

Body mass estimation in non-avian bipeds using a theoretical conversion to quadruped stylopodial proportions

Nicolás E. Campione^{1,2,3*}, David C. Evans^{1,4}, Caleb M. Brown^{1,5} and Matthew T. Carrano⁶

¹Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks St., Toronto, ON M5S 3B2, Canada;

²Palaeobiology Programme, Department of Earth Sciences, Uppsala University, Villavägen 16, SE-752 36 Uppsala, Sweden;

³Subdepartment of Evolution and Development, Department of Organismal Biology, Uppsala University, Norbyvägen 18A, SE-752 36 Uppsala, Sweden; ⁴Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, ON M5S 2C6, Canada; ⁵Royal Tyrrell Museum of Palaeontology, PO Box 7500, Drumheller, AB T0J 0Y0, Canada; and ⁶Department of

Paleobiology, Smithsonian Institution, National Museum of Natural History, PO Box 37012, MRC 121, 20013-7012 Washington, DC, USA

Summary

1. Body mass is strongly related to both physiological and ecological properties of living organisms. As a result, generating robust, broadly applicable models for estimating body mass in the fossil record provides the opportunity to reconstruct palaeobiology and investigate evolutionary ecology on a large temporal scale.

2. A recent study provided strong evidence that the minimum circumference of stylopodial elements (humerus and femur) is conservatively associated with body mass in living quadrupeds. Unfortunately, this model is not directly applicable to extinct bipeds, such as non-avian dinosaurs.

3. This study presents a new equation that mathematically corrects the quadruped equation for use in bipeds. It is derived from the systemic difference in the circumference-to-area scaling relationship of two circles (hypothetical quadruped) and one circle (hypothetical biped), which represent the cross-section of the main weight-bearing limb bones.

4. When applied to a newly constructed data set of femoral circumferences and body masses in living birds, the new equation reveals errors that are significantly lower than other published equations, but significantly higher than the error inherent in the avian data set. Such errors, however, are expected given the unique overall femoral circumference–body mass scaling relationship found in birds.

5. Body mass estimates for a sample of bipedal dinosaurs using the new model are consistent with recent estimates based on volumetric life reconstructions, but, in contrast, this equation is simpler to use, with the concomitant potential to provide a wider set of body mass estimates for extinct bipeds.

6. Although it is evident that no one estimation model is flawless, the combined use of the corrected quadrupedal equations and the previously published quadrupedal equation offer a consistent approach with which to estimate body masses in both quadrupeds and bipeds. These models have implications for conducting large-scale macroevolutionary analyses of body size throughout the evolutionary history of terrestrial vertebrates, and, in particular, across major changes in body plan, such as the evolution of bipedality in archosaurs and quadrupedality in dinosaurs.

Key-words: body mass estimation, dinosaurian, evolutionary biology, linear models, macroevolution, software, statistics, terrestrial bipeds

Introduction

Strong correlations exist between body mass and many physiological and ecological attributes in extant organisms (e.g. Brown, Marquet & Taper 1993; Burness, Diamond & Flannery 2001; Gillooly *et al.* 2001). Accurate estimates of body mass are therefore critical to understanding the palaeobiology of extinct taxa and the evolution of community structure through the history of life (e.g. Erickson, Rogers & Yerby

2001; Varricchio *et al.* 2008; Codron *et al.* 2012). Dinosaurs exhibit a large body mass range, with several species likely approaching the upper body mass limit for terrestrial vertebrates (Burness, Diamond & Flannery 2001; Sookias, Benson & Butler 2012). In addition, non-avian dinosaurs underwent major evolutionary shifts in limb posture and gait, including several transitions from bipedality to quadrupedality (Maidment & Barrett 2012) that may be associated with order of magnitude level increases in body mass. As a result, dinosaurs provide a valuable model for understanding body-size evolution and evolutionary ecology in terrestrial vertebrates (Carr-

*Correspondence author. E-mail: nicolas.campione@geo.uu.se

ano 2006; Turner *et al.* 2007; Brown *et al.* 2012; Codron *et al.* 2012; Sookias, Butler & Benson 2012; Benson *et al.* 2014). However, the capacity to reconstruct these patterns hinges on the ability to obtain accurate, consistent estimates of body mass across a large sample of taxa (Benson *et al.* 2014).

Campione & Evans (2012) showed that, despite previous criticisms, the relationship between total stylopodial (humerus + femur) circumferences and body mass is independent of gait, limb posture and phylogenetic history and that limb scaling models based on this relationship [first proposed by Anderson, Hall-Martin & Russell (1985)] provide a robust, consistent method with which to estimate body mass in terrestrial quadrupeds. Given that all limbs support weight in a quadruped, the model's applicability to extinct quadrupeds is evident from its integration of both fore and hind limb measurements. Weight-bearing constraints do not apply to the humerus of bipeds; thus, the quadrupedal equation (QE) does not directly apply to bipeds. Nevertheless, ~45% of known Mesozoic dinosaurs are bipedal theropods (genus-level data set in Barrett, McGowan & Page 2009), and both sauropodomorphs and ornithischians include bipedal taxa. It is likely that over half of all known Mesozoic dinosaur taxa had a bipedal gait. Consequently, investigations into the evolution of body size across major body plan transitions in dinosaurs – for example parallel evolution of quadrupedalism in sauropodomorphs, thyreophorans, marginocephalians and ornithopods (Maidment & Barrett 2012); the evolution of miniaturization and locomotion across the origin of birds (Carrano 1998; Turner *et al.* 2007; Allen *et al.* 2013; Dececchi & Larsson 2013; Puttick, Thomas & Benton 2014) – require a consistent model for estimating body mass in both quadrupeds and bipeds.

Current empirically-based equations for estimating body masses in bipeds are derived from avian data sets (Campbell & Marcus 1992; Field *et al.* 2013). Although these models have clear implications for estimating body masses in extinct birds, their applicability to extinct non-avian bipeds, such as non-avian dinosaurs, is limited because 1) scaling patterns of femoral circumference to body mass are not conserved in birds (Campbell & Marcus 1992; Doube *et al.* 2012; Field *et al.* 2013) as they are in extant quadrupeds (Campione & Evans 2012) and 2) the uppermost body mass of extant birds is almost two orders of magnitude below that of many non-avian theropods. As a result, estimates for non-avian bipeds (e.g. Turner *et al.* 2007) often rely on dinosaur-specific skeletal scaling equations using independently determined body masses of life reconstructions (Anderson, Hall-Martin & Russell 1985; Christiansen & Fariña 2004; O'Gorman & Hone 2012). Unfortunately, the errors associated with the inherent assumptions made by reconstructions (e.g. volume of lungs, muscle volume and tissue densities; see Hutchinson, Ng-Thow-Hing & Anderson 2007; Campione & Evans 2012; Brassey & Sellers 2014 for more detailed discussions) are difficult to constrain objectively or quantitatively, and hence their effect on estimation equations is unknown (previous equations are provided in Table S1).

Here we develop a new equation to estimate body mass in extinct bipeds based on a mathematical correction of the

quadrupedal equation (henceforward, the cQE). We test this new model within the context of (1) a large data set of extant birds, representing the only significantly diverse living bipeds and (2) a small sample of humans, of which we use the largest for comparison purposes. Finally, we apply the equation to a series of bipedal non-avian dinosaurs to compare results with previous estimates.

Mathematical details

The quadrupedal equation developed by Campione & Evans (2012) uses the combined circumferences of the major weight-bearing bones (humerus and femur). Circumference is simple to obtain and provides a proxy for cross-sectional surface area, which should be directly associated with the limb's weight-bearing capacity (although this still remains to be tested empirically) and therefore directly related to an animal's mass (Rubin & Lanyon 1984). As a result, given a constant body mass, the combined cross-sectional areas of the humerus and femur of a quadruped should equal that of the femur of a biped. Constant body mass should translate to equal cross-sectional area for the main weight-bearing bones, but this consistency will not translate to circumference, which will be higher in a quadruped compared to a biped of the same mass (Fig. 1). The difference in circumferences should be systemic and thus a purely mathematical factor (α) could be derived that permits use of QE to estimate a biped's mass, without resorting to outside volumetric model data (e.g. Anderson, Hall-Martin & Russell 1985; Seebacher 2001; Christiansen & Fariña 2004; O'Gorman & Hone 2012).

