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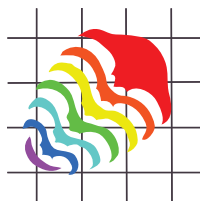


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HOW BIG WAS 'BIG AL'? QUANTIFYING THE EFFECT OF SOFT TISSUE AND OSTEOLOGICAL UNKNOWNNS ON MASS PREDICTIONS FOR ALLOSAURUS (DINOSAURIA:THEROPODA)

Karl T. Bates, Peter L. Falkingham, Brent H. Breithaupt, David Hodgetts, William I. Sellers, and Phillip L. Manning

ABSTRACT

MOR693, nicknamed 'Big Al,' is the most complete skeleton of the non-avian theropod *Allosaurus* and therefore provides the best opportunity to investigate the mass properties of this important Jurassic theropod through accurate physical or digital volumetric models. In this study, laser scanning and computer modelling software have been used to construct volumetric models of MOR693. A long-range laser scanner has been used to digitize the mounted cast of MOR693, allowing the reconstruction of body volumes and respiratory structures around and within the three-dimensional (3D) skeletal model. The digital medium offered the facility to modify model properties non-destructively in a detailed sensitivity analysis to quantify the effects of the many unknown parameters involved in such reconstructions. In addition to varying the volumes of body segments and respiratory structures, we also extend the sensitivity analysis to include uncertainties regarding osteological articulations in non-avian dinosaurs, including effects of inter-vertebral spacing and the orientation or 'flare' of the rib cage in MOR693. Results suggest body mass and inertial values are extremely uncertain and show a wide range in plausible values, whilst the CM (centre of mass) position is well constrained immediately in front and below the hip joint in MOR693, consistent with similar reconstructions of non-avian theropods.

Karl T. Bates. Adaptive Organismal Biology Research Group, Faculty of Life Sciences, University of Manchester, Stopford Building, Oxford Road, Manchester, M13 9PL United Kingdom, karl.bates@postgrad.manchester.ac.uk.

Peter L. Falkingham. School of Earth, Atmospheric and Environmental Science, University of Manchester, Williamson Building, Oxford Road, Manchester, M13 9PL, United Kingdom, peter.falkingham@manchester.ac.uk.

Brent H. Breithaupt. Geological Museum, University of Wyoming, Laramie, WY 82071, USA, uwgeoms@umyo.edu.

David Hodgetts. School of Earth, Atmospheric and Environmental Science, University of Manchester, Williamson Building, Oxford Road, Manchester, M13 9PL, United Kingdom, david.hodgetts@manchester.ac.uk.

William I. Sellers. Adaptive Organismal Biology Research Group, Faculty of Life Sciences, University of

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Manchester, Stopford Building, Oxford Road, Manchester, M13 9PL United Kingdom, william.sellers@manchester.ac.uk.

Phillip L. Manning. The Manchester Museum, University of Manchester, Oxford Road, Manchester, M13 9PL, United Kingdom, and School of Earth, Atmospheric and Environmental Science, University of Manchester, Williamson Building, Oxford Road, Manchester, M13 9PL, United Kingdom, phil.manning@manchester.ac.uk.

Key words: Allosaurus; 'Big Al'; body mass; centre of mass; inertia; LiDAR; modeling

INTRODUCTION

In 1991, the most complete dinosaur known from Wyoming was excavated from the Upper Jurassic Morrison Formation in the eastern Bighorn Basin near the town of Shell (Breithaupt 2001). Although the theropod *Allosaurus* has been known for over 100 years, this specimen (nicknamed 'Big Al') had one of the most complete skulls and skeletons of this genus yet to be found. This specimen is particularly important as it represents a partially articulated, 95% complete, pathologic (i.e., with broken, fractured, and infected bones) skeleton of a sub-adult *Allosaurus fragilis* (although it may represent a new species). Consequently, MOR 693 has gained international recognition, as the scenarios of its painful life, early death, and rapid burial have been determined through various paleontological analyses. The Museum of the Rockies molded MOR 693 and provided a permanent display cast to the University of Wyoming Geological Museum.

Such complete skeletons provide an opportunity to investigate the mass properties of extinct animals by allowing accurate physical or digital volumetric models to be produced (Colbert 1962; Alexander 1985, 1989; Farlow et al. 1995; Henderson 1999; Hutchinson et al. 2007; Bates et al. 2009). These models can be used to characterize the mass, centre of mass (CM) and inertial properties of body segments, providing information necessary for numerical biomechanical assessments of functional morphology (e.g., Hutchinson et al. 2007). Bates et al. (2009) used laser scanning and computer modelling software to construct volumetric models of five specimens of non-avian dinosaurs. A long-range laser (LiDAR) scanner was used to digitize mounted skeletons allowing the reconstruction of body volumes and respiratory structures around and within the 3D skeletal model. The digital medium offered the facility to modify model properties non-destructively, such that a detailed sensitivity analysis could be con-

ducted to quantify the effect of the many unknown parameters involved in such reconstructions. By varying the volume of body segments and respiratory structures, it was possible to constrain the maximum plausible range of mass set values within broad limits. In this study the same approach is used to constrain the maximum plausible range in mass values for *Allosaurus* MOR 693 and by inference specimens of similar skeletal proportions. Sensitivity analyses have only recently begun to be applied in dinosaur body volumetric reconstructions and the few previous studies (Henderson and Snively 2003; Hutchinson et al. 2007; Bates et al. 2009) have not directly addressed the affects of ambiguities in the articulation or mounting of dinosaur skeletons on volumetric reconstructions. In this study the sensitivity analysis is extended to include additional uncertainties regarding osteological articulations in non-avian dinosaurs, with specific focus on the effects of inter-vertebral spacing (i.e., the unknown volume of inter-vertebral discs) and the orientation or 'flare' of the rib cage in MOR 693.

MATERIALS AND METHODS

A RIEGL LMS-Z420i 3D terrestrial Light Detection and Range (LiDAR) scanner was used to digitize the University of Wyoming (UW) Geological Museum's mounted cast of MOR 693 (Figures 1.1, 1.2). The CAD package Maya (www.autodesk.com/maya) was used to construct body outlines around the digital skeletal model, following the approach of Bates et al. (2009; figures 1.3, 1.4). The skull of MOR 693 was mediolaterally distorted during post-mortem burial and so was re-inflated by 20% prior to head volume reconstruction, based on observations of published descriptions of *A. fragilis* (Madsen 1976). Each reconstructed body segment was given a density of 1000 kg m⁻³, in accordance with previous studies (Alexander 1985, 1989; Henderson 1999; Hutchinson et al. 2007).

