-Scherer, 1993; Biknevicius, 1999), and body size to mass relations vary within groups of extant mammals, as between larger categories of dinosaurs (Seebacher, 2001). Accordingly, for this study we chose to restrict the data sample to non-avian theropods exclusively.

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Appendicular bones are rather frequently preserved with fragmentary theropod skeletons (Lyman, 1994). Traditionally, when using appendicular bones to assign a mass value to a theropod specimen (e.g. Currie and Zhao, 1993; Russell and Dong, 1993a,b; Varricchio, 1993; Peczkis, 1994; Chure, 1995; Carpenter *et al.*, 1997; Azuma and Currie, 2000; Currie and Carpenter, 2000), the results of Anderson *et al.* (1985) are used, also on "reptiles" (e.g. Hurlburt, 1999).

This is not satisfactory, since Anderson *et al.* (1985) studied the relationship between appendicular bones and inferred body mass in a sample of extant, quadrupedal mammals of markedly different somatic proportions (from guinea pig to hippo and giraffe). The markedly different physical proportions of mammals from non-avian theropod would render this study dubious in terms of assigning mass values to theropods. Anderson *et al.* (1985) also did not analyse the predictive reliability of the computed equations using modern methods (standard error of the estimate (%SEE) and percent prediction error (%PE)) but relied on the correlation coefficient. Relying exclusively on the correlation coefficient for evaluation of the predictive power of an equation does not take into account the possibility of high residuals or curvilinearity (e.g. Smith, 1981; 1984; Bertram and Biewener, 1990; Christiansen, 1999b). In this paper, we attempt to provide some simple means of estimating the approximate mass of fragmentary non-avian theropod specimens.

MATERIALS AND METHODS

A sample of 16 theropods known from reasonably complete skeletal remains was used (Table I), spanning a wide estimated size range, from 16.5 to 6300 kg. Body masses of the included taxa had been found by displacement methods of scale models, based on measurements taken directly from mounted skeletons (Christiansen, 1998). We decided to perform regression analyses on the appendicular parameters exclusively (Table I), because these are rather frequently found, even with more fragmentary skeletons, or even individually. Additionally, appendicular bones have the advantage of being directly involved in support of mass, unlike other frequently used parameters for mammalian body mass prediction, such as dental variables (see discussion in Hylander, 1985; Smith, 1985).

Following log transformation of the variables bivariate regression equations (model II, Reduced Major Axis) were fitted to the data. As appropriately (Smith, 1981; 1984), we computed not just the correlation coefficient, but also the %SEE and %PE, since these are frequently superior to the correlation coefficient in evaluating the predictive power of

the equations (see also Christiansen, 2004), and may even be directly incorporated into the final mass estimates (Christiansen, 2004a). The %PE provides a measure of the average percent difference between the predicted masses and the actual masses of the individual specimens. The %SEE provides an indication of the predictive power of the equations, since 68% of the actual masses would fall within $\pm$ %SEE, assuming a normal (Poisson) distribution (see, e.g. Van Valkenburg, 1990; Christiansen, 1999a; 2004). Additionally, we computed the F statistic and assigned confidence limits (95% CI) to both slope and intercept.

Multivariate analyses were also performed on the variables. Multivariate regression introduces potential intercorrelation of the "independent" variables. This can be evaluated by computing the eigen and tolerance values and the condition indices (see Christiansen, 2002), but these were not used, since variable intercorrelation is probably unavoidable in biological samples (Christiansen, 2002). Multiple "independent" variables can, however, result in variable redundancy. This was evaluated by a two tailed p test, and the significance level for rejection of the equation was set at $p > 0.10$. For two "independent" osteological variables all possible combinations were attempted. However, in order to avoid circularity some parameters were not combined. For instance, a perimeter measurement was not combined with a diaphysial diameter (antero-posterior or lateromedial, Table II) since these are too closely related to the perimeter. This narrowed the analyses number down to 144. Initially, we also anticipated doing analyses with three or more "independent" variables, but since most of the bivariate regressions and all of the multivariate regressions with just two "independent" variables resulted in high correlations, addition of more variables in all cases led to variable redundancy. As with the bivariate analyses the correlation coefficient, F-statistic and confidence limits for slopes and intercepts were computed for each sample. In the multiple regression analyses the traditional standard error of the estimate (s.e.) was computed.