To derive α , one needs the relationship between circumference and area (Fig. 1). We initially model cross-sectional shape

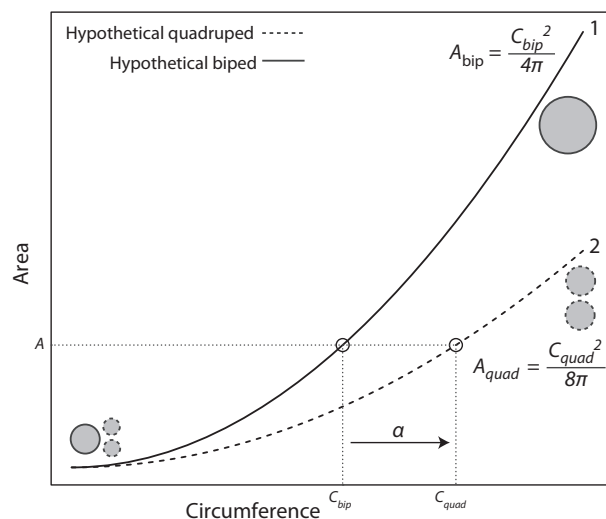


Fig. 1. Theoretical basis for deriving the correction factor. Functions are based on the relationship between the circumference and area of a circle. Solid line represents the relationship between the circumference and area of one circle (i.e. a hypothetical biped); line (1), and the dashed line represents the relationship between the total circumferences and total areas of two circles (i.e. a hypothetical quadruped), line (2). Dotted line depicts differences in circumference given constant area. Alpha (α) represents the correction factor that transforms line 1 into line 2.

as a circle, but later test for effects of cross-sectional shape on α . The circumference (C) to area (A) relationship of one circle (i.e. a hypothetical biped) is defined by:

$$A_{\text{bip}} = \frac{C_{\text{bip}}^2}{4\pi} \quad \text{eqn 1}$$

and the relationship between combined circumferences and the combined areas of two circles of equal size (i.e. a hypothetical quadruped) is:

$$A_{\text{quad}} = \frac{C_{\text{quad}}^2}{8\pi} \quad \text{eqn 2}$$

Given a constant body mass, the combined cross-sectional area of a quadruped will equal that of a biped (i.e. $A_{\text{bip}} = A_{\text{quad}}$). Therefore,

$$\frac{C_{\text{bip}}^2}{4\pi} = \frac{C_{\text{quad}}^2}{8\pi} \quad \text{eqn 3}$$

The systemic bias in the circumference of a biped and a quadruped in relation to area indicates that both values will be proportional to one another such that

$$C_{\text{bip}} \propto C_{\text{quad}} \quad \text{eqn 4}$$

and \therefore

$$\alpha \cdot C_{\text{bip}} = C_{\text{quad}} \quad \text{eqn 5}$$

where α is the bipedal correction factor of interest. Equation 5 is then inserted into eqn 3, and solved for α ; resulting in $\alpha = \sqrt{2}$.

Insertion of α into the phylogenetically corrected QE of Campione & Evans (2012) results in:

$$\log_{10} \text{BM} = 2.754 \cdot \log_{10}(C_{\text{femur}} \cdot \sqrt{2}) - 1.097 \quad \text{eqn 6}$$

thus making the cQE:

$$\log_{10} \text{BM}_{\text{bip}} = 2.754 \cdot \log_{10}(C_{\text{femur}}) - 0.683 \quad \text{eqn 7}$$

where BM_{bip} is the body mass of the biped and C_{femur} is its femoral circumference.

Methodological assumptions

The derivation of the cQE demonstrates that α is determined by taking the square root of the quotient of the intercept values of the two hypothetical models (i.e. b in the power function $b \cdot x^m$). In its raw form, α pre-supposes that the humerus and femur of a quadruped are equal in circumference (i.e. $C_h/C_f = 1$). However, animals rarely have humeri and femora of the same size (Table 1; see also Carrano 2001), a pattern that is most evident in euarchontoglires (mean $C_h/C_f = 0.845$; 1 SD = ± 0.143) and marsupial (0.855 ± 0.146) mammals, and even more pronounced in quadrupedal dinosaurs [e.g. *Edmontosaurus regalis*, $C_h/C_f \approx 0.517$ (Campione in press); *Apatosaurus louisae*, $C_h/C_f \approx 0.744$ (Anderson, Hall-Martin & Russell 1985)]. It may therefore be expected that proportional differences between these bones will have an effect on α . To test this, α was re-derived using a modified hypothetical quadrupedal relationship, in which $C_h/C_f = 0.5$. Based on this criterion,

Table 1. Average proportional differences between the circumference of the humerus and femur in a sample on extant terrestrial tetrapods

Clade	<i>N</i>	mean C_h/C_f	SD	95% CI
Tetrapoda	255	0.943*	0.176	0.921 to 0.964
Mammalia	200	0.932*	0.184	0.906 to 0.957
Carnivora	48	1.011	0.131	0.973 to 1.049
Euarchontoglires	81	0.845*	0.143	0.813 to 0.876
Marsupialia	14	0.855*	0.146	0.77 to 0.939
Ungulata	41	1.008	0.136	0.965 to 1.051
Reptilia	47	0.968	0.113	0.934 to 1.001
Lissamphibia	8	1.069	0.229	0.878 to 1.261

Data are from Campione & Evans (2012). *Denotes a significant difference from unity ($P < 0.05$); *N*, sample size; C_h , humeral circumference; C_f , femoral circumference; SD, one standard deviation.

the revised function is:

$$A_{\text{quad}} = \frac{5 \cdot C_{\text{quad}}^2}{36\pi} \quad \text{eqn 8}$$

and the associated $\alpha = \sqrt{1.8}$. However, $C_h/C_f = 0.5$ represents a much larger difference between stylopodial bones than the average for mammals and reptiles, the empirical basis for the QE. A more realistic proportion, $C_h/C_f = 0.9$ (Table 1), results in the hypothetical quadrupedal function:

$$A_{\text{quad}} = \frac{2263 \cdot C_{\text{quad}}^2}{18050\pi} \approx 0.0399 \cdot C_{\text{quad}}^2 \quad \text{eqn 9}$$

in which $\alpha = \sqrt{9025/4526} \approx \sqrt{1.994}$. Such a small difference suggests that proportional differences in the size of the humerus and femur will not play a major role in the final body mass estimates of bipedal taxa.

The correction factor also assumes equal cross-sectional shape of the proximal weight-bearing bones between bipeds and quadrupeds, and between the fore- and hind limb of quadrupeds. On average, terrestrial vertebrates exhibit subcircular cross-sections. Carrano (2001) found that the proportional difference between mediolateral and anteroposterior diameters (i.e. eccentricity) of the femur was not significantly different from unity in both mammals ($D_{\text{ML}}/D_{\text{AP}} = 1.129 \pm 0.228$) and bipedal dinosaurs ($D_{\text{ML}}/D_{\text{AP}} = 1.027 \pm 0.233$). However, the wide standard deviations around these means suggest that several taxa deviate from circularity. At least in dinosaurs, this deviation is associated with body size such that larger taxa have distinctly elliptical cross-sections, which is hypothesized to better accommodate increased mediolateral forces generated at large size (Wilson & Carrano 1999; Carrano 2001; Maidment *et al.* 2012). To accommodate these empirical observations, we modified the hypothetical quadrupedal function using the mean eccentricity of the femur ($D_{\text{ML}}/D_{\text{AP}} = 1.027$) as observed in mammals by Carrano (2001), and the mean humeral eccentricity ($D_{\text{ML}}/D_{\text{AP}} = 0.831$) calculated from a carnivoran sample (Bertram & Biewener 1990). These, in combination with an approximate 10% difference in the circumference of the humerus and femur (see previous paragraph), result in the function: $A_{\text{quad}} \approx 0.0394 \cdot C_{\text{quad}}^2$. Because the hypothetical bipedal function depends on femoral

eccentricity, we present a range of α values that can be incorporated into the cQE (See Table S2). Although any of these correction factors can be used, eccentricity is not expected to greatly affect α as even the most extreme values differ by an $\alpha < 0.15$.