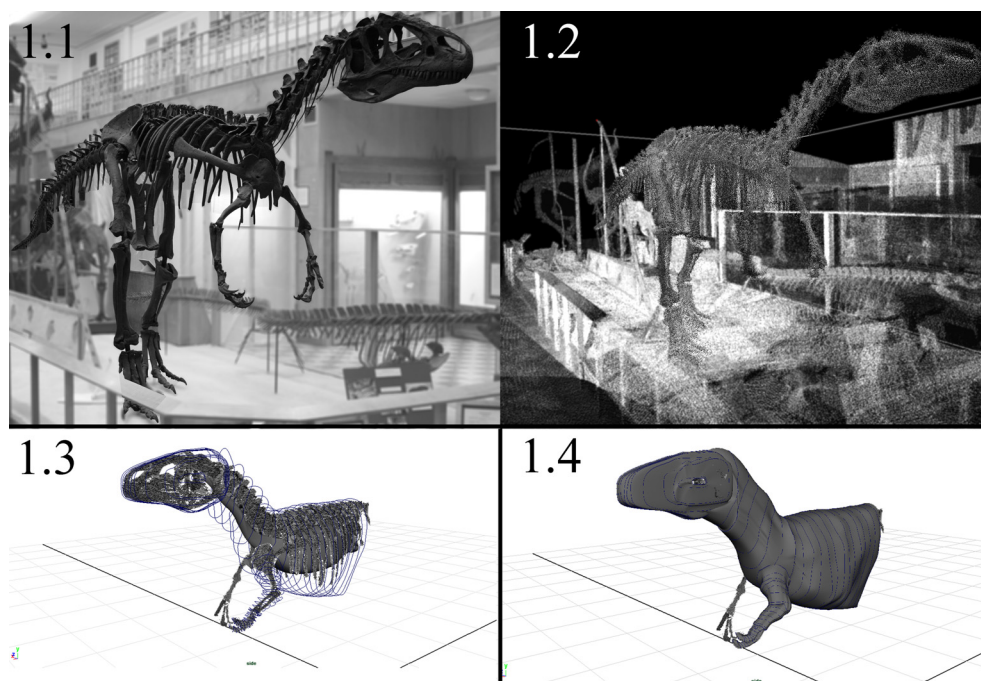


FIGURE 1. (1) Cast of 'Big Al' (MOR 693) at the University of Wyoming Geological Museum. (2) Raw LiDAR point cloud of the specimen and surroundings. (3) Triangulated skeletal model of upper body area, surrounded by Non-Uniform Rational B-Spline (NURBs) circles. (4) Surface lofted through NURBs circles to produce body volume.

After producing a 'best estimate model' (see discussion below) a sensitivity analysis was conducted to investigate the effects of initial assumptions and estimate a realistic range of mass set values for MOR 693. Mass properties were calculated for a single gracile (minus 7.5%) and two larger models (+ 7.5% and +15%), by changing the diameter of the NURBs circles that defined the neck, thoracic, sacral, tail and hind limb segments (thigh, shank and metatarsal). Bates et al. (2009) found that the + 15% models far exceeded the likely maximum body segment volumes for the five animals studied. In an attempt to better constrain the likely maximum mass set values for MOR 693 an additional + 11.25% model was constructed. To investigate uncertainties regarding the relative proportions of body segments, a series of trunk and leg segments from the respective models were interchanged. In addition to segment volumes, the effects of having larger and smaller zero density respiratory structures in our thoracic and neck segments were also tested.

Even near-complete specimens suffer from uncertainties about precise articulation of the skeleton, yet no physical or digital mass reconstruction to-date has tested for the effects of these unknowns on mass set predictions (Bates et al. 2009). As a first step towards quantifying uncer-

tainties in mass predictions related to the mounting of dinosaur skeletons additional models were produced in which the articulation of trunk elements were varied. Specifically, the effects of two uncertainties in dinosaur skeletal reconstructions are tested; the medio-lateral angulation or flare of the ribcage and relative spacing of individual vertebrae (i.e., inter-vertebral disc length). First, the best estimate thoracic volume was adjusted after increasing and decreasing the orientation or flare of the rib cage ± 10 degrees. Second, the best estimate reconstruction was modified by increasing the separation between vertebrae and their associated NURBs outline by 0.005 m to mimic an enlarged inter-vertebral disc cavity. The original spacing of vertebrae from the dorsal and caudal series in the casted skeleton can be found in the appendix (Table 26).

RESULTS

The best estimate mass model of MOR 693 (Figure 2, Animations 1-2) has a total body mass of 1500.91 kg, with the whole body CM positioned 0.184 m and 0.141 m in front and below the acetabulum. Table 1 summarizes the mass data for each of the initial gracile and larger models produced in the sensitivity analysis, a suite of which

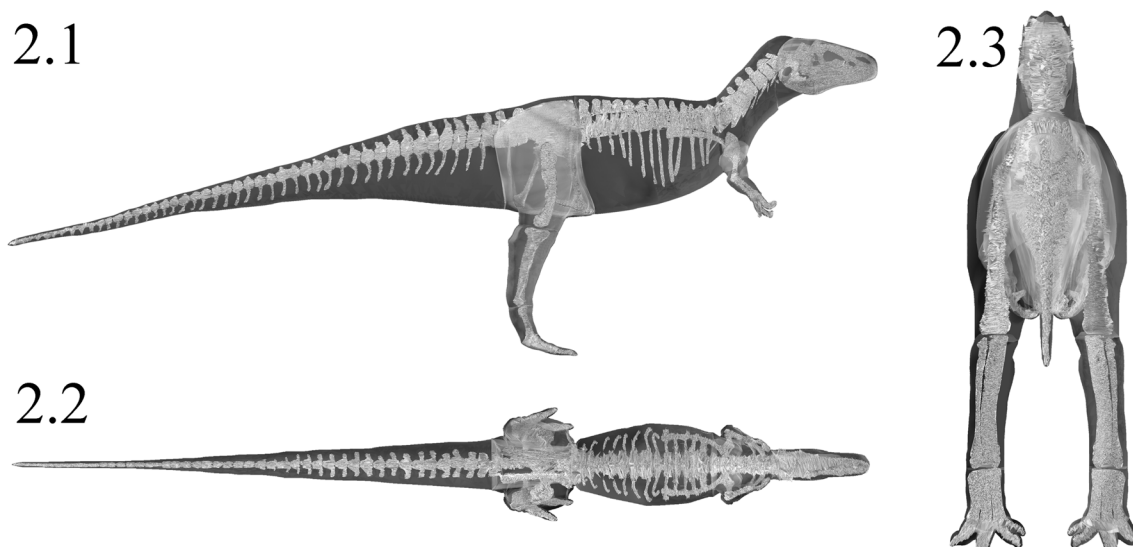
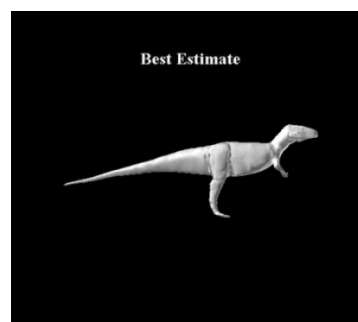


FIGURE 2. Best estimate reconstruction of MOR 693 in (1) right lateral; (2) dorsal; and (3) cranial views (not to scale, respiratory structures not shown). See also Animation 1 & 2.