RESULTS

Seven of the bivariate regression analyses resulted in correlation coefficients equal to or above 0.975, and these are presented in Table II. A number of other variables resulted in quite high correlation coefficients ($r > 0.95$) but these were discarded, due to the rapidly decreasing explanatory power of the equations with decreasing correlation coefficients (square of the decrease). The femur is the best bone for predictions of body mass (Fig. 1A and B),

TABLE I Theropod body masses (kg) and long bone dimensions (mm)

Species	Body mass (kg)	Femur					Tibia					Fibula							
		length	per	Diaphysis		Distal	length	per	Diaphysis		Distal	length	per	Diaphysis		Proximal		Distal	
				ap	lm	lm			ap	lm	lm			ap	lm	ap	lm	ap	lm
Albertosaurus	1685	905	298	74.5	115	297	987	268	99.5	71	198	801	101	23.5	41	170	34	53.5	21.5
Tarbosaurus	1650	854	312	96.5	102	216	799	281	82	97	211	724	95	40	20.5	163	42	50	31
Daspletosaurus	2700	1006	389	114.5	133	257	1017	347	79.5	141.5	207								
Tyrannosaurus	6300	1273	540	161.5	182.5	344	1199	468	128	170	368	1163	154	64	34	258	92	113	57
Gallimimus	490	673	216	66	72	138.5	737	193	55	68	115	679	60	24	14	113	38	21	14
Anserimimus	170	433	145	43	49	65	472	125	38	41.5	74	427	29	13	5.5	71.5	23	17	11
Struthiomimus	175	486	127	46.5	34.5	70	534	103	25	40.5	61	526	40	14	11.5	72	18	16.5	8
Ornithomimus	155	443	107	39.5	29	64	498	97	23.5	38.5	57	439	28	10.5	7	59	10	15	9
Dromiceiomimus	160	454	132	47.5	36.5	65	537	113	28	44	65	507	30	12	7	76	10.5	10.5	9
Allosaurus fragilis	1620	874	293	100	86.5	188	747	265	75.5	93.5	194	620	97	34	27.5	147	55	58	39
Sinraptor dongi	1700	884	283	92.5	87.5	186	820	232	57	90.5	190	681	88	25	31	135	52	79	38
Dilophosaurus	325	551	185	51.5	66.5	105	537	128	47	34.5	75	517	57	20	16	86	30	48	41
Elaphrosaurus	245	519	165	47	58		608	132	38	46									
Ornitholestes	16.5	210	64	15	25.5	39.5	165	41	14.5	11.5	24.5	162	24	6.5	8.5	30	9	13	10
Saurornitholestes	22.5	214	63	16.5	23.5	40	283	63	16	24	42								
Oviraptor	58	303	93	32.5	26.5	47.5	388	83	21.5	31	52.5								

ap, anteroposterior diameter; lm, lateromedial diameter; per, perimeter.

TABLE II   Bivariate and multivariate equations obtained. In all cases $\log_{10} y =$ is $\log_{10}$ body mass in kg. The p values for the constants in the multivariate equations are 2-tailed p

Bivariate

$\log_{10} y = -6.288 \pm 0.500 + 3.222 \pm 0.181 \times \log_{10}\text{FL}$
$n = 16$; $r = 0.995$;%SEE $= 19.26$; %PE $= 13.81$; $F = 1432.221$; $p \ll 0.001$

$\log_{10} y = -3.607 \pm 0.461 + 2.738 \pm 0.203 \times \log_{10}\text{FP}$
$n = 16$; $r = 0.992$; %SEE $= 26.08$; %PE $= 18.57$; $F = 821.292$; $p \ll 0.001$

$\log_{10} y = -2.028 \pm 0.462 + 2.641 \pm 0.263 \times \log_{10}F$ dia AP
$n = 16$; $r = 0.985$; %SEE $= 36.48$; %PE $= 22.26$; $F = 449.637$; $p \ll 0.001$

$\log_{10} y = -2.284 \pm 0.654 + 2.377 \pm 0.317 \times \log_{10}F$ distal LM
$n = 15$; $r = 0.975$; %SEE $= 51.04$; %PE $= 30.72$; $F = 249.877$; $p \ll 0.001$

$\log_{10} y = -3.135 \pm 0.516 + 2.611 \pm 0.235 \times \log_{10}\text{TP}$
$n = 16$; $r = 0.988$; %SEE $= 32.39$; %PE $= 22.64$; $F = 555.837$; $p \ll 0.001$

$\log_{10} y = -2.099 \pm 0.540 + 2.337 \pm 0.267 \times \log_{10}T$ distal LM
$n = 15$; $r = 0.982$; %SEE $= 42.41$; %PE $= 26.52$; $F = 344.640$; $p \ll 0.001$

$\log_{10} y = -2.905 \pm 0.575 + 2.787 \pm 0.286 \times \log_{10}\text{Fib}$ *prox* AP
$n = 12$; $r = 0.989$; %SEE $= 28.05$; %PE $= 15.05$; $F = 462.591$; $p \ll 0.001$

Multivariate "independent" variables

$\log_{10} y = -5.285 \pm 0.790 + 2.012 \pm 0.860 \times \log_{10}\text{FL} + 1.030 \pm 0.731 \times \log_{10}\text{FP}$
$n = 16$; $r = 0.997$; s.e. $= 0.061$; $F = 1144.218$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.000$, $b2 : p = 0.009$