Empirical tests

METHODS

To empirically test the cQE (as originally derived, $\alpha = \sqrt{2}$), we applied it to a data set of femoral circumferences collected from 161 extant bird species spanning almost 3.5 orders of magnitudes in body mass (from 53 g *Coccyzus melacoryphus* to 139 kg *Struthio camelus*). All avian measurements were taken from specimens for which live body mass is known. We also measured the length of the femur and the circumferences and lengths of the humerus and tibiotarsus. Circumference was measured at the thinnest part of the limb bone (as per Anderson, Hall-Martin & Russell 1985; Campbell & Marcus 1992; Campione & Evans 2012; Field *et al.* 2013), and length was taken as the maximum articular length of the bone (see Data S1).

In addition to testing the cQE (eqn 6 and 7), we estimate the body masses of avian specimens using the following three alternative equations: (1) the extant avian regression equation of femoral circumference and body mass of Campbell & Marcus (1992; CM) based on their sample of 795 non-passerine specimens representing 391 species; (2) the bipedal equation of Anderson, Hall-Martin & Russell (1985; AHR), based on the same slope obtained from their quadrupedal regression and the intercept corrected based on a volumetric mass estimate of *Troodon formosus*; and (3) the femoral circumference-to-body mass equation of Christiansen & Fariña (2004; CF) based on measurements of 16 non-avian theropods for which body masses were determined by calculating the volume of clay models and an assumed body density of 0.95 g/cm³. The standard error of the estimate and the per cent prediction error (PPE = $(|BM_{\text{true}} - BM_{\text{estimate}}| / BM_{\text{estimate}}) \times 100$) were calculated for each equation, as well as for the regression between the true body mass and femoral circumference; PPE values were compared using a two-tailed *t*-test.

As an additional evaluation of α , we applied it to the heaviest individual (following Campione & Evans 2012) within a

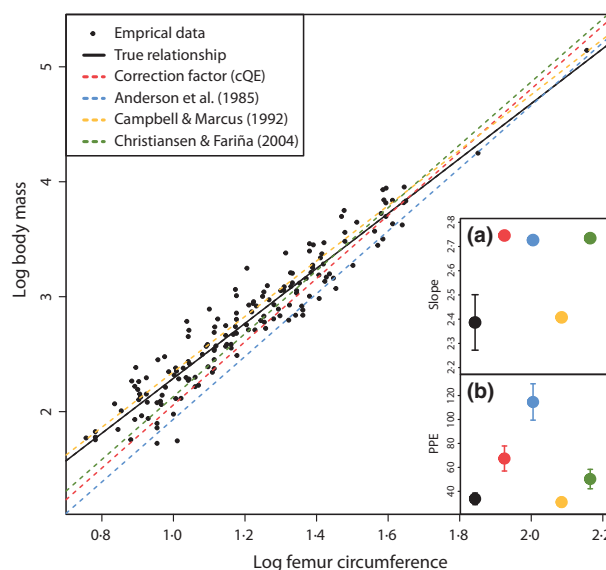


Fig. 2. Plot and regression of femoral circumference to body mass in a sample of 161 extant birds. Solid black line indicates the true relationship of the avian data (based on the black points). Dashed lines represent the regression equations that can be used to estimate the body mass of a biped from femoral circumference. Insets on the bottom right show the slope for each equation (Inset a) and the mean and 95% confidence intervals of the per cent prediction error associated with each model (Inset b). Avian data set and the values used in the insets can be found in the supporting information (see Data S1 and Table S3, respectively).

sample of ten humans for which body mass was known (see Data S2). Results were graphically examined within the context of the quadrupedal data presented by Campione & Evans (2012). Most analyses were conducted using standard statistical packages within R (R Development Core Team 2012; e.g. 'stats'). Line-fitting analyses used 'smatr' (Warton *et al.* 2011) and mass estimations, using cQE, QE, AHR, CM and CF, as well as PPEs and SEEs were generated through the new package 'MASSTIMATE' (Appendix S1).

RESULTS

In the sample of 161 avians, the relationship between femoral circumference and body mass exhibits the strongest support values (Table 2), followed by the relationship between tibiotar-

Table 2. OLS regression results between various limb measurements (*x*-axis) and body mass (*y*-axis) in extant birds. Scaling equation in format $y = mx + b$. AIC, Akaike Information Criterion, PPE, mean per cent prediction error, SEE standard error of the estimate; C, circumference; L, length

Proxy	<i>N</i>	<i>m</i>	<i>m</i> 95% CI	<i>b</i>	<i>b</i> 95% CI	<i>R</i> ²	PPE	SEE	AIC
<i>C</i> _{femur}	161	2.39	2.275 to 2.505	−0.1	−0.241 to 0.041	0.914	33.8	0.175	−98
<i>L</i> _{femur}	161	2.432	2.28 to 2.585	−1.479	−1.749 to −1.209	0.862	45.7	0.222	−21
<i>C</i> _{tibiotarsus}	148	2.407	2.272 to 2.542	0.018	−0.141 to 0.177	0.895	38.5	0.193	−60
<i>L</i> _{tibiotarsus}	148	2.054	1.878 to 2.231	−1.286	−1.64 to −0.932	0.784	60.5	0.275	44
<i>C</i> _{humerus}	108	2.478	2.304 to 2.651	−0.274	−0.49 to −0.058	0.883	41.5	0.193	−43
<i>L</i> _{humerus}	109	1.916	1.685 to 2.146	−0.802	−1.235 to −0.368	0.717	79.2	0.299	52

sal circumference and body mass. These results corroborate those of Campione & Evans (2012) and Field *et al.* (2013) in that circumferences correlate better with body mass than lengths, and that mass is best predicted by stylopodial, rather than zeugopodial, limb bones. In contrast to Field *et al.* (2013), our data set indicates that the humerus of birds is weakly correlated with body mass. Although this difference may be due to sample size and/or differences in data collection practices (e.g. use of actual vs. mean body masses), it most likely reflects variation in taxonomic sampling. Our data set is intentionally biased towards terrestrial birds and includes palaeognaths, which were excluded by Field *et al.* (2013) as they were interested in generating estimates for flying birds. Despite the low mean PPE calculated for the femoral circumference-to-body mass regression (33.8%) relative to other measurements, it is significantly higher than the mean PPE obtained in the relationship between combined stylopodial circumferences and body mass in terrestrial quadrupeds (Campione & Evans 2012: 25.6%; $t = 2.82$; $P \ll 0.01$). A higher mean PPE value (and lower coefficient of determination) supports the assertion that extant birds exhibit greater variation in limb scaling patterns than extant quadrupeds (Doube *et al.* 2012). Body mass estimates based on the cQE reveal a mean PPE of 68.8% (Fig. 2), which is significantly higher than that present in the empirical data ($t = 5.331$, $P \ll 0.01$). The CF model has a mean PPE of 50.3% and is also significantly higher than the true mean PPE ($t = 3.445$, $P \ll 0.01$). The CM model exhibits a low mean PPE that is virtual identical to that calculated from the empirical data set (PPE = 31%; $t = -0.884$, $P = 0.378$). Most notably, the commonly used AHR model exhibits a very high PPE at 114.6%, significantly higher than that obtained from both the cQE and true mean PPE ($t = 5.523$; $P \ll 0.01$; $t = 10.019$, $P \ll 0.01$, respectively).

Figure 2 shows a bivariate plot between femoral circumference and body mass of the extant avian data set on which the regression lines of proposed body mass estimation equations have been superimposed (dashed lines). These reveal possible systemic differences between estimates and the avian empirical data. Such differences are also evident in that the slope and intercept coefficients of estimated lines do not fall within the 95% confidence intervals of the bird data set (Fig. 2, inset a). Systemic error is most evident in the AHR model, which underestimates small-bodied taxa (Fig. 2, inset B). In comparison, the cQE and particularly the CF equations overestimate large-bodied birds. Not surprisingly, estimates based on the CM avian model provide the best fit to the avian sample (Fig. 2, inset b).

Finally, to test the hypothesis that the cQE can be applied to humans, the correction factor ($\alpha = \sqrt{2}$) was applied to the heaviest individual (70 kg) in a sample of ten humans. The corrected datapoint occurs within the range of variation of extant quadrupeds and within the 95% prediction intervals (Fig. 3).