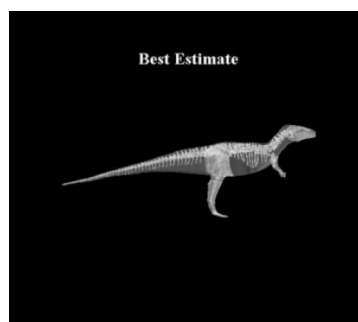
can be seen in the accompanying animations (Animations 3-10). The largest model (Figure 3.4) represented an increase of 31.7% (457.94 kg) in total body mass over the best estimate prediction, while the smallest model (Figure 3.1, Animations 3-4) was 12.9% (193.22 kg) lighter than initial predictions (Table 1). Best estimate centre of mass positions were most affected by altering the combinations of body segment volumes; the combination of large thoracic and neck segments with reduced tail segments resulted in the most cranial CM positions (0.375 m in front of the acetabulum), while enlarged tails and reduced anterior body segments brought the CM closest to the acetabulum (0.05 m in front of the joint). However, the CM remained in front and below the hip joint in all models. The full mass set results for the model generated can be found in the appendix (Appendix: Tables 2-25).

DISCUSSION

The reconstructions presented here provide the first comprehensive mass set values for *Allosaurus*, based on the single most complete specimen currently known and thus providing a firm basis to constrain the likely maximum range in mass properties for this dinosaur. As in a previous study (Bates et al. 2009), reconstruction of best estimate body segment and respiratory volumes was guided by the anatomy of the skeletal model and information from extant archosaurs. It was ensured that the ventral outline of the sacral segment passed close to the pelvis (ischium and



Animation 1. Animation of initial best guess reconstruction of MOR 693 body volumes. (For animations, see web site, palae-electronica.org/2009_3/index.html.)



Animation 2. Animation of best guess reconstruction of MOR 693 body volumes. Body volume translucent to allow view of size of reconstruction around skeleton.

Table 1. Summary of results for volumetric models of MOR 693.

Model	Net Density (kg m-3)	Volume (kg m2)	Mass (kg)	CM (x,y,z) (m)
Best estimate	933.983	1.607	1500.91	0.214, 1.696, 0
Minus 7.5%	910.648	1.436	1307.69	0.215, 1.704, 0
+ 7.5%	922.644	1.849	1705.97	0.211, 1.689, 0
+ 11.25%	928.18	1.973	1831.3	0.21, 1.687, 0
+ 15%	932.916	2.119	1976.85	0.213, 1.686, 0
Expanded rib cage	933.983	1.713	1564.44	0.248, 1.7, 0
Contracted rib cage	949.792	1.487	1412.34	0.17, 1.691, 0
Inter-vertebral spacing +0.005m	928.021	1.657	1537.73	0.228, 1.698, 0

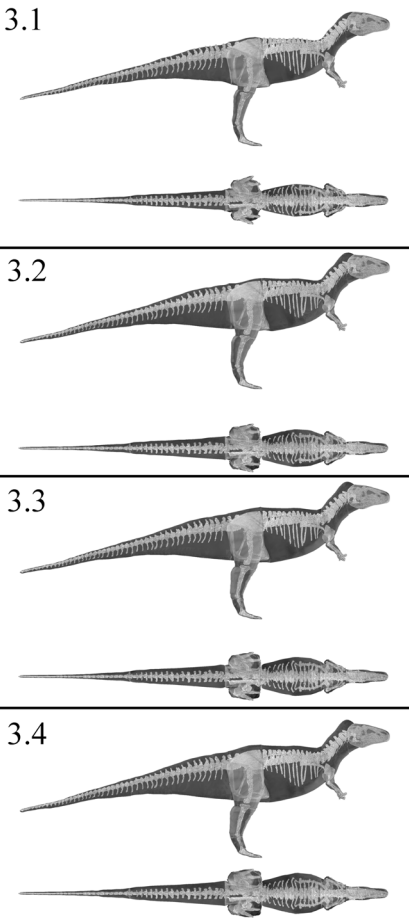
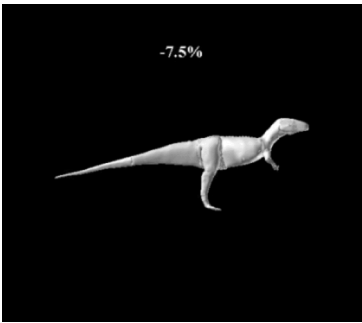
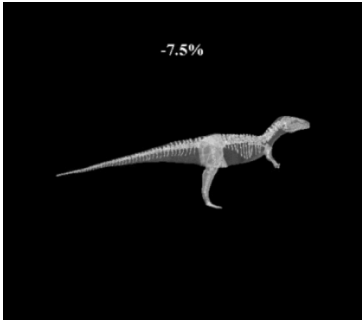


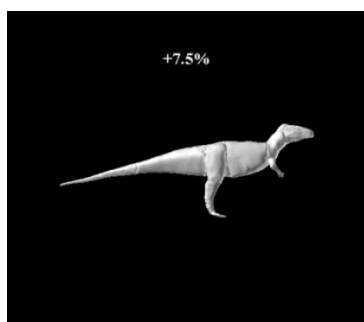
FIGURE 3. Right lateral and dorsal of body outline smaller and larger models of MOR 693. (1) -7.5% from best estimate; (2) +7.5%; (3) +11.25%; and (4) +15%. See also Animations 3-10.



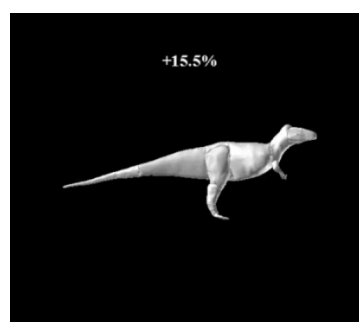
Animation 3. Animation of minus 7.5% reconstruction of MOR 693 body volumes.