$\log_{10} y = -5.656 \pm 0.718 + 2.714 \pm 0.498 \times \log_{10}\text{FL} + 0.431 \pm 0.413 \times \log_{10}F$ dia LM
$n = 16$; $r = 0.997$; s.e. $= 0.067$; $F = 927.963$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.000$, $b2 : p = 0.042$

$\log_{10} y = -5.509 \pm 0.859 + 2.593 \pm 0.637 \times \log_{10}\text{FL} + 0.466 \pm 0.470 \times \log_{10}F$ distal LM
$n = 15$; $r = 0.997$; s.e. $= 0.068$; $F = 910.281$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.000$, $b2 : p = 0.052$

$\log_{10} y = -5.263 \pm 0.693 + 2.159 \pm 0.646 \times \log_{10}\text{FL} + 0.868 \pm 0.519 \times \log_{10}\text{TP}$
$n = 16$; $r = 0.998$; s.e. $= 0.056$; $F = 1340.365$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.000$, $b2 : p = 0.003$

$\log_{10} y = -5.512 \pm 0.891 + 2.674 \pm 0.580 \times \log_{10}\text{FL} + 0.447 \pm 0.467 \times \log_{10}T$ dia AP
$n = 16$; $r = 0.996$; s.e. $= 0.069$; $F = 885.348$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.000$, $b2 : p = 0.059$

$\log_{10} y = -5.622 \pm 0.827 + 2.740 \pm 0.540 \times \log_{10}\text{FL} + 0.380 \pm 0.419 \times \log_{10}T$ dia LM
$n = 16$; $r = 0.996$; s.e. $= 0.070$; $F = 862.891$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.000$, $b2 : p = 0.072$

$\log_{10} y = -5.051 \pm 0.560 + 2.254 \pm 0.400 \times \log_{10}\text{FL} + 0.714 \pm 0.290 \times \log_{10}T$ distal LM
$n = 15$; $r = 0.999$; s.e. $= 0.043$; $F = 2236.407$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.000$, $b2 : p < 0.000$

$\log_{10} y = -6.003 \pm 0.690 + 2.985 \pm 0.334 \times \log_{10}\text{FL} + 0.241 \pm 0.203 \times \log_{10}\text{Fib}$ distal AP
$n = 12$; $r = 0.998$; s.e. $= 0.054$; $F = 939.622$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.000$, $b2 : p = 0.025$

$\log_{10} y = -6.202 \pm 0.625 + 3.093 \pm 0.285 \times \log_{10}\text{FL} + 0.202 \pm 0.191 \times \log_{10}\text{Fib}$ distal LM
$n = 12$; $r = 0.997$; s.e. $= 0.056$; $F = 852.704$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.000$, $b2 : p = 0.041$

$\log_{10} y = -4.324 \pm 0.807 + 2.179 \pm 0.519 \times \log_{10}\text{FP} + 0.715 \pm 0.650 \times \log_{10}T$ length
$n = 16$; $r = 0.994$; s.e. $= 0.087$; $F = 549.699$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.000$, $b2 : p = 0.034$

$\log_{10} y = -3.251 \pm 0.540 + 2.203 \pm 0.596 \times \log_{10}\text{FP} + 0.493 \pm 0.544 \times \log_{10}T$ dia LM
$n = 16$; $r = 0.994$; s.e. $= 0.092$; $F = 495.844$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.000$, $b2 : p = 0.072$

$\log_{10} y = -3.168 \pm 0.623 + 1.969 \pm 0.898 \times \log_{10}\text{FP} + 0.651 \pm 0.767 \times \log_{10}T$ distal LM
$n = 15$; $r = 0.994$; s.e. $= 0.094$; $F = 473.218$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.000$, $b2 : p = 0.089$

$\log_{10} y = -2.210 \pm 0.209 + 1.526 \pm 0.306 \times \log_{10}F$ dia AP $+ 1.040 \pm 0.276 \times \log_{10}F$ distal LM
$n = 15$; $r = 0.998$; s.e. $= 0.057$; $F = 1307.071$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.000$, $b2 : p < 0.000$

$\log_{10} y = -2.638 \pm 0.546 + 1.158 \pm 0.916 \times \log_{10}F$ dia AP $+ 1.461 \pm 0.906 \times \log_{10}\text{TP}$
$n = 16$; $r = 0.992$; s.e. $= 0.101$; $F = 409.726$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.017$, $b2 : p = 0.004$

$\log_{10} y = -1.931 \pm 0.323 + 1.683 \pm 0.527 \times \log_{10}F$ dia AP $+ 0.962 \pm 0.517 \times \log_{10}T$ dia AP
$n = 16$; $r = 0.993$; s.e. $= 0.094$; $F = 475.898$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.000$, $b2 : p = 0.001$

$\log_{10} y = -2.075 \pm 0.350 + 1.427 \pm 0.699 \times \log_{10}F$ dia AP $+ 1.081 \pm 0.619 \times \log_{10}T$ distal LM
$n = 15$; $r = 0.993$; s.e. $= 0.098$; $F = 431.077$ $p \ll 0.001$
p values, $a : p < 0.000$, $b1 : p < 0.001$, $b2 : p = 0.003$