Discussion

The cQE derived here provides an adjustment for the difference in intercepts between bipeds and quadrupeds and thereby

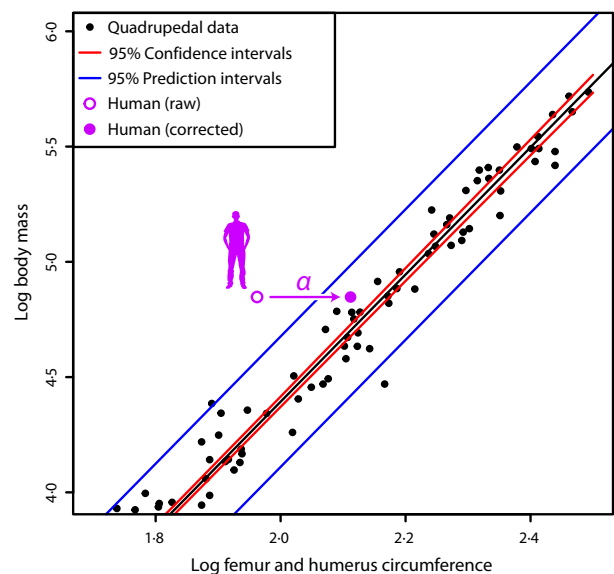


Fig. 3. Human femoral circumference and body mass within the context of extant quadrupeds. Quadrupedal data from Campione & Evans (2012) up-scaled to show the occurrence of adult humans. Human datapoint represents the largest individual in a sample of 10 specimens, displayed using both its raw femoral circumference data and that corrected using $\alpha = \sqrt{2}$.

permits use of the QE for estimating mass in bipeds. All body mass estimation techniques, however, have caveats that require further discussion. The cQE assumes that extinct bipeds exhibit a similar scaling coefficient (i.e. slope) to that of terrestrial quadrupeds. This assumption needs further discussion because (1) the femoral circumference-to-body mass scaling coefficient in extant birds [$m = 2.39$; 95% CI = ± 0.115 (See Table S3)] – the only extant bipedal group with a large sample size – is significantly below that of terrestrial quadrupeds [$m = 2.749 \pm 0.038$ (Campione & Evans 2012)], (2) the cQE exhibits a significantly higher mean PPE than that inherent to the avian data set (Fig. 2) and (3) many extinct bipeds (i.e. non-avian theropods) are stem-group birds (e.g. Turner *et al.* 2007). Consequently, should extinct non-avian bipeds follow the apomorphic scaling relationship recovered in birds, or do they retain the conserved and plesiomorphic relationship recovered in terrestrial quadrupeds?

Avians exhibit numerous derived attributes of skeletal limb morphology and ecology that could cause their femoral circumference-to-body mass scaling relationship to depart from the ancestral pattern. In particular, the majority of birds have highly pneumatic femora, which represent an invasion of the respiratory system into the major limb bones (Hutchinson 2001; O'Connor 2006). Biomechanically, pneumatic bones are generally considered to be weaker than marrow-filled bones (Cubo & Casinos 2000; Casinos & Cubo 2001), which may explain why avian femoral circumference follows patterns predicted by elastic ($m = 2.67$) or even static ($m = 2.5$) similarity (Table 2; McMahon 1973, 1975; Campbell & Marcus 1992; Cubo & Casinos 1998, 2000; Casinos & Cubo 2001). Greater relative levels of femoral robustness in birds were also

predicted because of their horizontally oriented femora, which incurs an increase in torsion (Carrano & Biewener 1999). It should be noted, however, that a trend towards a more horizontally oriented femur likely started prior to the origin of Aves (Allen *et al.* 2013). Nevertheless, given that non-avian bipedal dinosaurs do not possess pneumatic limb bones and most exhibit an upright femoral posture (O'Connor 2006; Benson *et al.* 2011), they may be expected to follow plesiomorphic scaling patterns exhibited by extant terrestrial quadrupeds. This assertion is supported by the observation that among birds both Charadriiformes and Gruiformes, which are clades of terrestrial or wading birds (i.e. walking) with apneumatic femora, appear to depart from the overall scaling pattern and exhibit higher scaling coefficients that are more similar to the quadrupedal pattern ($N = 44$, $m = 2.946$; $N = 21$, $m = 2.678$; See Fig. S1 and Table S4). Other clades of birds (for which a sample of ten or more could be obtained) exhibit lower scaling coefficients. These clades include some, if not all, species with pneumatic femora (See Data S1). Although this pattern requires further testing, it suggests that pneumaticity plays a role in dictating femoral circumference–body mass scaling patterns in extant birds. Current studies, however, indicate that femoral pneumaticity evolved after the common ancestor of Aves, and within neornithine birds (Casinos & Cubo 2001; Hutchinson 2001).

Scaling of femoral proportions in extinct bipedal dinosaurs (including non-avian theropods) also supports plesiomorphic body mass scaling relationships in non-avian bipeds. Carrano (1998) investigated femoral scaling patterns in dinosaurs within the context of extant mammals and birds and found that dinosaurian patterns (including non-avian bipedal dinosaurs) were more similar to extant mammals than to extant birds, leading to the assertion that the mammals (on which a large portion of the QE is based) may represent a better model for limb scaling patterns in non-avian dinosaurs.

Finally, the applicability of an avian scaling relationship to taxa such as non-avian dinosaurs is limited by the upper body mass limit of extant birds (~140 kg; See Data S1). Approximately 50% of currently known non-avian bipedal dinosaurs fall above the bird range [41% of non-avian theropods based on the data sets of O'Gorman & Hone (2012)], incurring significant extrapolation by as much as two orders of magnitude. By contrast, only 2% of theropods (such as *Tyrannosaurus rex*) may occur above the upper body mass limit of extant quadrupeds (>6000 kg), incurring less than half an order of magnitude extrapolation.

When applied to the bird data set, cQE exhibits high PPE values (Fig. 2). Therefore, we suggest that our results do not support the use of the cQE for estimating the body masses of extinct avians, for which bird-specific equations are clearly the model of choice. For instance, Field *et al.* (2013) found low prediction errors when using the maximum diameter of the coracoid glenoid in a sample of flying birds. However, high PPE values are explained, at least in part, by the observations that (1) extant birds exhibit apomorphic scaling patterns between body mass and stylopodial circumference relative to that exhibited in extant quadrupedal tetrapods and (2) avian

scaling trajectories vary between major clades. In combination with the observations that avian-based scaling equations can incur substantial extrapolation, and non-avian extinct bipeds (such as non-avian dinosaurs) exhibit limb-proportional scaling patterns that are consistent with those of non-avian rather than avian taxa, we argue that avian-based circumference–body mass equations are not adequate to estimate body mass in non-avian bipeds and advocate for the use of the cQE as an alternative.

Estimating body mass in non-avian bipeds

In addition to the cQE, both the AHR and CF models represent circumference-based mass estimation equations not generated via avian data sets. In their recent examination of dinosaur body size distributions, O'Gorman & Hone (2012) provide a similar equation to CF based on femur length. Campione & Evans (2012) showed that femur length is a poor predictor of body mass compared to circumference and hence this model was not examined here. When we apply all three circumference-based equations to the sample of 161 birds, the results reveal that they all exhibit a significantly higher amount of error compared to that inherent in the avian data set. However, the cQE and CF exhibit much lower errors relative to the widely used AHR, which showed, on average, errors above 100% (Fig. 2). Given such large errors, we strongly advocate against its usage and therefore do not discuss AHR further.

The CF model is similar in both coefficients and error to the cQE. Although the former has significantly lower PPE than the latter, both equations provide very similar estimates for a sample of bipedal dinosaurs (Table 3), and both are operationally straightforward. We note four advantages of the cQE model over that of CF. First, their model is generated from a sample of non-avian theropods that range from an estimated 16.5 kg to 6300 kg, thereby excluding small bipedal dinosaurs (e.g. Turner *et al.* 2007; Butler *et al.* 2009). Except for the largest order of magnitude (>10 tonnes), all non-avian dinosaurs occur within the body mass range of the extant quadrupedal data set of Campione & Evans (2012), limiting unnecessary extrapolation.

Secondly, the CF model is based on fleshed-out volumetric reconstructions of large non-avian theropods, which can have unpredictable results on estimation model equations. This unpredictability is evident when the model data from Table 3 (Paul 1997; Henderson 1999; Seebacher 2001) are included into the CF model, thereby increasing its sample size from 16 to 32, and its mass range from 2.5 to 4 orders of magnitude. In general, inclusion of additional data should help constrain a model, but in this case PPE increased significantly from 50% to 124% (Table S4). These drastic differences in support reflect the broad ranges of body masses that result from the various assumptions incurred when generating reconstructions. For instance, mass estimates based on reconstructions of the same specimens of *Giganotosaurus carolinii* and *Herrerasaurus ischigualastensis* vary by as much as 100% (Table 3). In contrast, the cQE is based on a large empirical data set that involves minimal assumptions, and errors are easy to constrain.

