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Downsizing a giant: Re-evaluating *Dreadnoughtus* body mass

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Key words: *Dreadnoughtus*, body mass, modeling, scaling equations.

Summary

Estimates of body mass often represent the founding assumption on which biomechanical and macroevolutionary hypotheses are based. Recently, a scaling equation was applied to a newly discovered titanosaurian sauropod dinosaur (*Dreadnoughtus*), yielding a 59,300kg body mass estimate for this animal. Herein

we use a modeling approach to examine the plausibility of this mass estimate for *Dreadnoughtus*. We find that 59,300kg for *Dreadnoughtus* is highly implausible, and demonstrate that masses above 40,000kg require high body densities and expansions of soft tissue volume outside the skeleton several times greater than found in living quadrupedal mammals. Similar results from a small sample of other archosaurs suggests that lower-end mass estimates derived from scaling equations are most plausible for *Dreadnoughtus*, based on existing volumetric and density data from extant animals. Although volumetric models appear to more tightly constrain dinosaur body mass there remains a clear need to further support these models with more exhaustive data from living animals. The relative and absolute discrepancies in mass predictions between volumetric models and scaling equations also indicate a need to systematically compare predictions across a wide size and taxonomic range to better inform studies of dinosaur body size.

INTRODUCTION

Sauropod dinosaurs include the largest terrestrial animals to have ever evolved, and mass properties are regarded as a crucial component of their functional, behavioural, and evolutionary dynamics [1]. Recently, Lacovara et al. [2] described a gigantic, near-complete titanosaurian sauropod, *Dreadnoughtus schrani***,** from Argentina. These authors used a scaling relationship between long bone (femoral plus humeral) circumference and body mass [3] to derive a mass estimate of 59,300kg for the holotype of *Dreadnoughtus*. This scaling equation is well supported statistically in living tetrapods and to-date has been used to estimate the body mass of extinct taxa to facilitate studies of physiology and growth [e.g. 4] and macroevolutionary dynamics [1]. However, the mass estimate seems high given that in overall skeletal proportions *Dreadnoughtus* only marginally exceeds those of near-complete specimens of other sauropods (e.g. *Apatosaurus*, *Giraffatitan*) whose masses have been estimated at 25-35,000kg by various methods [e.g. 3, 5]. In this paper we use a digital three-dimensional skeletal model and volumetric reconstructions to directly examine the plausibility of the 59,300kg mass estimate for *Dreadnoughtus*, and subsequently comment upon the use of scaling equations to estimate dinosaur body mass.

METHODS

A digital model of the *Dreadnoughtus* skeleton from Lacovara et al. [2] was used as a basis for a 3D volumetric model (Fig. 1). For comparative purposes we also modeled six extant taxa (three birds, two crocodilians and one lizard) and two other large sauropods using identical methods: *Giraffatitan brancai,* based on a laser scan of MB (Museum für Naturkunde, Berlin, Germany) SII from our previous study [5], and *Apatosaurus louisae*, based on a new 3D model of CM (Carnegie Museum, USA) 3018 generated using photogrammetry [6]. Each 3D skeletal model was posed in a standard 'neutral' posture, with the tail and neck extending horizontally and the limbs in a fully extended, vertical position (Fig. 1). Models were then divided into the following body segments: head, neck, 'trunk' (thorax & limb girdles), tail, thigh, shank, foot, humerus, forearm, and hand.

The holotype of *Dreadnoughtus* is missing most of the cervical vertebrae, as well the manus, skull and distal tip of the tail. Our convex hulling approach [5] to volumetric reconstruction involves tight-fitting 3D convex polygons to each body segment. As the extent of an object's convex hull is dictated solely by its geometric extremes, we were able to minimise the amount of skeletal reconstruction in our model (Fig. S1). For the hand and skull we used photogrammetric models of these elements from *Rapetosaurus* (FMNH PR 2209), another titanosaur, and re-scaled them using the reconstruction in Lacovara et al. ([2], their Fig. 2). To allow convex hulling to connect the 'trunk' and neck segments we duplicated the ninth cervical vertebra preserved in the specimen and placed its posterior surface above the most anterior point of pectoral girdle at a height consistent with the position of the preserved dorsal vertebrae. An additional 10% was added to the distal tail using the reconstruction of Lacovara et al. [2] as a guide (Fig. S1). In the supplementary material we provide extensive sensitivity tests of our skeletal reconstruction procedure (Figs S1-S8).