$\log_{10} y = -2.076 \pm 0.427 + 1.806 \pm 0.554 \times \log_{10}F \text{ dia AP} + 0.876 \pm 0.538 \times \log_{10}\text{FibP}$
$n = 12; \ r = 0.993; \ \text{s.e.} = 0.091; \ F = 321.370 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.000, \ b2 : p = 0.005$

$\log_{10} y = -1.809 \pm 0.410 + 2.163 \pm 0.336 \times \log_{10}F \text{ dia AP} + 0.535 \pm 0.296 \times \log_{10}\text{Fib dia LM}$
$n = 12; \ r = 0.994; \ \text{s.e.} = 0.086; \ F = 366.677 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.000, \ b2 : p = 0.003$

$\log_{10} y = -1.787 \pm 0.475 + 2.100 \pm 0.440 \times \log_{10}F \text{ dia AP} + 0.484 \pm 0.335 \times \log_{10}\text{Fib distal AP}$
$n = 12; \ r = 0.992; \ \text{s.e.} = 0.098; \ F = 279.416 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.000, \ b2 : p = 0.010$

$\log_{10} y = -2.858 \pm 0.538 + 0.733 \pm 0.795 \times \log_{10}F \text{ distal LM} + 1.801 \pm 0.873 \times \log_{10}\text{TP}$
$n = 15; \ r = 0.991; \ \text{s.e.} = 0.114; \ F = 319.548 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.068, \ b2 : p = 0.001$

$\log_{10} y = -2.116 \pm 0.428 + 1.395 \pm 0.507 \times \log_{10}F \text{ distal LM} + 1.064 \pm 0.534 \times \log_{10}T \text{ dia LM}$
$n = 15; \ r = 0.990; \ \text{s.e.} = 0.116; \ F = 306.235 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.000, \ b2 : p = 0.001$

$\log_{10} y = -4.295 \pm 1.102 + 1.656 \pm 0.621 \times \log_{10}\text{TL} + 1.343 \pm 0.500 \times \log_{10}\text{FibP}$
$n = 12; \ r = 0.990; \ \text{s.e.} = 0.108; \ F = 228.689 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.001, \ b2 : p < 0.000$

$\log_{10} y = -4.420 \pm 1.025 + 2.098 \pm 0.465 \times \log_{10}\text{TL} + 0.834 \pm 0.292 \times \log_{10}\text{Fib distal AP}$
$n = 12; \ r = 0.991; \ \text{s.e.} = 0.103; \ F = 252.284 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.000, \ b2 : p < 0.000$

$\log_{10} y = -2.634 \pm 0.500 + 1.939 \pm 0.586 \times \log_{10}\text{TP} + 0.581 \pm 0.612 \times \log_{10}\text{FibC}$
$n = 12; \ r = 0.993; \ \text{s.e.} = 0.090; \ F = 328.880 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.000, \ b2 : p = 0.060$

$\log_{10} y = -2.518 \pm 0.487 + 2.154 \pm 0.323 \times \log_{10}\text{TP} + 0.362 \pm 0.305 \times \log_{10}\text{Fib dia LM}$
$n = 12; \ r = 0.994; \ \text{s.e.} = 0.083; \ F = 392.056 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.000, \ b2 : p = 0.025$

$\log_{10} y = -2.464 \pm 0.448 + 2.062 \pm 0.326 \times \log_{10}\text{TP} + 0.387 \pm 0.267 \times \log_{10}\text{Fib distal AP}$
$n = 12; \ r = 0.995; \ \text{s.e.} = 0.075; \ F = 480.554 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.000, \ b2 : p = 0.009$

$\log_{10} y = -2.605 \pm 0.531 + 2.232 \pm 0.345 \times \log_{10}\text{TP} + 0.266 \pm 0.313 \times \log_{10}\text{Fib distal LM}$
$n = 12; \ r = 0.993; \ \text{s.e.} = 0.094; \ F = 306.664 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.000, \ b2 : p = 0.087$

$\log_{10} y = -1.733 \pm 0.414 + 1.355 \pm 0.424 \times \log_{10}T \text{ dia LM} + 1.165 \pm 0.469 \times \log_{10}\text{FibP}$
$n = 12; \ r = 0.993; \ \text{s.e.} = 0.093; \ F = 310.210 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.000, \ b2 : p = 0.000$

$\log_{10} y = -1.251 \pm 0.387 + 1.753 \pm 0.308 \times \log_{10}T \text{ dia LM} + 0.732 \pm 0.309 \times \log_{10}\text{Fib dia LM}$
$n = 12; \ r = 0.992; \ \text{s.e.} = 0.097; \ F = 287.956 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.000, \ b2 : p = 0.000$