Table 3. Body mass estimates (in kg) for a sample of non-avian bipedal dinosaurs using cQE (in bold) compared to those obtained using volumetric reconstructions and other equations. Ranges in brackets represent the 25% prediction error range (Campioni & Evans 2012). Eccentricity (ECC) values match those in Table S2, which correspond to a specific α value (if missing, $\alpha = \sqrt{2}$). Acronyms for the equation-based estimates follow those described in the text; H1999, estimates using Henderson (1999), sometimes reported in Butler *et al.* (2009), Therrien & Henderson (2007), or Henderson & Snively (2004); P1997, estimates from Paul (1997), S2001, estimates from Seebacher (2001)

Taxon	Sp #	C_f	D_{ML}	D_{AP}	ECC	Volumetric-based			Equation-based			
						P1997	H1999	S2001	CF	AHR	CM	cQE
Ornithischia												
<i>Fruitadens haagarorum</i>	LACM 115727	19.6	–	–	–	–	0.74	–	0.85	0.54	1.12	0.75 (0.56–0.94)
<i>Lesothosaurus diagnosticus</i>	BMNH RUB17	41.5	12.3	10.5	1.2	2.4	–	–	6.7	4.2	6.9	5.9 (4.4–7.4)
<i>Jeholosaurus shangyuanensis</i>	IVPP V15939	50.2	–	–	–	–	–	–	11.2	7	10.9	10 (7.5–12.5)
<i>Gasparinisaura cincosaltensis</i>	MUCPv 219	55	–	–	–	13 ¹	–	–	14.4	9	13.5	12.9 (6.7–16.1)
<i>Stegoceras validum</i>	UALVP 2	60.5	17.9	19.5	0.9	–	–	26.7	18.7	11.7	17	16.9 (12.6–21.1)
<i>Hyposilophodon foxii</i>	BMNH R192	70	21.2	22.2	1	–	–	–	27.9	17.4	24.2	25.4 (19.31–8)
<i>Homalocephale calathocercos</i>	MPC-D 100/1201	83	–	–	–	–	–	–	44.4	27.8	36.5	40.1 (30–50.1)
<i>Dryosaurus altus</i>	YPM 1876	138	42.1	40.3	1	103	–	104.3 ²	179	111	124	164 (124–206)
<i>Thescelosaurus neglectus</i>	AMNH 5891	183	61.2	56.3	1.1	–	–	–	387	240	245	356 (267–445)
Prosauropoda												
<i>Massospondylus carinatus</i>	BP/1/4934	209	–	–	–	–	–	–	557	345.2	338	510 (382–637)
<i>Plateosaurus engelhardti</i>	MBR 4398	253	79.4	64.7	1.2	–	–	–	939	582	536	855 (641–1069)
Theropoda												
<i>Mahakala omnogovae</i>	GI 100/1033	19.9	–	–	–	–	–	–	0.89	0.56	1.17	0.79 (0.59–0.98)
<i>Velociraptor mongoliensis</i>	MPC-D 100/25	64	17.1 ³	19.2 ³	0.9	11	–	–	21.8	13.7	19.5	19.7 (14.8–24.6)
<i>Ornithomimus edmontonicus</i>	ROM 851	110	25.3	29.2	0.9	111	–	–	96	59.9	71.9	87.5 (65.6–109)
<i>Deinonychus antirrhopus</i>	MCZ 4371	116	37.8	32.1	1.2	–	–	–	111	69.2	81.7	99.8 (74.8–125)
<i>Herrerasaurus ischigualastensis</i>	PVL 2566	170	55.1	54.4	1	124	64.33	348	316	196	205	292 (219–366)
<i>Gallimimus bullatus</i>	GI 100/11	216	–	–	–	438	–	586	609	378	366	558 (418–697)
<i>Majungasaurus crenatissimus</i>	FMNH PR 2278	323	–	–	–	–	–	–	1833	1133	965.4	1690 (1267–2112)
<i>Carnotaurus sastrei</i>	MACN-CH 894	325	94.6	95.6	1	2070	–	–	1864	1152.3	979.8	1743 (1306–2179)
<i>Albertosaurus sarcophagus</i>	ROM 807	340	123.6	85.2	1.5	2500	–	–	2110	1303	1092	1768 (1325–2210)
<i>Gigantoraptor erlianensis</i>	LH V0011	349	–	–	–	2000	–	–	2266	1400	1163	2092 (1569–2614)
<i>Allosaurus fragilis</i>	AMNH 680	381	129	115.7	1.6	–	–	–	2881	1778	1438	2681 (2010–3353)
<i>Daspletosaurus torosus</i>	AMNH 5438	390	–	–	–	2400	–	–	3071	1896	1521	2840 (2130–3550)
<i>Gorgosaurus libratus</i>	CMN 530	394	103	133	0.8	2340 ⁴	2795 ⁴	2465 ⁴	3158	1949	1559	2861 (2145–3577)
<i>Suchomimus tenerensis</i>	MNN GDF 500	408	145.2	85.7	1.7	2500	5207	3816	3475	2144	1696	2709 (2032–3387)
<i>Acrocanthosaurus atokensis</i>	NCSM 14345	427	142.7	123.6	1.2	4400	5672	–	3937	2428	1892	3613 (2708–4517)
<i>Mapusaurus roseae</i>	MCF-PVPH-108.234	455 ⁵	–	–	–	–	–	–	4682	2887	2205	4342 (3265–5427)
<i>Tyrannotitan chubutensis</i>	MPEF-PV 1156	500	–	–	–	–	–	–	6064	3735	2768	5630 (4221–7039)
<i>Giganotosaurus carolinii</i>	MUCPv-CH 1	521	174.6	152.4	1.1	6850	13 807	6595	6787	4179	3057	6349 (4759–7938)
<i>Tyrannosaurus rex</i>	CM 9380	534	–	–	1.2 ⁶	5700	7908	6651	7261	4470	3244	6688 (5014–8361)

¹Based on MUCPv-215; ²Based on numerous specimens including YPM 1876; ³Based on IGM 100/988; ⁴Based on AMNH 5458; ⁵Femur crushed;

⁶Based on the mean ECC in Table 5. For institutional abbreviations, please see Appendix S2.

Table 4. Comparisons of body mass estimates for extant facultative bipeds using the cQE and QE. The per cent prediction error (PPE) is shown for all taxa, along with the mean for each clade and the total sample used here. Standard deviation of the PPE (SD) and standard error of the estimate (SEE) were calculated for the clades and the total sample. SEE is calculated using log-transformed (base 10) data and results

Taxon	cQE			QE		
	PPE (%)	SD	SEE	PPE (%)	SD	SEE
Macropodidae	36.9	16.8	0.142	25.7	8.3	0.124
<i>Bettongia penicillata</i>	16.1	–	–	17.9	–	–
<i>Dendrolagus inustus</i>	32.7	–	–	37.4	–	–
<i>Macropus fuliginosus</i>	55.9	–	–	23.5	–	–
<i>Macropus rufus</i>	43.1	–	–	24	–	–
Primates	97.9	82.5	0.309	24.5	15.8	0.146
<i>Lemur catta</i>	29.2	–	–	31.8	–	–
<i>Macaca fuscata</i>	25.9	–	–	48.2	–	–
<i>Papio cynocephalus</i>	100.8	–	–	18.8	–	–
<i>Papio hamadryas</i>	104.3	–	–	15.6	–	–
<i>Pongo Pygmaeus</i>	229.4	–	–	8.1	–	–
TOTAL	70.8	67.4	0.249	25	12.3	0.147

Thirdly, cQE appears to better estimate the body mass of ratites, including the largest extant bird (*Struthio camelus*; 139 kg). Although small sample size ($N = 3$) precludes a meaningful statistical comparison, ratites exhibit a 25.7% mean PPE under the cQE, compared to 35.8% under the CF model.