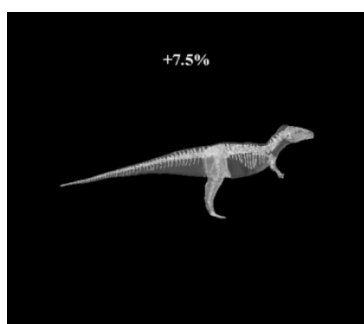
Animation 4. Animation of minus 7.5% reconstruction of MOR 693 body volumes. Body volume translucent to allow view of size of reconstruction around skeleton.



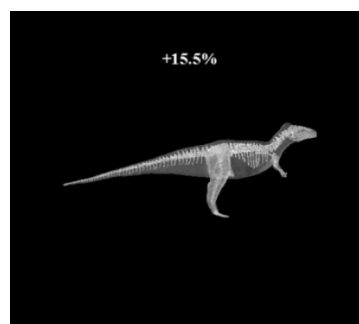
Animation 5. Animation of plus 7.5% reconstruction of MOR 693 body volumes.



Animation 9. Animation of plus 15% reconstruction of MOR 693 body volumes.



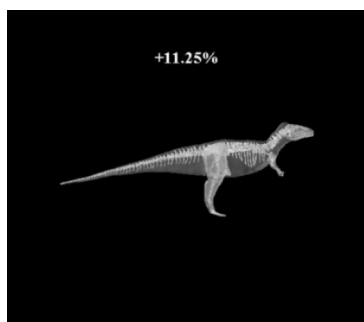
Animation 6. Animation of plus 7.5% reconstruction of MOR 693 body volumes. Body volume translucent to allow view of size of reconstruction around skeleton.



Animation 10. Animation of plus 15% reconstruction of MOR 693 body volumes. Body volume translucent to allow view of size of reconstruction around skeleton.



Animation 7. Animation of plus 11.25% reconstruction of MOR 693 body volumes.



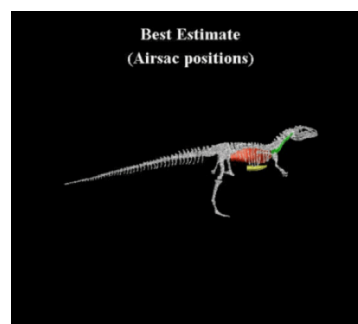
Animation 8. Animation of plus 11.25% reconstruction of MOR 693 body volumes. Body volume translucent to allow view of size of reconstruction around skeleton.

pubis) based on consideration of pelvic limb musculature (Hutchinson 2001) and the impressions of the pubic boot in trace fossils (Gierlinski et al. 2005). The lateral profile around the pectoral girdle has to pass under scapula-coracoids and is unlikely to extend below the level of the arms, which would severely restrict the range of movement. The gastralia form a shallow convexity linking the pubis and sternum in non-avian theropods, so the belly outline was constructed with a conservative amount of flesh beneath this plane, based on the relationship between the gastralia and the abdominal wall in extant crocodilians (Perry 1983; Claessens 2004). The amount of flesh reconstructed on the dorsal surface of the animal was likely to be of moderate depth based on the anatomy of extant archosaurs, though the dorsal outline of the anterior neck is expanded near its insertion on head segment to account for the musculature in the nuchal crest region, notably *M. transversospinalis capitis* (Snively and Russell 2007). The mediolateral expansion of trunk cavities is generally considered to be the most uncertain dimension in trunk reconstructions of non-avian dinosaurs (Henderson 1999). The best estimate

reconstruction of MOR 693 had around 35–40 mm of soft tissue between the proximal end of the ribs and the wall of the thoracic cavity, which represents 12% of the mediolateral width of one side of the reconstructed body volume.

The most gracile model has a total mass of 1307.69 kg (1280 kg with enlarged air sacs) but is highly emaciated, particularly in the torso (Figure 3.1, Animations 3–4). When the gracile model was subjected to the full volume reduction it resulted in the body outline moving within the rib cage, and this was manually adjusted (i.e., re-inflated) prior to mass calculations until the ribs were enclosed within the thoracic cavity. The largest model produced a mass estimate of 1976.85 kg (2000.03 kg with reduced air sacs), but was unrealistic in many areas and contained an excessive amount of flesh around the neck, torso, sacrum and proximal tail (Figure 3.4, Animation 9–10). However, all segments in the + 7.5% model and many of the segments in the + 11.25% model still appeared reasonable given the inherent levels of uncertainty (Figures 3.2–3.3, Animations 5–8). Both the mediolateral and dorso-ventral extent of the proximal parts of the neck and tail appear excessively large in the + 11.25% model, and the ventral outline of the body extended well below the level of the gastral basket (Figure 3.3, Animations 7–8). These considerations suggest that the model represents a close approximation to the likely maximum total body mass for MOR 693 given the current level of uncertainty surrounding body volumes in non-avian dinosaurs. It is therefore suggested that the total body mass of MOR 693 is constrained within 1350–1850 kg.

It is now clear from a number of independent studies that precise values chosen for volumes of respiratory structures have relatively little effect on body mass predictions in dinosaurs (Alexander 2006; Hutchinson et al. 2007; Bates et al. 2009), and the results in this study are consistent with this conclusion. The initial respiratory structures calculated for this study amounted to 8.8% of the total best estimate body volume and 11.5% for the Head-Arms-and-Trunk (HAT) volume (Appendix: Tables 2, 25, and Animation 11). Larger body air sacs increased this volume to 10.5% total body volume (13.6% HAT volume) when placed in the best estimate model, while smaller air sacs were equivalent to just 7.2% total volume or 9.4% HAT volume (Appendix: Tables 3–4, 25). Even changing air sac volumes in the largest and smallest models to exaggerate mass effects had less than $\pm 2.1\%$ effect on total body mass in these models (Appen-



Animation 11. Animation of skeleton of MOR 693 showing size and position of reconstructed respiratory structures.

dix: Tables 9, 14, 25). Addition of an abdominal air sac to the best estimate model had a modest effect on mass predictions, reducing total body by 0.93% (Appendix: Table 5), and so the current ambiguity surrounding the presence of this structure in non-avian theropods (see O'Connor and Claessens 2005 for discussion) does not greatly affect mass set predictions (Bates et al. 2009; Hutchinson et al. 2007).

