Minimum convex hull mass estimations of complete mounted skeletons

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Body mass is a critical parameter used to constrain biomechanical and physiological traits of organisms. Volumetric methods are becoming more common as techniques for estimating the body masses of fossil vertebrates. However, they are often accused of excessive subjective input when estimating the thickness of missing soft tissue. Here, we demonstrate an alternative approach where a minimum convex hull is derived mathematically from the point cloud generated by laser-scanning mounted skeletons. This has the advantage of requiring minimal user intervention and is thus more objective and far quicker. We test this method on 14 relatively large-bodied mammalian skeletons and demonstrate that it consistently underestimates body mass by 21 per cent with minimal scatter around the regression line. We therefore suggest that it is a robust method of estimating body mass where a mounted skeletal reconstruction is available and demonstrate its usage to predict the body mass of one of the largest, relatively complete sauropod dinosaurs: \textit{Giraffatitan brancai} (previously \textit{Brachiosaurus}) as 23200 kg.

Keywords: body mass estimation; laser scanning; convex hull

1. INTRODUCTION

The masses of organisms affect their morphology, physiology and ecology and understanding the relationships between these traits is of ongoing importance to both zoological and palaeontological studies [1]. Despite excellent skeletal preservation of many prehistoric organisms, the poor preservation of soft tissues prevents mass values being preserved directly [2]. Therefore, there has been considerable demand for accurate techniques to reliably estimate body mass from skeletal remains for over a century [3]. There are two standard approaches: the volumetric approach, where a model of the animal is produced and its body mass calculated from its density; and the predictive regression approach, where a relationship between linear dimensions and body mass is generated from empirical data (see [1] for review). Volumetric approaches have the advantage of maximizing the information content of the complete skeleton, but they have the disadvantage that they require considerable time-consuming user input to generate the body outline. Predictive regression approaches are objective and can be performed rapidly. However, they rely on specific skeletal features which can lead to problems of high variation and outliers, and they often perform very badly when used to extrapolate outside the calibrating dataset [2]. The aim of this paper is to test the idea that it is possible to combine the maximum data available from a fully mounted skeleton and predictive regression to produce better estimates of body mass.

2. MATERIAL AND METHODS

The calibration skeletons were scanned using a Z+F Imager-5006i LiDAR scanner at the Oxford University Museum of Natural History. Reconstruction was performed using \textit{Geomagic Studio} (www.geomagic.com) creating complete three-dimensional skeletal point cloud models of each animal. The model was subsequently divided into functional segments: hind and fore feet, metatarsus and metacarpus, shank and forearm, thigh and arm, tail, torso (which included the attached scapula), neck and head. Horns, when present, were removed from the head component. Each segment was then saved as a point cloud. The minimum convex hull was calculated using the \textit{MATLAB} qhull command that calculates the enclosed volume (www.mathworks.com). The total volume was the sum of the individual segment volumes. This volume was converted into a mass estimate using both segment-specific density values for horses and also using an overall weighted-mean body density of 893.36 kg m\textsuperscript{-3} [4]. Figure 1 illustrates this procedure showing the original skeleton, the point cloud and the final convex hulls derived from the data.

Unfortunately, body masses for the museum specimens were not available. However, it is possible to estimate body masses for extant animals with reasonable precision since detailed information is often available in the literature relating body mass to specific linear body dimensions. We measured appropriate dimensions (shoulder height for most species but femur length for \textit{Cervus elaphus} and body length for \textit{Ursus maritimus}) directly from the point clouds and calculated the predicted body mass based on literature derived scaling equations [5–22]. In most cases, there was good information available but the values for \textit{Diceros bicornis}, \textit{Megalosaurus giganteus} and \textit{Tapiro indica} are somewhat less reliable since no systematic assessment of body mass and dimensions could be found. More detailed descriptions of how each body mass was estimated can be found in the electronic supplementary material.

To assess the body mass of \textit{Giraffatitan brancai} (renamed following the reassessment of \textit{Brachiosaurus} [23]), we scanned the mounted skeleton at the Berlin Museum für Naturkunde using the Z+F scanner. The skeleton was fully reconstructed and converted into a computer aided design (CAD) model by Z+F Germany. The CAD model was used directly to generate the convex hulls.