Finally, the baseline data set used to develop cQE is the same as for the QE. Consequently, both equations can be used in concert, thereby offering a consistent method with which to estimate body masses in both quadrupeds and bipeds without the need to invoke multiple data sets (i.e. birds) or external data sources (i.e. volumetric reconstructions). In addition, given the broad extant sample on which the cQE is based and its possible applicability to humans (Fig. 3) and hence their bipedal ancestors, this new model is evidently not limited to bipedal dinosaurs, but rather offers the possibility to investigate the evolution of body size across all postural transitions in terrestrial tetrapod evolution (Spoor, Wood & Zonneveld 1994; Steudel 1996; Berman *et al.* 2000; Nesbitt & Norell 2006; Kivell & Schmitt 2009; Maidment & Barrett 2012).

One last discussion point regards the applicability of the cQE and QE to facultative bipeds (i.e. taxa that can locomote both quadrupedally and bipedally). Large-scale studies of body mass evolution in extinct vertebrates are likely to encounter such locomotor styles, especially those interested in reconstructing evolutionary patterns across the quadruped to biped transition and vice versa. We tested the cQE and the QE in a sample of nine extant facultative bipeds (including primates and macropods) from the data set of Campione & Evans (2012). The results (Table 4) indicate that, overall, the strict application of the QE outperforms the cQE, most notably in baboons and the orangutan. In other cases, however, the errors are comparable indicating that either could be used. Nevertheless, because of the larger range in errors (high standard deviations) obtained when using the cQE, we advocate

Table 5. Body mass (in kg) estimates of *Tyrannosaurus rex* using the cQE. Ranges in brackets provide the 25% prediction error range determined by Campione & Evans (2012). ECC, eccentricity, follows Table S2

Specimen	C_f (mm)	D_{ML}	D_{AP}	ECC	Body mass
FMNH PR 2081	579	188.1	119.9	1.6	7377 (5531–9224)
RSM P2523.8	570	–	–	1.2	8004 (6000–10 007)
CM 9380	534	–	–	1.2	6688 (5014–8361)
MOR 555	520	168.2	139	1.2	6216 (4660–7772)
BHI 3033	505	137.2	168	0.8	5667 (4248–7085)

for the use of QE when estimating the body mass of facultative bipeds.

Application to bipedal non-avian dinosaurs

We applied the cQE to a sample of 30 bipedal ornithischian and saurischian dinosaurs (Table 3). Body mass estimates were made using the newly developed ‘MASSTIMATE’ package in R (see Appendix S1; Campione 2013). These estimates are, in general, more consistent with those obtained using volumetric reconstruction methods than previous scaling equations, which predict much lower body mass estimates at larger sizes (>100 kg; Table 3). Based on femoral circumference, the tyrannosaurid, *Tyrannosaurus rex*, was the heaviest theropod with an estimated body mass as high as 8 tonnes for the largest specimens (RSM P2523.8 and FMNH PR 2081, Table 5). *Tyrannosaurus rex* is followed by three South American carcharodontosaurids, *Giganotosaurus carolinii* (6.4 tonnes), *Tyrannotitan chubutensis* (5.6 tonnes) and *Mapusaurus roseae* (4.3 tonnes). At the lower body mass range, the estimate for *Fruitadens haagarum*, putatively the smallest ornithischian at 750 g, is almost identical to that using a volumetric model (Butler *et al.* 2009) and is very similar in mass to the smallest non-avian theropod, *Mahakala omnogovae* (Turner *et al.* 2007), at 780 g.

Body mass estimates of *Tyrannosaurus rex* have been presented by nearly all mass estimation studies in dinosaurs (Colbert 1962; Alexander 1985; Anderson, Hall-Martin & Russell 1985; Campbell & Marcus 1992; Paul 1997; Henderson 1999; Seebacher 2001; Christiansen & Fariña 2004; Bates *et al.* 2009; Hutchinson *et al.* 2011). As a result, *T. rex* represents a model taxon for comparing estimates between methods. Results are presented in Fig. 4 and Table 5 and reveal similar patterns to that presented in Table 3, in which the cQE provides estimates more consistent with volumetric reconstructions than previous limb scaling equations (i.e. CM and AHR models). Although these results suggest a heavier mass estimate for the largest specimens of *T. rex* (FMNH PR 2081: 7.4 tonnes and RSM 2523.8: 8 tonnes; Table 5) than traditional estimates for the species (generally around 6 tonnes: e.g. Paul 1997; Seebacher 2001), it approximates the lower bounds recently published by Hutchinson *et al.* (2011; 10 tonnes) for the former specimen, and occurs very close to the 6000–8000 kg range that they suggested as a mean mass for this species. Based on the cQE, the

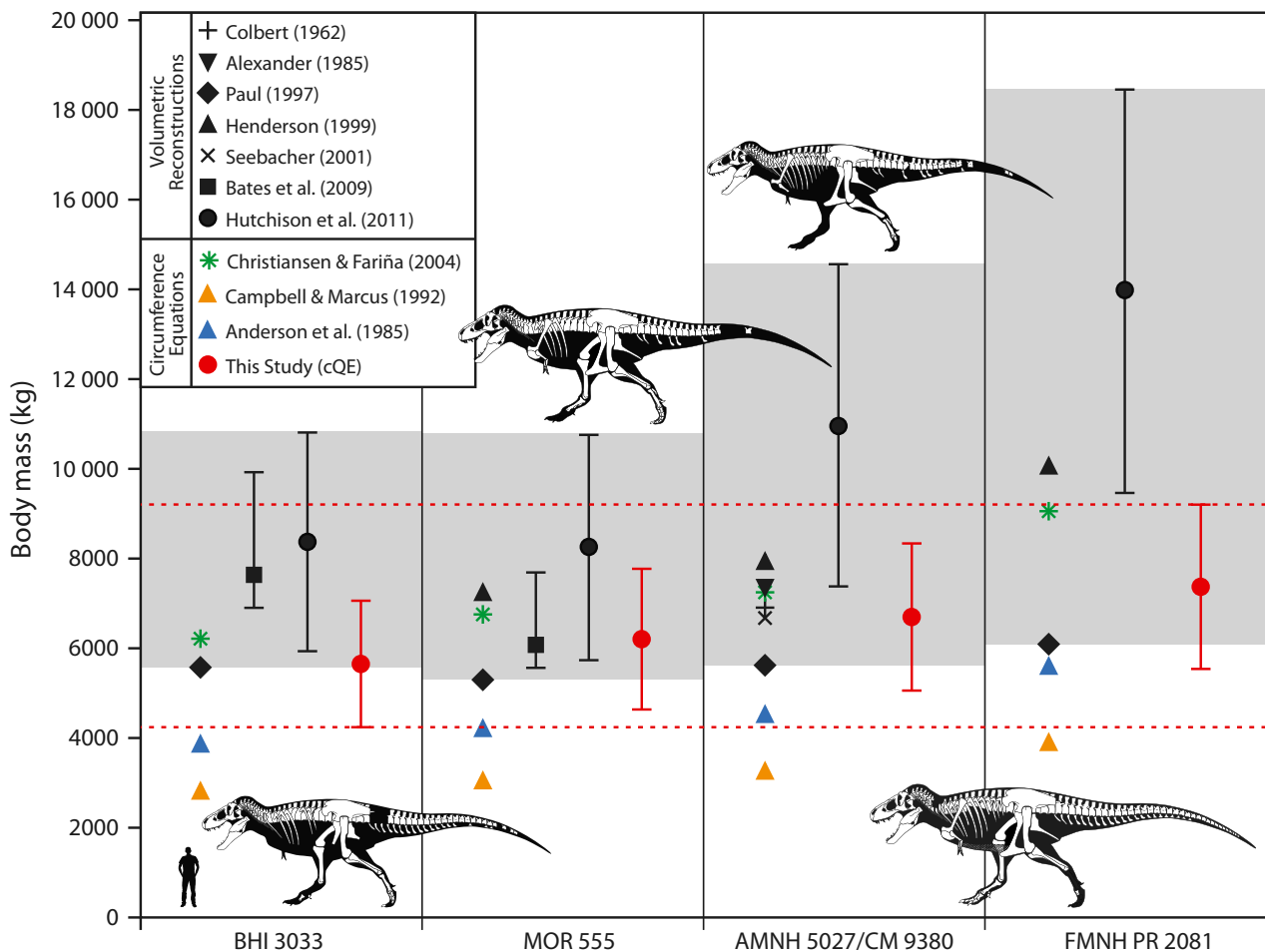


Fig. 4. Comparison of body mass estimates for four commonly cited specimens of *Tyrannosaurus rex*. Coloured symbols represent estimates based on equations of femoral circumference to body mass, and black symbols represent body mass estimates based on volumetric reconstructions. Error bars represent the ranges presented by the respective studies, and the grey area represents the total body mass range based on all volumetric reconstructions of each specimen. Dashed lines represent the body mass range provided by the cQE, incorporating a 25% error for each specimen (4248–9224 kg). Skeletal reconstructions depict the bones preserved for each specimen or composite (silhouettes and reconstructions are modified with permission from Scott Hartman).

four exemplars in Fig. 4, and a 25% mean prediction error, an adult *T. rex* ranged anywhere from 4248 to 9224 kg. Acknowledging such errors in estimates is rarely done, as shown by a lack of error bars in most *T. rex* mass estimates (Fig. 4), but represents a crucial component if one is to adequately interpret the ecology and physiology of *T. rex* and any other extinct taxon (e.g. growth rates; Erickson *et al.* 2004; Myhrvold 2013).