The minimum convex hull volume for each skeletal body segment was calculated using the MATLAB (www.mathworks.com) qhull command [5,7]. The total minimum convex hull volume provides the minimum volume estimate for each animal, and a baseline for our sensitivity analysis in which we generated three further models. In the first model the minimal convex hulls were geometrically expanded by 21%, following a previous study in which live body mass was estimated to have been on average 21% greater than that calculated from minimum convex hulls for a range of extant mammals [5]. We subsequently generated a 'maximal mass model' in which the volume of the trunk segment was increased by 50% and those of all other segments by 100%. Finally, we expanded the minimum convex hull model of *Dreadnoughtus* by the amount required to match the total body masses predicted by the scaling equation of [3].

For the sauropod models, body segments were given an initial density of 1000kg m^{-3}. Zero-density respiratory structures in the head, neck and 'trunk' segments were reconstructed and the volumes of these structures subtracted from their overall segment volume, as in previous volumetric studies of dinosaurs [8-10]. Homogeneous body densities were used for the extant taxa, based on published values for crocodiles and chickens [10].

RESULTS

The convex hull volume reconstruction of *Dreadnoughtus* results in a total body volume of 26.910m^3 (Fig. 1a, Table 1). Expanding this minimum convex hull volume by 21% raises whole-body volume to 32.534m^3 (Fig.1b), while the volume of our maximal model is 43.016m^3 (Fig. 1c). Deducting the volume of our reconstructed respiratory structures from each of these models yields total body masses of 22,117kg, 27,741kg and 38,225kg for the three model iterations. These data, and data from equivalent models of *Apatosaurus* and *Giraffatitan* (Fig. 2a-b), are shown in Table 1, while the data from extant taxa is tabulated in the supplementary information (Tables S1-6, Figs S8-9). Convex hull volumes are available in the supplementary information.

DISCUSSION AND CONCLUSIONS

The mass of *Dreadnoughtus* was estimated at 59,300kg using the raw bivariate predictive equation of Campione and Evans [3]. The masses of our three volumetric reconstructions of *Dreadnoughtus* (Fig. 1a-c, Table 1) are equivalent to 37%, 47% and 64% of the 59,300kg scaling equation mass. The 'average percent prediction error' from the bi-variate equation gives a minimum mass of

44,095kg (5,780kg or 15% higher than our 'maximal' model) and a maximum mass of 74,487kg (36,262kg or 95% higher than our 'maximal' model). The '95% prediction interval' from the equation yields a range of 32,000-109,000kg for *Dreadnoughtus*, which overlaps with model estimates (Fig. 2).

Convex hulling provides a close, objective approximation of the body volume defined by a skeleton alone [5,7]. A volume 2.38 times larger than that of our convex hull model is required for *Dreadnoughtus* to achieve the mean or 'best-estimate' scaling equation mass of 59,300kg, using our estimates for the size of respiratory structures (Fig. 1d). This represents an expansion more than 6.5 times greater than the average value found in a sample of quadrupedal mammals spanning major taxonomic groups [5]. This 2.38 times expanded model (Fig. 1d) has a bulk density of 925kg m^{-3}, which is higher than any presently published estimate for sauropods [range 791-900kg m^3; Table S7]. If lower-end estimates of 800kg m^{-3} for sauropod density [8] are correct, then achieving a body mass of 59,300kg for *Dreadnoughtus* would require body and respiratory volumes of 74.125m^3 and 14.825m^3 respectively, the latter representing a 310% expansion of our respiratory volumes (Fig. 1). Filling the entire ribcage with a zero-density respiratory structure (Fig. S7), which is obviously highly implausible, only produces a 212% increase in respiratory volume. It is clear from our model that bulk densities as low or approaching 800kg m^3 cannot be reconciled with a total body mass of 59,300kg given the skeletal proportions of *Dreadnoughtus* and the space available within the ribcage for low-density respiratory structures.