$\log_{10} y = -1.259 \pm 0.342 + 1.643 \pm 0.298 \times \log_{10}T \text{ dia LM} + 0.713 \pm 0.258 \times \log_{10}\text{Fib distal LM}$
$n = 12; \ r = 0.994; \ \text{s.e.} = 0.085; \ F = 368.235 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.000, \ b2 : p = 0.000$

$\log_{10} y = -2.487 \pm 1.021 + 1.780 \pm 0.381 \times \log_{10}T \text{ distal LM} + 0.564 \pm 0.612 \times \log_{10}\text{Fib length}$
$n = 12; \ r = 0.995; \ \text{s.e.} = 0.075; \ F = 481.493 \ p \ll 0.001$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.000, \ b2 : p = 0.067$

$\log_{10} y = -2.556 \pm 0.530 + 2.347 \pm 0.426 \times \log_{10}\text{Fib prox AP} + 0.355 \pm 0.310 \times \log_{10}\text{Fib distal AP}$
$n = 12; \ r = 0.994; \ \text{s.e.} = 0.086; \ F = 366.809 \ p \ll 0.000$
$p \ \text{values}, \ a : p < 0.000, \ b1 : p < 0.000, \ b2 : p = 0.029$

F, femur; T, tibia; Fib, fibula; L, length; dia AP, midshaft anteroposterior diameter; LM, midshaft lateromedial diameter; prox AP, proximal anteroposterior diameter; prox LM, proximal lateromedial diameter; distal AP, distal anteroposterior diameter; distal LM, distal lateromedial diameter; p, perimeter.

because no less than four variables resulted in high correlations (0.975–0.995). Femur length proved to be the best available measurement ($r = 0.995$), and particularly high correlations have been obtained previously in analyses of bone proportions to mass in extant mammals (Anderson *et al.*, 1985; Christiansen, 1999b). More importantly, the %SEE (19.26) and %PE (13.81) were also the lowest of the samples, indicating lower deviations from predicted values than in the other measurements.

The %SEE and %PE values (Table II) indicate that although the correlation coefficients of femoral diaphysis anteroposterior diameter ($r = 0.985$), tibia perimeter ($r = 0.988$; Fig. 1C) and fibula proximal anteroposterior diameter ($r = 0.989$; Fig. 1D) are nearly identical, the latter one is the most reliable predictor of body mass. The %SEE and %PE values further indicate that although the correlation coefficients are high there is a certain degree of divergence of the individual species from the predicted values.

In non-avian theropods there is a relationship between phylogenetic position and body proportions. More plesiomorphic taxa, e.g. ceratosaurs and carnosaurs, have proportionally longer bodies and tails and shorter legs than coelurosaurs (Christiansen and Bonde, 2002). Also, regardless of phylogenetic position small species universally have
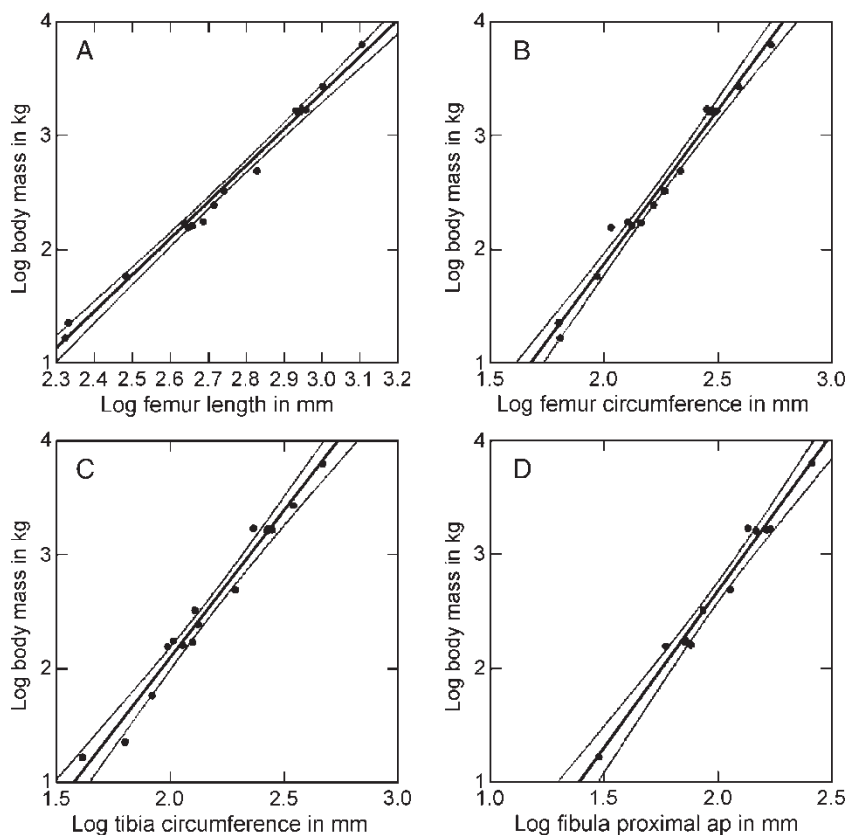
FIGURE 1   Bivariate regression plots with 95% confidence lines for the regression line of the four best variables (variables in log mm), which showed the highest correlation with estimated log body mass. A, femur length; B, femur diaphysial perimeter; C, tibia diaphysial perimeter; D, fibula proximal anteroposterior length of articulating surface.