The sensitivity analysis undertaken on rib cage orientation and inter-vertebral spacing provides the first insight to the effect of ambiguities in dinosaur joint articulation on mass set predictions. Manual adjustments of the best estimate thoracic cavity after increasing the mediolateral flare of the rib cage by 10 degrees resulted in a 20.3% (0.106 kg m^{-3}) increase in thoracic volume, similar to the 23% (0.12 kg m^{-3}) decrease incurred by contracting the rib cage by 10 degrees (Appendix: Tables 20–21; Fig. 4.1). However, expansion and contraction of the rib cage necessitates parallel changes to the thoracic air sac, which reduced the actual change in thoracic mass to +16.4% (63.53 kg) and -22.9% (88.57 kg) in the respective models (Figure 4.1). Whilst this represents a significant change to the mass and volume of the thoracic segment, the overall effect on total body mass is modest (Table 1). Increasing inter-vertebral spacing between caudal, dorsal and cervical vertebrae by 0.005 m effectively increased the length of our best estimate reconstruction by approximately 0.35 m and total body volume by 0.05 m^3 . However, once again the necessity of increasing air sac volume to maintain plausible respiratory anatomy (O'Connor and Claessens 2005) reduced the actual body mass increase to just 36.82 kg or 2.5% (Appendix: Table 22; Figure 4.2).

The sensitivity analysis strongly suggests that the trunk CM must lie well in front and below the

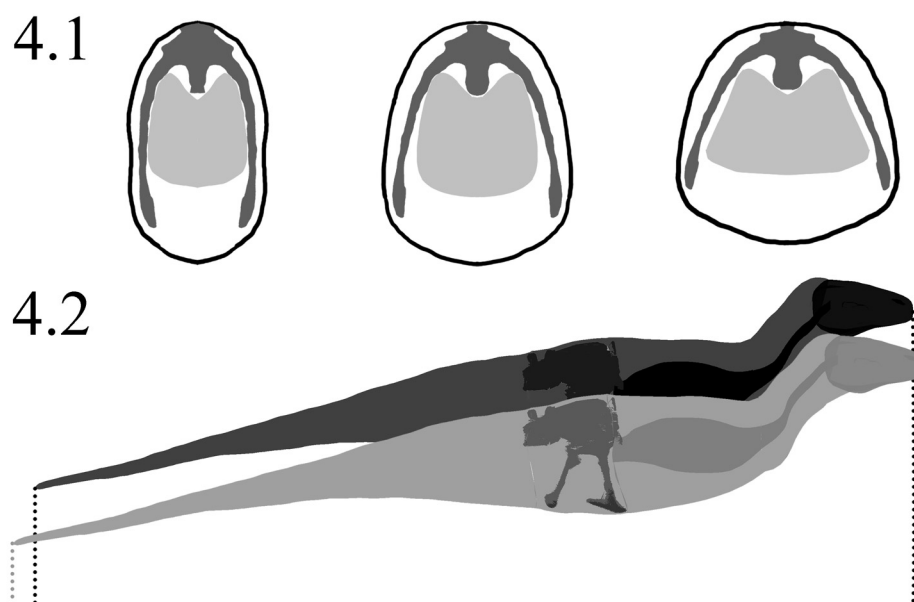


FIGURE 4. Sensitivity analysis of osteological articulations in MOR 693. (1) Schematic diagrams of the reconstructed thoracic outline and respiratory structure around the seventh dorsal rib with the mediolateral orientation of the rib cage reduced (left) and increased (right) by 10 degrees relative to the skeletal mount of MOR 693 (centre). (2) Trunk volume reconstruction with inter-vertebral spacing increased by 5 mm (grey) with the best estimate reconstruction (black) shown for comparison.

acetabulum in *Allosaurus* (Figure 5; Table 1, 23). Even in models with significantly enlarged tails and reduced thoracic and neck segments, the CM remained comfortably in front of the hip joint. The same remained true in sensitivity analyses conducted on volumetric models of *Tyrannosaurus*, *Acrocanthosaurus*, *Struthiomimus* and *Edmontosaurus* in previous studies (Hutchinson et al. 2007; Bates et al. 2009). Varying the volume of thoracic and pharyngeal air sacs had a relatively modest effect on CM positions, shifting the CM by just ± 0.02 m along x (horizontal) and y (vertical) axes (Appendix). Similarly, the changes made to skeletal articulation (rib cage flare and inter-vertebral spacing) failed to shift the CM by more than 0.045 m (Table 1, Appendix: Table 23). Overall, the positions of the Head-Arms-and-Trunk CM and the total body CM from the models of MOR 693 are similar to those calculated for *Acrocanthosaurus*, rather than *Tyrannosaurus* (Hutchinson et al. 2007; Bates et al. 2009), consistent with the relative phylogenetic placement of these taxa within the Theropoda and the relatively larger tails and smaller heads in allosauroids. These results suggest that even with the significant soft tissue and osteological unknowns, it may be possible to test hypotheses regarding phylogenetic trends in CM positions, such as the gradual cranial migration of CM within

Theropoda on the on-line to crown-group birds (Gatesy 1990, 1995).

Mass and inertial properties also underpin biomechanical assessments of absolute and relative performance in both extant and extinct taxa (Winter 1990). For example, Sellers and Manning (2007) used estimated mass properties to conduct a forward simulation of locomotion with the aim of predicting the maximum running speed of *Allosaurus*. A subsequent sensitivity analysis tested for the effect of these estimated mass properties on predicted running speed by individually substituting initial values for numbers sampled from the range of published estimates for *Allosaurus*, in addition to data from extant vertebrates (Bates et al. in press). The volumetric reconstructions and sensitivity analysis presented here suggest the range of mass values tested in this former study far exceed the plausible range for an *Allosaurus* of the skeletal dimensions used. Of particular significance are the leg-to-trunk volume ratios obtained here for *Allosaurus* (Appendix: Table 24), which support earlier inferences that medium to large non-avian theropods are likely to have a lower proportion of total body mass as hind limb muscle than extant avian bipeds (Hutchinson et al. 2007; Bates et al. 2009; see Paul 1998, 2008 for contrary arguments). Bates et al. (in press) tested muscle force values