Comparison of mass predictions from volumetric reconstructions of near-complete skeletons of *Apatosaurus* and *Giraffatitan* (Fig. 2) to the mean scaling equation masses, produces a qualitatively similar result: scaling equation mass predictions exceed those of our maximal models (Fig 2c-d). The disparity between the two approaches increases further if the whole-body densities of these models are set to lower-end estimates for sauropods (800kg m^{-3} [8]) rather than predicting density by inclusion of respiratory structures. In the case of both *Apatosaurus* and *Giraffatitan* there is clear overlap between the lowest scaling equation estimates and our maximal models, although as with *Dreadnoughtus* there remains no overlap between the lowest scaling equation masses and those derived from the upper bounds of the mammalian convex hull expansion exponent (Fig. 2).

Convex hull volumes for extant taxa produced here required scaling exponents of between 1.18-1.91 (Tables S1-6, Fig. S8-9) to reach actual measured body masses, with three animals (American alligator 1.69; guineafowl 1.91; leghorn chicken 1.87) requiring exponents greater than that applied in our 'maximal' models (Fig. 1). However, increasing convex hull volume by 2.38, as required for our reconstruction of *Dreadnoughtus* to reach the mean scaling equation mass, results in substantial mass overestimates for all modelled extant taxa (23-102% overestimates; see Tables S1-6).

Our analysis emphasises a number of important points that should be considered in future studies. Firstly, it is vital that uncertainties and likely error magnitudes are explicitly acknowledged in mass estimates derived from all methods, including scaling equations. Our analysis also reveals that the higher range estimates predicted by bivariate scaling equations [3] appear to be highly incompatible with volumetric models that are based directly on currently available volume and density data from living vertebrates ([5]; Tables S1-6).

Indeed, in the case of *Dreadnoughtus,* the mean, and perhaps even some lower-end, scaling equation estimates appear to be implausible based on current data (Figs 1-2). The high scaling equation mass for *Dreadnoughtus* also appears to result in a discrepancy in relative mass predictions between the modelled sauropods; our convex hull volumes (which provide a close approximation of the body volume defined by the preserved skeleton) of *Apatosaurus* and *Giraffatitan* represent 0.9 and 0.985 that of *Dreadnoughtus*, which appears congruent with the overlap in gross linear body proportions (Fig. S11). By contrast, mean scaling equation mass predictions for *Apatosaurus* and *Giraffatitan* are 0.57 and 0.70 that of *Dreadnoughtus* (Fig. 2). While differences in skeletal:extra-skeletal dimensions should be expected [3], even in relatively closely related taxa (Tables S1-6) it seems unlikely that differences in skeletal proportions of these three sauropods (Figs 2 & S11) are sufficient to account for the 20-25,000kg difference in body mass predicted by the scaling equation. Thus, even physiological and macroevolutionary studies that use relative mass values or distribute taxa into discrete mass 'categories' based on scaling equation estimates should take the maximum range of values or error inherent in these equations into account.

Recently a similar pattern of divergence between volumetric and linear-based mass estimates was found an for exceptionally complete *Stegosaurus* skeleton [7]. The authors attributed this discrepancy to the ontogenetic status of the individual. Certain skeletal features may indicate that the *Dreadnoughtus* holotype was still growing at the time of death [2]. As an organism's body proportions change with age, the application of a scaling equation derived from modern adult skeletons to the limb bones of a sub- or young adult may be erroneous. At least some of the inconsistency we find here between mass estimation techniques may therefore be due to the ontogenetic stage of the specimen. Given the absence of confirmed 'adult' skeletal material for *Dreadnoughtus* however, it would be challenging to account for this phenomenon.