All point cloud data and analysis software are available from www.animalsimulation.org.

3. RESULTS

The calculated masses, using both a single weighted-mean body density and individual segment densities, as well as the predicted body masses of the specimens based on literature values, are shown in table 1. Using segment-specific densities makes minimal difference. The biggest discrepancy is 3.5 per cent for the giraffe, which probably reflects the fact that its segmental proportions are very different from the horse that was used to generate the weighted-mean body density. To investigate the utility of the minimum convex hull approach for predicting body mass, we investigated the relationship between the datasets by line fitting of both the raw and log-transformed data. There is considerable debate in the literature about which line fitting algorithm to use: linear regression (LR), major axis estimation (MA) or standardized major axis...
Following the arguments of Smith [25], we propose that LR with minimum convex hull as the x-axis is the most suitable since the main purpose of this study is to generate predictive equations. Figure 2 shows the relationships generated using LR, MA, SMA and also LR, where the line is forced through the origin (LMO) for the untransformed data. All the line fitting techniques give very similar answers, and the results obtained using the segment-specific and overall mean body densities are almost indistinguishable. All lines are statistically significant \( p < 0.0005 \) and the coefficient of determination \( r^2 \) values are very high. Occam’s Razor would suggest that simple approaches are to be preferred when there is no clear advantage in more complex ones. Indeed, we would suggest that LMO makes better biological sense and furthermore, this model gives the highest \( r^2 \) although these are not equivalently calculated [26]. LMO, using the mean density approach, gives:

\[
predicted mass = \frac{1.206}{\text{mean body density}} \times \frac{\text{convex hull volume}}{\text{mean body density}}.
\]

The 95% CI for the constant is 1.091–1.322. Using the 95 per cent predictive intervals, the body mass for \( G. \) brancai is calculated as 23 200 \( + \) 2200 kg using a density of 800 kg m\(^{-3} \) [23,27].

4. DISCUSSION

The proposed relationship has an \( r^2 \) of 0.975, which is extremely encouraging even though the sample size \( (n = 14) \) is relatively small. Equations predicting body mass from morphological measurements are very variable in their precision. Equations for polar bears have \( r^2 \) values from 0.7 to 0.99 [28] and similar ranges are found for elephants [11,14,15]. The value for the Sumatran rhinoceros \( Dicerorhinus \) sumatrensis is a clear outlier. An alternative relationship based on black rhinoceros \( Diceros \) bicornis data predicts a body mass of 470.3 kg which is almost exactly on the regression line [22]. Using this value, the predicted mass is \( \frac{1.193}{\text{mean body density}} \times \text{convex hull volume} \) \( (r^2 = 0.990) \). The fact that a simple relationship is supported can be explained because the missing volume from such a convex hull is primarily limb muscle and it is generally considered that body muscle is a relatively fixed proportion of the total body mass [29], although we are not aware that this has been rigorously tested. When comparing reindeer, hare and greyhound, the proportion of limb muscle compared with body mass is 26.6 per cent, 27.2 per cent and 35.4 per cent, respectively [30], which supports this argument. Such a relationship between convex hull

Table 1. Measured volumes and derived body masses for the species studied. The alternative literature value for \( Dicerorhinus \) sumatrensis is 470.3 kg [22].