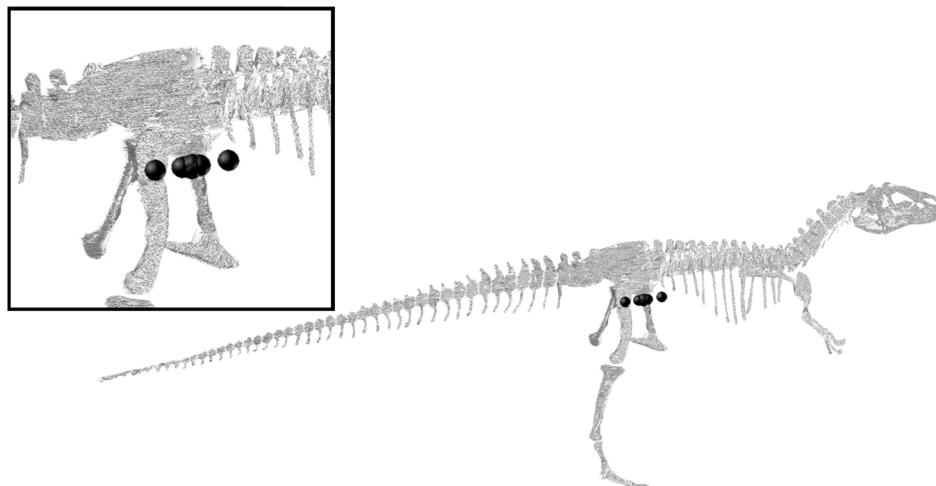


FIGURE 5. Whole body CM positions for all models of MOR 693 produced in the sensitivity analysis. The CM positions of all models are closely clustered together in a region in front and below the hip joint. The most anterior CM is where tail reconstruction is smallest (-7.5%) and thoracic/neck reconstructions are maximum (+15%), and the most posterior CM is where the tail reconstruction is largest (+15%), and torso reconstructions are smallest (-7.5%).

equivalent to values for the muscle mass of a single hind limb between 11.93 – 33.78% total body mass for *Allosaurus*. Although the minimum value falls close to that suggested in this study, the maximum value far exceeds the plausible ratio based on volumetric reconstructions (Appendix: Table 24). Reconstructing MOR 693 with the largest leg volumes (plus 15%) and smallest trunk volume (minus 7.5%) yields a hind limb volume equivalent to 17.79% total body mass, the highest value possible using the reconstructions presented here. This significantly reduces the uncertainty in running performance in *Allosaurus* resulting from unknown muscle mass values. Although an increase in sophistication and anatomical realism of these ‘evolutionary robotic’ models may yield predictions of higher locomotor performance for dinosaurs, the results presented here cast doubt on speeds above 8 m/s for *Allosaurus* based on current simulations (but see Bates et al. in press for discussion of uncertainty resulting from unknown physiological factors).

CONCLUSIONS

This study confirms yet expands upon the results of the few previous sensitivity analyses performed on volumetric reconstructions of non-avian dinosaurs; body mass and inertial values are highly uncertain and show a wide range in plausible values, whilst the CM position is well constrained immediately in front and below the hip joint (Hen-

derson 1999; Hutchinson et al. 2007; Bates et al. 2009). This analysis is the first to demonstrate the relatively modest effect of re-articulating poorly constrained osteological articulations on mass predictions. Increasing inter-vertebral spacing had a modest effect on total body mass and similarly little effect on CM position (as spacing anterior and posterior to the CM were increased), while the impact of altering the mediolateral orientation of the rib cage was largely negated by the necessary concomitant changes to the size of respiratory structures.

In addition to highlighting the importance of sensitivity analyses in soft tissue reconstructions of extinct taxa, these studies also provide the numerical data necessary for more robust evaluation of dinosaur anatomy. For example, whilst it is possible to postulate very large body masses for non-avian dinosaurs from volumetric reconstructions, these are only plausible if the skeleton is strong enough to withstand the forces generated during minimal locomotor exertion (e.g., walking, standing up). Although beyond the scope of this study, data generated from sensitivity analyses such as that reported here must subsequently be assessed in a functional context to further constrain plausible mass properties of non-avian dinosaurs.

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REFERENCES

- Alexander, R.M. 1985. Mechanics of gait and posture of some large dinosaurs, *Zoological Journal of the Linnean Society*, 83:1-25.
- Alexander, R.M. 1989. *Dynamics of Dinosaurs and Other Extinct Giants*. Columbia University Press, New York.
- Alexander, R.M. 2006. Dinosaur biomechanics, *Proceedings of the Royal Society of London B*, 273:1849-1855.
- Bates K.T., Manning, P.L., Hodgetts, D., and Sellers, W.I. 2009. Estimating the mass properties of dinosaurs using laser imaging and 3D computer modeling, *PLoS ONE* 4(2):e4532 doi:10.1371.
- Bates, K.T., Manning, P.L., Margetts, L., and Sellers, W.I. In press. Sensitivity analysis in evolutionary robotic simulations of bipedal dinosaur running. *Journal of Vertebrate Paleontology* 30(1).
- Breithaupt, B.H. (2001) The case of "Big Al" the Allosaurus: a study in paleodetective partnerships, p. 95-106 In Santucci, V.L. and McClelland, L. (eds.) *Proceedings of the 6th Fossil Resource Conference (National Park Service, U.S. Department of the Interior, Geologic Resources Division Technical Report (NPS/NRGRD/GRDTR-01/01)* p. 226.
- Claessens, L.P.A.M. 2004. Dinosaur gastralia: Origin, morphology, and function, *Journal of Vertebrate Paleontology*, 24:90-106.
- Colbert, E.H. 1962. The weights of dinosaurs, *American Mus. Novit.*, 2181:1-24.
- Farlow, J.O., Smith, M.B., and Robinson, J.M. 1995. Body mass, bone 'strength indicator' and cursorial potential of *Tyrannosaurus rex*, *Journal of Vertebrate Paleontology*, 15:713-725.
- Gatesy, S.M. 1990. Caudofemoralis musculature and the evolution of theropod locomotion, *Paleobiology*, 16:170-186.
- Gatesy, S.M. 1995. Functional evolution of the hindlimb and tail from basal theropods to birds, p. 219-234. In Thomason, J.J. (ed.), *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, Cambridge, UK.
- Gierlinski G., Lockley, M., and Milner, A.R.C. 2005. Traces of early Jurassic crouching dinosaurs, p. 4. In *Proceedings of Tracking Dinosaur Origins*, Dixie State College, St. George, Utah.
- Henderson, D.M. 1999. Estimating the Masses and Centers of Masses of Extinct Animals by 3-D Mathematical Slicing, *Paleobiology*, 25:88-106.
- Henderson, D.M. and Snively, E. 2003. *Tyrannosaurus* en pointe: allometry minimized rotational inertia of large carnivorous dinosaurs, *Proceedings of the Royal Society of London B Supplement: Biology Letters* 271:S57-S60.
- Hutchinson, J.R. 2001. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes), *Zoological Journal of the Linnean Society*, 131:123-168.
- Hutchinson J.R., Thow-Hing, V.Ng., and 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.
- Madsen, J.H. 1976. *Allosaurus fragilis*: A revised osteology. Bulletin 109 Utah Geological Survey, pp. 163.
- O'Connor, P.M. and Claessens, L.P.A.M. 2005. Basic avian pulmonary design and flow-ventilation in non-avian theropod dinosaurs, *Nature*, 436:253-256.
- Paul, G.S. 1998. Limb design, function and running performance in ostrich-mimics and Tyrannosaurs, *Gaia*, 15:257-270.
- Paul, G.S. 2008. The Extreme Lifestyles and Habits of the Gigantic Tyrannosaurid Superpredators of the Late Cretaceous of North America and Asia, p. 307-354. In Larson, P. and Carpenter, K. (eds.), *Tyrannosaurus Rex, The Tyrant King*. Indiana University Press, Bloomington.
- Perry, S.F. 1983. Reptilian lungs: functional anatomy and evolution, *Advances in Anatomy, Embryology, and Cell Biology*, 79:1-81.
- Sellers, W.I. and P.L. Manning, 2007. Estimating dinosaur maximum running speeds using evolutionary robotics. *Proceedings of the Royal Society B* 274 :2711-2716.
- Snively, E. and Russell, A.P. 2007. Functional variation of neck muscles and their relation to feeding style in Tyrannosauridae and other large theropod dinosaurs, *The Anatomical Record*, 290:934-957.
- Winter, D.A. 1990. *Biomechanics and motor control of human movement*. John Wiley and Sons, New York, pp 277.