Estimating the mass of extinct animals is challenging [3,5,7,9-10]. By directly using the determinates of mass (volume and density) and maximising skeletal evidence, volumetric approaches allow inherent uncertainties in mass predictions to be explicitly assessed (Figs 1-2) and plausible limits established based on data and models of extant taxa. Our analysis reveals the importance of extending current analyses of dinosaur body mass in two ways; first and foremost by addition of further volumetric and density data on living taxa in order to more tightly constrain maximum plausible values for extinct animals. Second, a systematic comparison of dinosaur mass predictions from modelling and scaling equations, across a wide taxonomic and size range, is needed to identify and explain discrepancies between the two approaches (Fig. 2). Such a study would not only lead to more informed estimates of dinosaur body mass, but could also shed light on musculoskeletal adaptations for large body size in different dinosaur lineages.

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Data accessibility. Convex hull models are downloadable from Dryad (doi:XXXX).

Author contributions. K.T.B., S.C.R.M., C.A.B and P.L.F designed the experiments; K.T.B. S.M. and P.L.F. collected the data; K.T.B., C.A.B, S.C.R.M. and S.M. analysed the data; all authors contributed to the manuscript.

Conflict of interest. The authors declare that they have no competing interests.

Figure 1. *Dreadnoughtus* 3D skeletal model and the ***(a)*** convex hull, ***(b)*** plus21%, ***(c)*** maximal and ***(d)*** scaling equation mass volumetric reconstructions in lateral, oblique and aerial views. Black structures are respiratory volumes.

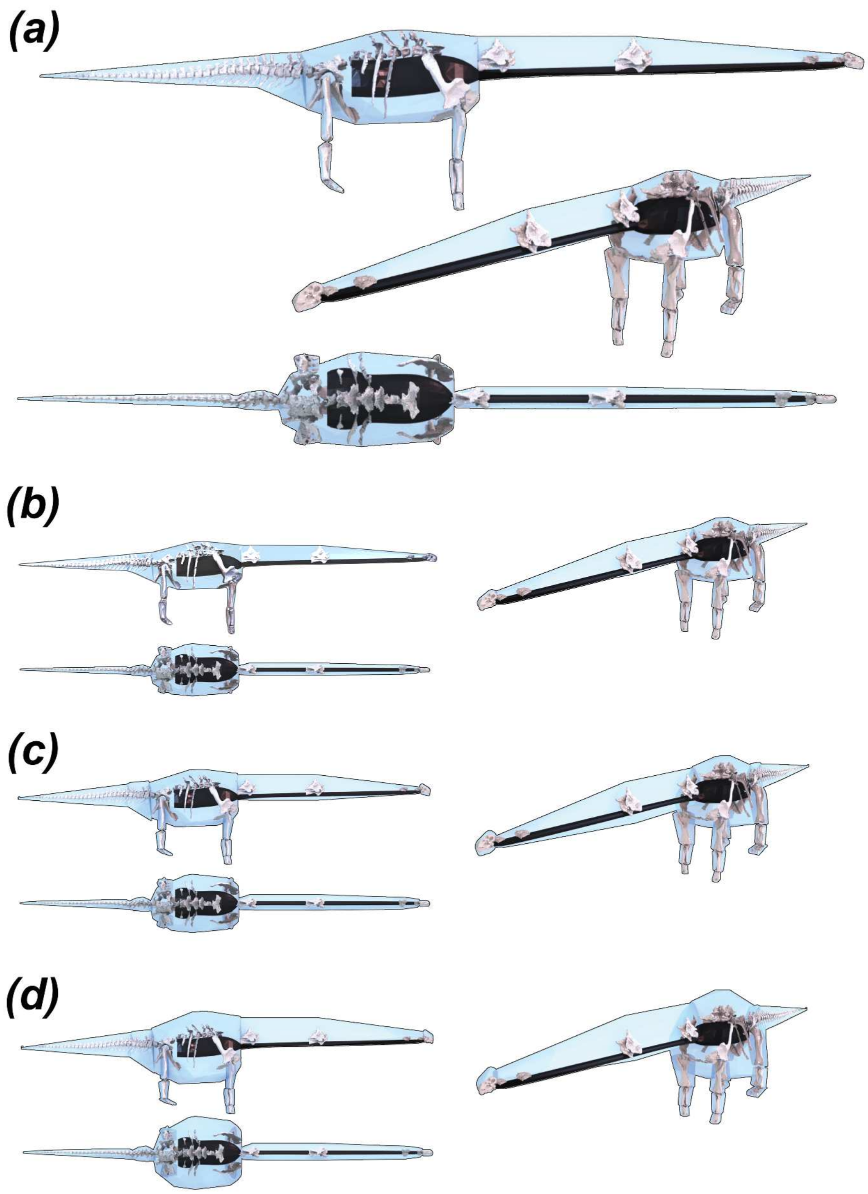
Figure 2. Comparison of skeletal proportions and convex hull volumes for *Apatosaurus* (top), *Dreadnoughtus* (middle) and *Giraffatitan* (bottom) in ***(a)*** dorsal and ***(b)*** lateral views. Comparison of mass predictions from the models in this study to masses derived from the scaling equation [2], with ***(c)*** model mass and density calculated using reconstructed zero-density respiratory structures, and ***(d)*** density artificially set to 800 kg m^{-3} [8]. The positive error bar on our maximal models represents the mass predicted by expanding convex hull volumes by the highest exponent (x1.91) for mammals [5] and archosaurs to-date. The 'PPE' error bars on scaling equation represent the average 'percent prediction error', while '95PI' error bars represent the '95% prediction interval.'