The relative consistency between recent reconstruction-based estimates and those presented here provides further support that the cQE is a useful tool for generating large data sets of body mass in extinct tetrapods (in particular non-avian dinosaurs). However, unlike volumetric reconstructions, the cQE is much simpler, and, because it does not rely on the complete reconstruction and preservation of an individual, it can be applied to a larger proportion of taxa and specimens with preserved femora, but that are otherwise incomplete (Benton 2008; Mannion & Upchurch 2010; Brown *et al.* 2013). Taken together, the QE and cQE provide a powerful approach for investigating macroevolutionary patterns of body size in deep

time (e.g. Benson *et al.* 2014), and possible associations with changing Earth systems (Smith *et al.* 2010; Sookias, Benson & Butler 2012).

Acknowledgements

We thank M. Peck, O. Haddrath, A. Baker, K. Seymour and B. Iwama for access to ROM collections. Special thanks to R. Kim and G. Oliveira Cunha for the assistance collecting the ROM bird data, M. Ryan (CMNH) for providing femoral measurements from a human sample and J. L. Carballido for providing a circumference measurement for *Tyrannotitan*. Thanks also to R. Benson, R. Blob, A. Dececchi, J. Hutchinson, H. Larsson, R. Reisz and M. Silcox for discussions related to this project. Thanks also to the members of the Evans and Reisz laboratories for their support and discussions. Finally, we greatly appreciate the comments made by the editors, R. Freckleton and L. Revell, and reviewers, J. Hutchinson and two anonymous, that improved the quality of the manuscript. Funding for this project was provided by an NSERC Postgraduate Scholarship and Queen Elizabeth II Graduate Scholarship in Science and Technology (to NEC), an NSERC Discovery Grant (to NEC) and an NSERC Canadian Graduate Scholarship (to CMB).

Data accessibility

All the new data used in this study are included as part of the Supporting Information.

References

- Alexander, R.M. (1985) Mechanics of posture and gait of some large dinosaurs. *Zoological Journal of the Linnean Society*, **83**, 1–25.
- Allen, V., Bates, K.T., Li, Z. & Hutchinson, J.R. (2013) Linking the evolution of body shape and locomotor biomechanics in bird-line archosaurs. *Nature*, **497**, 104–107.
- Anderson, J.F., Hall-Martin, A. & Russell, D.A. (1985) Long-bone circumference and weight in mammals, birds and dinosaurs. *Journal of the Zoological Society of London A*, **207**, 53–61.
- Barrett, P.M., McGowan, A.J. & Page, V. (2009) Dinosaur diversity and the rock record. *Proceedings of the Royal Society B*, **276**, 2667–2674.
- Bates, K.T., Manning, P.L., Hodgetts, D. & Sellers, W.I. (2009) Estimating mass properties of dinosaurs using laser imaging and 3D computer modelling. *PLoS One*, **4**, e4532. doi:10.1371/journal.pone.0004532.
- Benson, R.B.J., Butler, R.J., Carrano, M.T. & O'Connor, P.M. (2011) Air-filled postcranial bones in theropod dinosaurs: physiological implications and the 'reptile'-bird transition. *Biological Reviews*, **87**, 168–193.
- Benson, R.B.J., Campione, N.E., Carrano, M.T., Mannion, P.D., Sullivan, C., Upchurch, P. & Evans, D.C. (2014) Rates of dinosaur body mass evolution indicate 170 million years of sustained ecological innovation on the avian stem lineage. *PLoS Biology*, **12**, e1001853.
- Benton, M.J. (2008) How to find a dinosaur, and the role of synonymy in biodiversity studies. *Journal Information*, **34**, 516–533.
- Berman, D.S., Reisz, R.R., Scott, D., Henrici, A.C., Sumida, S.S. & Martens, T. (2000) Early Permian bipedal reptile. *Science*, **290**, 969–972.
- Bertram, J.E.A. & Biewener, A.A. (1990) Differential scaling of the long bones in the terrestrial Carnivora and other mammals. *Journal of Morphology*, **204**, 157–169.
- Brassey, C.A. & Sellers, W.I. (2014) Scaling of convex hull volume to body mass in modern primates, non-primate mammals and birds. *PLoS One*, **9**, e91691.
- Brown, J.H., Marquet, P.A. & Taper, M.L. (1993) Evolution of body size: consequences of an energetic definition of fitness. *The American Naturalist*, **142**, 573–584.
- Brown, C.M., Campione, N.E., Corrêa Giacomini, H., O'Brien, L.J., Vavrek, M.J. & Evans, D.C. (2012) Ecological modelling, size distributions and taphonomic size bias in dinosaur faunas: a comment on Codron et al. (2012). *Biology Letters*, **9**, 20120582.
- Brown, C.M., Evans, D.C., Campione, N.E., O'Brien, L.J. & Eberth, D.A. (2013) Evidence for taphonomic size bias in the Dinosaur Park Formation (Campanian, Alberta), a model Mesozoic terrestrial alluvial-paralic system. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **372**, 108–122.
- Burness, G.P., Diamond, J. & Flannery, T. (2001) Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. *Proceedings of the National Academy of Science*, **98**, 14518–14523.
- Butler, R.J., Galton, P.M., Porro, L.B., Chiappe, L.M., Henderson, D.M. & Erickson, G.M. (2009) Lower limits of ornithischian dinosaur body size inferred from a new Upper Jurassic heterodontosaurid from North America. *Proceedings of the Royal Society B*, **277**, 375–381.
- Campbell, K.E. Jr & Marcus, L. (1992) The relationships of hindlimb bone dimensions to body weight in birds. *Natural History Museum of Los Angeles County Science Series*, **36**, 395–412.
- Campione, N.E. (2013) *MASSTIMATE: Body Mass Estimation Equations for Vertebrates*. R package version 1.2. <http://cran.r-project.org/web/packages/MASSTIMATE/>.
- Campione, N.E. (in press) Postcranial anatomy of *Edmontosaurus regalis* (Hadrosaurinae) from the Horseshoe Canyon Formation, Alberta, Canada: description and photographic atlas of the paratype. *HADROSAURS: Proceedings of the International Hadrosaur Symposium at the Royal Tyrrell Museum* (eds D.C. Evans & D.A. Eberth), pp. 208–244. Indiana University Press, Bloomington, Indiana.
- Campione, N.E. & Evans, D.C. (2012) A universal scaling relationship between body mass and proximal limb bone dimensions in quadrupedal terrestrial tetrapods. *BMC Biology*, **10**, 60.
- Carrano, M.T. (1998) Locomotion in non-avian dinosaurs: integrating data from hindlimb kinematics, in vivo strains, and bone morphology. *Paleobiology*, **24**, 450–469.
- Carrano, M.T. (2001) Implications of limb bone scaling, curvature and eccentricity in mammals and non-avian dinosaurs. *Journal of Zoology*, **254**, 41–55.
- Carrano, M.T. (2006) Body-size evolution in the Dinosauria. *Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles* (eds M.T. Carrano, R.W. Blob, T.J. Gaudin & J.R. Wible), pp. 225–268. University of Chicago Press, Chicago, Illinois.
- Carrano, M.T. & Biewener, A.A. (1999) Experimental alteration of limb posture in the chicken (*Gallus gallus*) and its bearing on the use of birds as analogs for dinosaur locomotion. *Journal of Morphology*, **240**, 237–249.
- Casinos, A. & Cubo, J. (2001) Avian long bones, flight and bipedalism. *Comparative Biochemistry and Physiology Part A*, **131**, 159–167.
- Christiansen, P. & Fariña, R.A. (2004) Mass prediction in theropod dinosaurs. *Historical Biology*, **16**, 85–92.
- Codron, D., Carbone, C., Müller, D.W.H. & Clauss, M. (2012) Ontogenetic niche shifts in dinosaurs influenced size, diversity and extinction in terrestrial vertebrates. *Biology Letters*, **8**, 620–623.
- Colbert, E.H. (1962) The weights of dinosaurs. *American Museum Novitates*, **2076**, 1–16.
- Cubo, J. & Casinos, A. (1998) Biomechanical significance of cross-sectional geometry of avian long bones. *European Journal of Morphology*, **36**, 19–28.
- Cubo, J. & Casinos, A. (2000) Incidence and mechanical significance of pneumatization in the long bones of birds. *Zoological Journal of the Linnean Society*, **130**, 499–510.
- Dececchi, T.A. & Larsson, H.C.E. (2013) Body and limb size dissociation at the origin of birds: uncoupling allometric constraints across a macroevolutionary transition. *Evolution*, **67**, 2741–2752.
- Doube, M., Yen, S.C.W., Kosowski, M.M., Farke, A.A., Hutchinson, J.R. & Shefelbine, S.J. (2012) Whole-bone scaling of the avian pelvic limb. *Journal of Anatomy*, **221**, 21–29.
- Erickson, G.M., Rogers, K.C. & Yerby, S.A. (2001) Dinosaurian growth patterns and rapid avian growth rates. *Nature*, **412**, 429–433.
- Erickson, G.M., Makovicky, P.J., Currie, P.J., Norell, M.A., Yerby, S.A. & Brochu, C.A. (2004) Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. *Nature*, **430**, 772–775.
- Field, D.J., Lynner, C., Brown, C. & Darroch, S.A.F. (2013) Skeletal correlates for body mass estimation in modern and fossil flying birds. *PLoS One*, **8**, e82000.
- Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. (2001) Effects of size and temperature on metabolic rate. *Science*, **293**, 2248–2251.
- Henderson, D.M. (1999) Estimating the masses and centers of mass of extinct animals by 3-D mathematical slicing. *Paleobiology*, **25**, 88–106.
- Henderson, D.M. & Snively, E. (2004) *Tyrannosaurus* en pointe: allometry minimized rotational inertia of large carnivorous dinosaurs. *Biology Letters*, **271**, S57–S60.
- Hutchinson, J.R. (2001) The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society*, **131**, 169–197.
- Hutchinson, J.R., Ng-Thow-Hing, V. & Anderson, F.C. (2007) A 3D interactive method for estimating body segmental parameters in animals: application to the turning and running performance of *Tyrannosaurus rex*. *Journal of Theoretical Biology*, **246**, 660–680.
- Hutchinson, J.R., Bates, K.T., Molnar, J., Allen, V. & Makovicky, P.J. (2011) A computational analysis of limb and body dimensions in *Tyrannosaurus rex* with implications for locomotion, ontogeny, and growth. *PLoS One*, **6**, e26037.
- Kivell, T.L. & Schmitt, D. (2009) Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. *Proceedings of the National Academy of Sciences*, **106**, 14241–14246.
- Maidment, S.C.R. & Barrett, P.M. (2012) Does morphological convergence imply functional similarity? A test using the evolution of quadrupedalism in ornithischian dinosaurs. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 3765–3771.
- Maidment, S.C.R., Linton, D.H., Upchurch, P. & Barrett, P.M. (2012) Limb-bone scaling indicates diverse stance and gait in quadrupedal ornithischian dinosaurs. *PLoS One*, **7**, e36904.
- Mannion, P.D. & Upchurch, P. (2010) Completeness metrics and the quality of the sauropodomorph fossil record through geological and historical time. *Journal Information*, **36**, 283–302.
- McMahon, T. (1973) Size and shape in biology. *Science*, **179**, 1201–1204.
- McMahon, T.A. (1975) Using body size to understand the structural design of animals: quadrupedal locomotion. *Journal of Applied Physiology*, **39**, 619–627.
- Myhrvold, N.P. (2013) Revisiting the estimation of dinosaur growth rates. *PLoS One*, **8**, e81917.
- Nesbitt, S.J. & Norell, M.A. (2006) Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda). *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1045–1048.
- O'Connor, P.M. (2006) Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. *Journal of Morphology*, **267**, 1199–1226.
- O'Gorman, E.J. & Hone, D.W.E. (2012) Body size distribution of the dinosaurs. *PLoS One*, **7**, e51925.