APPENDIX

Table 2. Results for the best estimate model of MOR 693.

Segment	Net Density (kg m ⁻³)	Volume (m ³)	Mass (kg)	CM (x,y,z) (m)	Ixx Iyy Izz (kg m ²)
Head	990.536	0.069	68.347	2.397, 2.52, 0	34.083, 301.742, 335.221
Air sacs	0	0.0007	0	-	-
Neck	946.09	0.121	114.477	1.758, 2.160, 0	21.471, 243.96, 263.925
Pharyngeal cavity	0	0.006	0	-	-
Thorax	742.04	0.521	386.603	0.917, 1.796, 0	29.796, 199.55, 221.557
Lungs	0	0.135	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.467, 32.593, 43.15
Tail	1000	0.317	317.484	-0.193, 1.644, 0	25.228, 995.577, 1016.57
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	1.009, 18.091, 18.181
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.072, 1.259, 1.297
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.179, 1.451, 1.599
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.068, 0.513, 0.569
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.327, 21.314, 21.645
Thigh	1000	0.146	146.198	0.002, 1.606, -0.268	12.752, 4.44, 14.88
Shank	1000	0.041	41.352	-0.152, 0.839, -0.293	1.682, 0.546, 1.879
Metatarsus	1000	0.009	9.214	-0.18, 0.301, -0.313	0.089, 0.052, 0.086
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.008, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.202	202.772	-0.039, 1.346, -0.277	14.536, 5.09, 16.898
HAT	885.5	1.237	1095.37	0.3081, 1.826, 0	126.701, 1816.05, 1923.72
Whole Body	933.983	1.607	1500.91	0.214, 1.696, 0	-

Table 3. Results for the best estimate model of MOR 693 with enlarged respiratory structures.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	33.650, 306.729, 339.776
Air sacs	0	0.0007	0	-	-
Neck	929.8	0.121	112.511	1.758, 2.162, 0	20.563, 245.186, 264.87
Pharyngeal cavity	0	0.008	0	-	-
Thorax	693.067	0.521	361.088	0.917, 1.808, 0	26.823, 194.551, 218.255
Lungs	0	0.16	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.573, 30.373, 41.036
Tail	1000	0.317	317.484	-0.193, 1.644, 0	25.761, 977.993, 999.519
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	1.027, 18.536, 18.645
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.074, 1.285, 1.326
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.181, 1.483, 1.634
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.069, 0.524, 0.582
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.352, 21.829, 22.187
Thigh	1000	0.146	146.198	0.002, 1.606, -0.268	12.752, 4.44, 14.88
Shank	1000	0.041	41.352	-0.152, 0.839, -0.293	1.682, 0.546, 1.879
Metatarsus	1000	0.009	9.214	-0.18, 0.301, -0.313	0.089, 0.052, 0.086
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.008, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000		202.772	-0.039, 1.346, -0.277	14.536, 5.09, 16.898
HAT	863.29	1.237	1067.89	0.291, 1.83, 0	123.079, 1798.49, 1907.83
Whole Body	916.882	1.607	1473.43	0.2, 1.697 0	-

Table 4. Results for the best estimate model of MOR 693 with reduced respiratory structures.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	Ixx Iyy Izz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	34.359, 297.264, 331.02
Air sacs	0	0.0007	0	-	-
Neck	958.818	0.121	116.017	1.759, 2.16, 0	21.961, 242.4, 262.589
Pharyngeal cavity	0	0.005	0	-	-
Thorax	789.338	0.521	411.245	0.918, 1.788, 0	32.346, 209.989, 218.213
Lungs	0	0.11	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.404, 34.7, 45.194
Tail	1000	0.317	317.484	-0.193, 1.644, 0	24.896, 1011.65, 1032.32
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	0.997, 17.693, 17.771
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.071, 1.235, 1.272
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.177, 1.423, 1.569
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.067, 0.503, 0.558
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.312, 20.853, 21.17
Thigh	1000	0.146	146.198	0.002, 1.606, -0.268	12.752, 4.44, 14.88
Shank	1000	0.041	41.352	-0.152, 0.839, -0.293	1.682, 0.546, 1.879
Metatarsus	1000	0.009	9.214	-0.18, 0.301, -0.313	0.089, 0.052, 0.086
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.008, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.202	202.772	-0.039, 1.346, -0.277	14.536, 5.09, 16.898
HAT	906.669	1.237	1121.55	0.324, 1.823, 0	129.59, 1837.71, 1931.67
Whole Body	950.274	1.607	1527.09	0.228, 1.696, 0	-

Table 5. Results for the best estimate model of MOR 693 with an abdominal air sac.