Table 1. Mass property data for convex hull reconstructions of *Dreadnoughtus, Apatosaurus* and *Girafffatitan*, and summary of whole-body mass data from different model iterations.

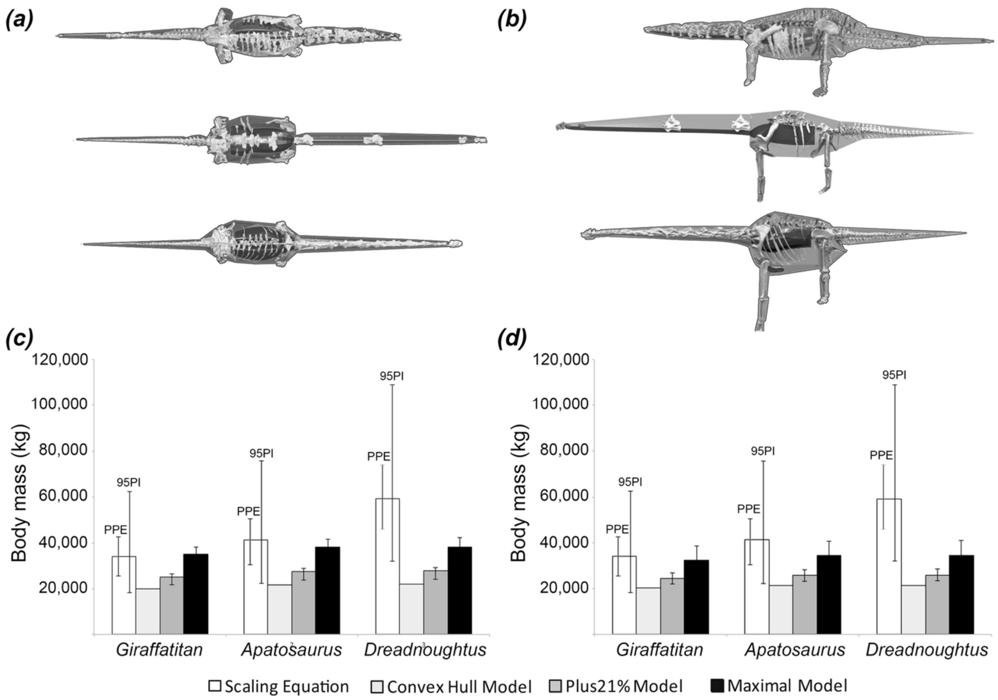
Table 1. Mass property data for convex hull reconstructions of *Droughnoughtus, Apatosaurus* and *Girafffatitan*, and summary of whole-body mass data from different model iterations.