<table>
<thead>
<tr>
<th>species</th>
<th>data source</th>
<th>volume (m(^3))</th>
<th>mass using segment densities (kg)</th>
<th>mass using mean body density (kg)</th>
<th>mass derived from literature (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>( B. ) bison</td>
<td>[5]</td>
<td>0.4733</td>
<td>422.8</td>
<td>422.8</td>
<td>558.5</td>
</tr>
<tr>
<td>( B. ) taurus</td>
<td>[6]</td>
<td>0.2191</td>
<td>196.6</td>
<td>195.7</td>
<td>323.7</td>
</tr>
<tr>
<td>Camelus dromedaries</td>
<td>[7]</td>
<td>0.3315</td>
<td>300.6</td>
<td>296.1</td>
<td>427.0</td>
</tr>
<tr>
<td>( C. ) elaphus</td>
<td>[8]</td>
<td>0.0840</td>
<td>76.0</td>
<td>75.1</td>
<td>89.5</td>
</tr>
<tr>
<td>( D. ) sumatrensis</td>
<td>[9,10]</td>
<td>0.3634</td>
<td>325.7</td>
<td>324.7</td>
<td>876.7</td>
</tr>
<tr>
<td>( E. ) maximus</td>
<td>[11]</td>
<td>2.0930</td>
<td>1913.4</td>
<td>1869.8</td>
<td>2352.0</td>
</tr>
<tr>
<td>( E. ) caballus</td>
<td>[12]</td>
<td>0.3698</td>
<td>333.1</td>
<td>330.3</td>
<td>517.5</td>
</tr>
<tr>
<td>Giraffa camelopardalis</td>
<td>[13]</td>
<td>0.4468</td>
<td>413.5</td>
<td>399.1</td>
<td>638.2</td>
</tr>
<tr>
<td>Loxodonta africana</td>
<td>[14,15]</td>
<td>2.7480</td>
<td>2519.6</td>
<td>2455.0</td>
<td>2734.9</td>
</tr>
<tr>
<td>Megaloceros giganteus</td>
<td>[16,17]</td>
<td>0.3012</td>
<td>271.4</td>
<td>269.0</td>
<td>435.6</td>
</tr>
<tr>
<td>Rangifer tarandus</td>
<td>[18]</td>
<td>0.0757</td>
<td>68.4</td>
<td>67.6</td>
<td>95.8</td>
</tr>
<tr>
<td>Sus scrofa</td>
<td>[19]</td>
<td>0.0785</td>
<td>70.5</td>
<td>70.2</td>
<td>107.4</td>
</tr>
<tr>
<td>Tapirus indicus</td>
<td>[20]</td>
<td>0.1718</td>
<td>154.1</td>
<td>153.5</td>
<td>295.3</td>
</tr>
<tr>
<td>Ursus maritimus</td>
<td>[21]</td>
<td>0.1109</td>
<td>101.5</td>
<td>99.1</td>
<td>206.1</td>
</tr>
</tbody>
</table>
volume and body mass has the advantage of being potentially robust when used for extrapolating body masses for very large vertebrates.

The major advantage of volumetric reconstructions in general is that they use the maximum information from the complete skeleton [1] and therefore avoid the single bone problem, where a species or an individual has limbs of unusual size that can lead to large errors. However, volumetric reconstructions are not without difficulties. They require an accurate, complete reconstruction, which is not possible unless a reasonable proportion of the skeleton has been preserved, and it is mounted accurately. Most of the mass is in the torso, therefore reconstructing the torso properly is essential and requires accurate rib placing which can be difficult to achieve. The importance of the diameter of the torso has long been known since the so-called 'heart girth' is often considered the best single measurement for predicting body mass in a range of mammals [31].

Finally, the 21 per cent value has been obtained empirically from large mammals. Whether the value for extant reptiles and birds is similar is unknown, and whether this value is appropriate for a specific group of extinct fossil organisms is a subject for debate. Future work should include a wider range of taxa, body masses and alternative segmentation strategies and segment densities, especially for taxa with heavy tails and long necks. Additionally, the residuals from the predicted relationship may reveal interesting biomechanical information. The body mass estimation for *G. brancai* is very close to other recent volumetric estimates (e.g. 23 337 kg, [23]) but avoided any arbitrary scaling factors in its derivation and is a largely automated technique. Assuming the skeletal reconstruction is accurate, we propose this method is as precise an estimate as can be currently expected given the modest amount of work required. We will never know the exact body mass since all estimation techniques have

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Figure 2. Graphs showing the relationships between the masses predicted from the convex hull and the masses derived from the literature. LR, linear regression; MA, major axis estimation; SMA, standardized major axis estimation, LRO, linear regression through the origin. (a,c) Use individual segment densities; (b,d) use a single weighted-mean density. For (a,b), the raw data are used and for (c,d), the data are log-transformed.
appreciable noise in individual cases. Similarly, animals fluctuate in mass depending on nutrition and hydration. However, we suggest that using a robust volumetric technique backed up by neontological data is the best approach currently available.

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