proportionally longer limbs than closely related large species (Christiansen and Bonde, 2002; see also Christiansen, 1998). This is also evident in the present analysis where ornithomimids have very long tibiae and fibulae for their body mass compared to other taxa. Large carnosaurs (*Allosaurus*, *Sinraptor*) also have shorter lower limb bones than comparably-sized coelurosaurs (tyrannosaurids *Albertosaurus* and *Tarbosaurus*). These differences are not present in femur length, and accordingly this was the only bone where length showed an intimate relationship with estimated body mass (Tables I and II). Thus, even correlations as high as the ones presented here should not be taken as indicative of a mass estimate that will necessarily be very close to the true value.

Combining two "independent" variables often lead to significantly increased correlations and enhanced reliability and explanatory powers. All multivariate analyses resulted in high correlation coefficients. Accordingly we decided to use only the very best with $r > 0.990$. The resulting 32 equations are shown in Table II. These will allow reliable predictions to be made even if fragmentary limb bones are recovered (e.g. femoral distal lateromedial diameter and tibia diaphysial perimeter; $r = 0.991$). Even if only the fibula is recovered a reliable body mass estimate may be obtained from combining

the anteroposterior diameters of the proximal and distal ends (Table II; $r = 0.994$).

DISCUSSION

The present analysis will allow a reasonable estimate of body mass to be made even if the skeleton is fragmentary or even partially encased in matrix, providing that the limb bones are recovered and not distorted. Using a datasample such as the present violates the assumptions of a regression analysis, however, since the body mass data are not data *per se*, i.e. they were not obtained from measurements, but from displacement analyses based on scale models (Christiansen, 1998). They were, accordingly, derived from reconstructions, which are naturally open to debate. It is, however, preferable to use a sample consisting of animals of roughly similar stature and/or phylogenetically closely related species for mass prediction, instead of relying on a sample of extant mammals, which bear little overall resemblance to non-avian theropod dinosaurs.

It would be possible to construct a sample of mass data and osteological variables on extant (avian) dinosaurs. This could be a superior sample to the present, in terms of the mass data representing true

data (see Campbell and Marcus, 1992). It is dubious, however, if the criteria of overall similarity are met satisfactorily. A good number of anatomical changes have occurred from advanced non-avian theropods and primitive avialeans (*Archaeopteryx* and others) compared to extant neornithine dinosaurs, notably a reduction of the tail, forwards displacement of the centre of mass, and a major reorganization of the femoral posture and associated musculature (e.g. Gatesy, 1990; 1991; Gatesy and Dial, 1996; Carrano, 1997; 1998; Gatesy and Middleton, 1997; Christiansen, 1999c; Jones *et al.*, 2000; Christiansen and Bonde, 2002).

This would imply that femoral diaphysial dimensions, and probably also proximal and distal parameters, would lead to significant overestimation of body mass in most non-avian theropods (see also Christiansen and Bonde, 2002). The tibia would be more comparable in the two, owing to greater similarities in overall loading pattern and overall proportions (Carrano, 1998; Christiansen, 1998; 1999c; Farlow *et al.*, 1999). One would, nonetheless, have to accept the comparison of a monophyletic (neornithine dinosaurs) to a paraphyletic (non-avian theropods) assemblage.

Finally, in mass prediction analyses it is sometimes possible to analyse the bias (systematic error) and imprecision (random error) of the equations (Damuth and MacFadden, 1990) by examination of the residuals. However, is not possible for a sample such as the present, as it would require knowledge of the true morphology in detail and possibly also ecology of the included species. Such knowledge is obviously not available for extinct, non-avian theropods. Even the best models, be they three dimensional as used here, or illustrations (Henderson, 1999; Hurlburt, 1999; Christiansen, 2001) are subjective estimates of body proportions.

However, this does not equal mere guesswork, and detailed comparisons with the extant fauna will serve to refine the estimates of proportions, but they remain estimates. It would be possible to examine residuals for bias in terms of taxonomy (Sokal and Rohlf, 1995; see also Christiansen, 1999c). As indicated above some taxa (e.g. ornithomimids) diverged in several aspects. A systematic elimination of such outliers would, however, compromise the purpose of providing equations for body mass estimation of theropods *per se*, not just of some small subgroup. Such refined analyses are common for mammals (Damuth and MacFadden, 1990) but impossible for non-avian theropods, because the "data"-sample is also extinct.