Convex Hull		***Dreadnoughtus***			***Apatosaurus***			***Giraffatitan***	
Body Segments	Volume (m^3)	Density (kg m^{-3})	Mass (kg)	Volume (m^3)	Density (kg m^{-3})	Mass (kg)	Volume (m^3)	Density (kg m^{-3})	Mass (kg)
Head	0.033	1000	33.49	0.02	1000	23.46	0.06	1000	59.45
Neck	3.110	1000	3109.99	2.62	1000	2615.16	2.46	1000	2461.00
Trunk	20.382	1000	20381.96	20.12	1000	20187.65	19.85	1000	19850.92
Tail	1.011	1000	1011.35	1.86	1000	1861.20	0.78	1000	774.76
Humerus	0.186	1000	186.08	0.23	1000	232.34	0.30	1000	298.78
Forearm	0.097	1000	97.36	0.10	1000	103.01	0.16	1000	160.67
Hand	0.024	1000	24.11	0.03	1000	25.96	0.09	1000	85.98
Humerus	0.186	1000	186.08	0.28	1000	275.31	0.30	1000	298.78
Forearm	0.097	1000	97.36	0.10	1000	103.01	0.16	1000	160.67
Hand	0.024	1000	24.11	0.03	1000	25.96	0.09	1000	85.98
Thigh	0.246	1000	246.13	0.35	1000	351.27	0.29	1000	294.19
Shank	0.110	1000	109.86	0.21	1000	208.57	0.19	1000	193.06
Foot	0.042	1000	41.91	0.08	1000	84.62	0.04	1000	35.69
Thigh	0.246	1000	246.13	0.35	1000	351.27	0.29	1000	294.19
Shank	0.110	1000	109.86	0.21	1000	208.57	0.19	1000	193.06
Foot	0.042	1000	41.91	0.08	1000	84.62	0.04	1000	35.69
Axial total	25.50	1000	24536.80	24.62	1000	24687.47	23.15	1000	23146.13
Hind limb total	0.796	1000	795.80	1.289	1000	1288.92	1.046	1000	1045.88
Fore limb total	0.614	1000	615.09	0.722	1000	722.62	1.092	1000	1090.87
Whole body	26.91	1000	25947.68	26.63	1000	26699.01	25.28	1000	25282.88
Respiratory structures									
Head	0.003	1000	3.43	0.001	1000	0.99	0.0036	1000	3.60
Neck	4.30	1000	4303.67	4.60	1000	4602.86	5.00	1000	5000.39
Trunk	0.49	1000	486.48	0.29	1000	291.95	0.33	1000	332.54

Model Iteration									
Minimum									
Convex Hull	26.91	821.9	22117.98	26.63	818.8	21803.21	25.284	788.8	19946.35
Plus 21% Model	32.53	852.7	27741.68	32.26	850.5	27363.56	30.54	825.2	25204.65
Maximal Model	43.02	888.6	38224.57	43.08	886.4	38187.23	40.40	867.9	35060.42



Dreadnoughtus 3D skeletal model and the (a) convex hull, (b) plus21%, (c) maximal and (d) scaling equation mass volumetric reconstructions in lateral, oblique and aerial views. Black structures are respiratory volumes.
288x400mm (300 x 300 DPI)



Comparison of skeletal proportions and convex hull volumes for Apatosaurus (top), Dreadnoughtus (middle) and Giraffatitan (bottom) in (a) dorsal and (b) lateral views. Comparison of mass predictions from the models in this study to masses derived from the scaling equation [2], with (c) model mass and density calculated using reconstructed zero-density respiratory structures, and (d) density artificially set to 800 kg m-3 [8]. The positive error bar on our maximal models represents the mass predicted by expanding convex hull volumes by the highest exponent (x1.91) for mammals [5] and archosaurs to-date. The 'PPE' error bars on scaling equation represent the average 'percent prediction error', while '95PI' error bars represent the '95% prediction interval.'
127x90mm (300 x 300 DPI)