- Paul, G. (1997) Dinosaur models: the good, the bad, and using them to estimate the mass of dinosaurs. *Dinofest International* (eds D.L. Wolberg, E. Stump & G.D. Rosenberg), pp. 39–45. The Academy of Natural Sciences, Arizona State University, Phoenix, AZ.
- Puttick, M.N., Thomas, G.H. & Benton, M.J. (2014) High rates of evolution preceded the origin of birds. *Evolution*, **68**, 1497–1510.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rubin, C.T. & Lanyon, L.E. (1984) Dynamic strain similarity in vertebrates: an alternative to allometric limb bone scaling. *Journal of Theoretical Biology*, **107**, 321–327.
- Seebacher, F. (2001) A new method to calculate allometric length-mass relationships of dinosaurs. *Journal of Vertebrate Paleontology*, **21**, 51–60.
- Smith, F.A., Boyer, A.G., Brown, J.H., Costa, D.P., Dayan, T., Ernest, S.K.M. *et al.* (2010) The evolution of maximum body size of terrestrial mammals. *Science*, **330**, 1216–1219.
- Sookias, R.B., Benson, R.B.J. & Butler, R.J. (2012) Biology, not environment, drives major patterns in maximum tetrapod body size through time. *Biology Letters*, **8**, 674–677.
- Sookias, R.B., Butler, R.J. & Benson, R.B.J. (2012) Rise of dinosaurs reveals major body-size transitions are driven by passive processes of trait evolution. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 2180–2187.
- Spoor, F., Wood, B. & Zonneveld, F. (1994) Implications of early hominid labyrinthine morphology for evolution of human bipedal locomotion. *Nature*, **369**, 645–648.
- Steudel, K. (1996) Limb morphology, bipedal gait, and the energetics of hominid locomotion. *American Journal of Physical Anthropology*, **99**, 345–355.
- Therrien, F. & Henderson, D.M. (2007) My theropod is bigger than yours...or not: estimating body size from skull length in theropods. *Journal of Vertebrate Paleontology*, **27**, 108–115.
- Turner, A.H., Pol, D., Clarke, J.A., Erickson, G.M. & Norell, M.A. (2007) A basal dromaeosaurid and size evolution preceding avian flight. *Science*, **317**, 1378–1381.
- Varricchio, D.J., Moore, J.R., Erickson, G.M., Norell, M.A., Jackson, F.D. & Borkowski, J.J. (2008) Avian paternal care had dinosaur origin. *Science*, **322**, 1826–1828.
- Warton, D.I., Duursma, R.A., Falster, D.S. & Taskinen, S. (2011) smatr 3-an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution*, **3**, 257–259.
- Wilson, J.A. & Carrano, M.T. (1999) Titanosaurs and the origin of “wide-gauge” trackways: a biomechanical and systematic perspective on sauropod locomotion. *Journal of Paleontology*, **25**, 252–267.

Received 15 November 2013; accepted 16 June 2014

Handling Editor: Liam Revell

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Code for the main functions available through the R-package ‘MASSTIMATE’, for estimating body mass in terrestrial tetrapods.

Appendix S2. Institutional abbreviations for specimens referred to in this study.

Data S1. Limb measurements and body mass data for the sample of 161 bird species used in this study.

Data S2. Limb measurements and body mass data for 10 human specimens.

Fig. S1. Bivariate plot and fitted lines (sample size permitting) between femoral circumference and body mass in a sample of 161 bird species.

Table S1. Previously proposed equations for estimating body mass in extinct bipeds from femoral circumference.

Table S2. A list of possible correction factors that can be incorporated into the cQE based on various levels of femoral eccentricity.

Table S3. Slopes, mean per cent prediction errors, and standard errors of the estimate of the regression lines in Fig. 2.

Table S4. Line-fitting results between femoral circumference and body mass in avian groups with $N > 10$.