References

Anderson, J.F., Hall-Martin, A. and Russell, D.A. 1985. Long-bone circumference and weight in mammals, birds and dinosaurs. *Journal of Zoology (London)* **207**, 53–61.

Anyonge, W. 1993. Body mass in large extant and extinct carnivores. *Journal of Zoology (London)* **231**, 339–350.

Azuma, Y. and Currie, P.J. 2000. A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. *Canadian Journal of Earth Sciences* **37**, 1735–1753.

Bertram, J.E.A. and Biewener, A.A. 1990. Differential scaling of the long bones in the terrestrial Carnivora and other mammals. *Journal of Morphology* **204**, 157–169.

Biknevicius, A.R. 1999. Body mass estimation in armoured mammals: cautions and encouragements for the use of parameters from the appendicular skeleton. *Journal of Zoology (London)* **248**, 179–187.

Calder, W.A. 1984. *Size, Function, and Life History*. Harvard University Press, Cambridge.

Campbell, K.E. Jr. and Marcus, L. 1992. The relationships of hindlimb bone dimensions to body weight in birds. *In Papers in Avian Paleontology honoring Pierce Brodkorb*, edited by K.E. Campbell Jr., pp. 395–412. Natural History Museum of Los Angeles County, Science Series 36.

Carrano, M.T. 1997. Mammals versus birds as models for dinosaur limb kinematics. *Journal of Vertebrate Paleontology* **17**(Suppl. 3), 36A.

Carrano, M.T. 1998. Locomotion in non-avian dinosaurs: integrating data from hindlimb kinematics, *in vivo* strains, and bone morphology. *Paleobiology* **24**, 450–469.

Carpenter, K., Russell, D.A., Baird, D. and Denton, R. 1997. Redescription of the holotype of *Dryptosaurus aquilunguis* (Dinosauria: Theropoda) from the Upper Cretaceous of New Jersey. *Journal of Vertebrate Paleontology* **17**, 561–573.

Christiansen, P. 1998. Strength indicator values of theropod long bones, with comments on limb proportions and cursorial potential. *Gaia* **15**, 241–255.

Christiansen, P., 1999a. What size was *Arctodus simus* and *Ursus spelaeus* (Carnivora: Ursidae)? *Annales Zoologici Fennici* **36**, 93–102.

Christiansen, P., 1999b. Scaling of the limb long bones to body mass in terrestrial mammals. *Journal of Morphology* **239**, 167–190.

Christiansen, P., 1999c. Long bone scaling and limb posture in non-avian theropods: evidence for differential allometry. *Journal of Vertebrate Paleontology* **19**, 666–680.

Christiansen, P. 2001. Dinosaur biomechanics. *In* Paul, G.S. (ed) *The Scientific American Book of Dinosaurs*, pp 65–75. St Martin's Press, New York.

Christiansen, P. 2002. Locomotion in terrestrial mammals: the influence of body mass, limb length and bone proportions on speed. *Zoological Journal of the Linnean Society* **136**, 685–714.

Christiansen, P. 2004. Body size in proboscideans, with notes on elephant metabolism. *Zoological Journal of the Linnean Society* **140**, 523–549.

Christiansen, P. 2004a. The body size of *Smilodon populator* (Mammalia: Felidae). *Mammalia*.

Christiansen, P. and Bonde, N. 2002. Limb proportions and avian terrestrial locomotion. *Journal für Ornithologie* **143**, 356–371.

Chure, D.J. 1995. A reassessment of the gigantic theropod *Saurophagus maximus* from the Morrison Formation (Upper Jurassic) of Oklahoma, USA. *In* Sun, A. and Wang, Y. (eds) *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota*, pp 103–106. China Ocean Press, Beijing.

Currie, P.J. and Carpenter, K. 2000. A new species of *Acrocanthosaurus atokensis* (Theropoda: Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas* **22**, 207–246.

Currie, P.J. and Zhao, X.-J. 1993. A new Carnosaur (Dinosauria: Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences* **30**, 2037–2081.

Damuth, J. and MacFadden, B.J. (eds) 1990. *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge University Press, Cambridge.

Eisenberg, J.F. 1981. *The Mammalian Radiations*. University of Chicago Press, Chicago.

Fariña, R.A., Vizcaino, S.F. and Bargo, M.S. 1998. Body mass estimations in Lujanian (Late Pleistocene-Early Holocene of South America) mammal megafauna. *Mastozoologia Neotropical* **5**, 87–108.

Farlow, J.O., Gatesy, S.M., Holtz, Jr, T.R., Hutchinson, J.R. and Robinson, J.M. 1999. Theropod locomotion. *American Zoologist* **40**, 640–663.

Gatesy, S.M. 1990. Caudofemoral musculature and the evolution of theropod locomotion. *Paleobiology* **16**, 170–186.

Gatesy, S.M. 1991. Hindlimb scaling in birds and other theropods: implications for terrestrial locomotion. *Journal of Morphology* **209**, 83–96.

Gatesy, S.M. and Dial, K.P. 1996. Locomotor modules and the evolution of avian flight. *Evolution* **50**, 331–340.

Gatesy, S.M. and Middleton, K.M. 1997. Bipedalism, flight, and the evolution of theropod locomotor diversity. *Journal of Vertebrate Paleontology* **17**, 308–329.

Gingerich, P.D. 1990. Prediction of body mass in mammalian species from long bone lengths and diameters. *Contributions of the Museum of Paleontology, University of Michigan* **28**, 79–92.

Hartwig-Scherer, S. 1993. Body weight prediction in early fossil hominids: towards a taxon-independent approach. *American Journal of Physical Anthropology* **92**, 17–36.

Henderson, D.M. 1999. Estimating the masses and centers of mass of extinct animals by 3-D mathematical slicing. *Paleobiology* **25**, 88–106.

Hurlburt, G. 1999. Comparison of body mass estimation techniques using recent reptiles and the pelycosaur *Edaphosaurus boanerges*. *Journal of Vertebrate Paleontology* **19**, 338–350.

Hylander, W.L. 1985. Mandibular function and biomechanical stress and scaling. *American Zoologist* **30**, 315–330.

Janis, C. 1990. Correlation of cranial and dental variables with body size in ungulates and macropodoids. *In* Damuth, J. and MacFadden, B.J. (eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, pp 255–299. Cambridge University Press, New York.

Jerison, H.J. 1973. *Evolution of Brain and Intelligence*. Academic Press, New York.

Jones, T.D., Farlow, J.O., Ruben, J.A., Henderson, D.M. and Hillenius, W.J. 2000. Cursoriality in bipedal archosaurs. *Nature* **406** (6797), 716–718.

Kurtén, B. 1967. Pleistocene bears of North America. 2. Genus *Arctodus*, short-faced bears. *Acta Zoologia Fennica* **117**, 1–60.

Lyman, R.L. 1994. *Vertebrate Taphonomy*. Cambridge University Press, Cambridge.

Mazzetta, G., Fariña, R.A. and Vizcaíno, S.F. 1998. Notes for the palaeobiology of the South American horned theropod *Carnotaurus*. In *Gaia, Theropod Paleobiology Special Volume*, edited by Pérez-Moreno, B., Holtz, T.R. Jr., Sanz, J.L. and Moratalla, J.J., **15**, 185–192.

MaMahon, T.A. and Bonner, J.T. 1983. *On Size and Life*. W.H. Freeman, New York.

Peczkis, J. 1994. Implications of body-mass estimates for dinosaurs. *Journal of Vertebrate Paleontology* **14**, 520–533.

Richards, R.L. and Turnbull, W.D. 1995. Giant short-faced bear (*Arctodus simus yukonensis*) remains from Fulton County, Northern Indiana. *Fieldiana Geology* **20**, 1–34.

Ruff, C. 1990. Body mass and hindlimb bone cross-sectional and articular dimensions in anthropoid primates. *In* Damuth, J. and MacFadden, B.J. (eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, pp 119–149. Cambridge University Press, New York.

Russell, D.A. and Dong, Z.-M. 1993a. The affinities of a new theropod from the Alxa Desert, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences* **30**, 2107–2127.

Russell, D.A. and Dong, Z.-M. 1993b. A nearly complete skeleton of a new troodontid dinosaur from the Early Cretaceous of the Ordos Basin, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences* **30**, 2163–2173.

Schmidt-Nielsen, K. 1984. *Scaling: Why is Animal Size so Important?*. Cambridge University Press, Cambridge.

Scott, K.P. 1990. Postcranial dimensions of ungulates as predictors of body mass. *In* Damuth, J. and MacFadden, B.J. (eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, pp 301–335. Cambridge University Press, New York.

Seebacher, F. 2001. A new method to calculate allometric length–mass relationships of dinosaurs. *Journal of Vertebrate Paleontology* **21**, 51–60.

Smith, R.J. 1981. Interpretation of correlations in interspecific allometry. *Growth* **45**, 291–297.

Smith, R.J. 1984. Allometric scaling in comparative biology: problems of concept and method. *American Journal of Physiology* **15**, R152–R160.

Smith, R.J. 1985. The present as a key to the past: body weight of Miocene hominids as a test of allometric methods for paleontological inference. *In* Jungers, W.L. (ed) *Size and Scaling in Primate Biology*, pp 437–447. Plenum Press, New York.

Sokal, R.R. and Rohlf, F.J. 1995. *Biometry*. W.H. Freeman and Co., New York.

Van Valkenburg, B. 1990. Skeletal and dental predictors of body mass in carnivores. *In* Damuth, J. and MacFadden, B.J. (eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, pp 181–205. Cambridge University Press, New York.

Varricchio, D.J. 1993. Bone microstructure of the Upper Cretaceous theropod dinosaur *Troodon formosus*. *Journal of Vertebrate Paleontology* **13**, 99–104.