Segment	Net Density (kg m ⁻³)	Volume (m ³)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m ²)
Head	990.536	0.069	68.347	2.397, 2.52, 0	33.639, 304.463, 337.498
Air sacs	0	0.0007	0	-	-
Neck	946.09	0.121	116.017	1.759, 2.16, 0	21.114, 247.127, 266.734
Pharyngeal cavity	0	0.006	0	-	-
Thorax	715.15	0.521	372.593	0.913, 1.808, 0	27.617, 196.254, 216.182
Lungs	0	0.135	0	-	-
Abdominal air sac	0	0.014	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.576, 31.365, 42.031
Tail	1000	0.317	317.484	-0.193, 1.644, 0	25.776, 985.939, 1007.48
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	1.028, 18.334, 18.443
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.074, 1.273, 1.314
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.182, 1.468, 1.62
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.069, 0.519, 0.576
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.353, 21.594, 21.953
Thigh	1000	0.146	146.198	0.002, 1.606, -0.268	12.752, 4.44, 14.88
Shank	1000	0.041	41.352	-0.152, 0.839, -0.293	1.682, 0.546, 1.879
Metatarsus	1000	0.009	9.214	-0.18, 0.301, -0.313	0.089, 0.052, 0.086
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.008, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.202	202.772	-0.039, 1.346, -0.277	14.536, 5.09, 16.898
HAT	874.179	1.237	1081.36	0.299, 1.83, 0	124.429, 1808.34, 1913.83
Whole Body	925.264	1.607	1486.9	0.207, 1.698, 0	-

Table 6. Results for the best estimate model of MOR 693 with enlarged (+15%) legs.

Segment	Net Density (kg m ⁻³)	Volume (m ³)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m ²)
Head	990.536	0.069	68.347	2.397, 2.52, 0	34.083, 301.742, 335.221
Air sacs	0	0.0007	0	-	-
Neck	946.09	0.121	114.477	1.758, 2.160, 0	21.471, 243.96, 263.925
Pharyngeal cavity	0	0.006	0	-	-
Thorax	742.04	0.521	386.603	0.917, 1.796, 0	29.796, 199.55, 221.557
Lungs	0	0.135	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.467, 32.593, 43.15
Tail	1000	0.317	317.484	-0.193, 1.644, 0	25.228, 995.577, 1016.57
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	1.009, 18.091, 18.181
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.072, 1.259, 1.297
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.179, 1.451, 1.599
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.068, 0.513, 0.569
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.327, 21.314, 21.645
Thigh	1000	0.193	193.347	0.004, 1.57, -0.283	19.299, 6.927, 22.623
Shank	1000	0.051	51.24	-0.171, 0.796, -0.295	1.771, 0.889, 2.084
Metatarsus	1000	0.012	12.074	-0.188	0.118, 0.079, 0.112
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.008, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.262	262.669	-0.039, 1.327, -0.288	14.536, 5.09, 16.898
HAT	885.5	1.237	1095.37	0.3081, 1.826, 0	126.701, 1816.05, 1923.72
Whole Body	920.334	1.761	1620.708	0.214, 1.696, 0	-

Table 7. Results for the best estimate model of MOR 693 with reduced (- 7.5%) legs.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	34.083, 301.742, 335.221
Air sacs	0	0.0007	0	-	-
Neck	946.09	0.121	114.477	1.758, 2.160, 0	21.471, 243.96, 263.925
Pharyngeal cavity	0	0.006	0	-	-
Thorax	742.04	0.521	386.603	0.917, 1.796, 0	29.796, 199.55, 221.557
Lungs	0	0.135	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.467, 32.593, 43.15
Tail	1000	0.317	317.484	-0.193, 1.644, 0	25.228, 995.577, 1016.57
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	1.009, 18.091, 18.181
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.072, 1.259, 1.297
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.179, 1.451, 1.599
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.068, 0.513, 0.569
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.327, 21.314, 21.645
Thigh	1000	0.127	126.54	0.006, 1.631, -0.259	10.353, 3.543, 12.109
Shank	1000	0.036	36.393	-0.144, 0.859, -0.292	1.626, 0.422, 1.787
Metatarsus	1000	0.00079	7.908	-0.18, 0.3, -0.311	0.073, 0.039, 0.07
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.008, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.17	176.849	-0.034, 1.361, -0.27	14.536, 5.09, 16.898
HAT	885.5	1.237	1095.37	0.3081, 1.826, 0	126.701, 1816.05, 1923.72
Whole Body	918.42	1.577	1448.348	0.214, 1.696, 0	-

Table 8. Results for the - 7.5% best estimate model of MOR 693.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	33.484, 302.116, 334.996
Air sacs	0	0.0007	0	-	-
Neck	938.621	0.103	96.678	1.75, 2.1566, 0	16.896, 203.955, 219.999
Pharyngeal cavity	0	0.006	0	-	-
Thorax	695.372	0.444	308.745	0.91, 1.795, 0	18.802, 156.171, 174.624
Lungs	0	0.135	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.616, 32.422, 43.128
Tail	1000	0.272	271.764	-1.286, 1.651, 0	20.304, 844.849, 861.996
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	1.035, 18.124, 18.24
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.075, 1.261, 1.302
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.183, 1.454, 1.606
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.069, 0.514, 0.571
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.361, 21.352, 21.72
Thigh	1000	0.127	126.54	0.006, 1.631, -0.259	10.353, 3.543, 12.109
Shank	1000	0.036	36.393	-0.144, 0.859, -0.292	1.626, 0.422, 1.787
Metatarsus	1000	0.00079	7.908	-0.18, 0.3, -0.311	0.073, 0.039, 0.07
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.003, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.17	176.849	-0.034, 1.361, -0.27	12.066, 4.054, 14.020
HAT	866.831	1.097	950.914	0.307, 1.832, 0	105.828, 1582.22, 1678.18
Whole Body	910.648	1.436	1307.69	0.215, 1.704, 0	-

Table 9. Results for the - 7.5% best estimate model of MOR 693 with enlarged lungs.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	32.973, 307.883, 340.252
Air sacs	0	0.0007	0	-	-
Neck	919.534	0.103	94.712	1.75, 2.159, 0	16.003, 204.995, 220.772
Pharyngeal cavity	0	0.008	0	-	-
Thorax	536.55	0.444	238.23	0.909, 1.811, 0	15.771, 150.335, 170.424
Lungs	0	0.16	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.757, 29.878, 40.725
Tail	1000	0.272	271.764	-1.286, 1.651, 0	20.848, 827.573, 845.264
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	1.058, 18.64, 18.779
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.078, 1.292, 1.336
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.186, 1.49, 1.646
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.07, 0.527, 0.586
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.392, 21.948, 22.346
Thigh	1000	0.127	126.54	0.006, 1.631, -0.259	10.353, 3.543, 12.109
Shank	1000	0.036	36.393	-0.144, 0.859, -0.292	1.626, 0.422, 1.787
Metatarsus	1000	0.00079	7.908	-0.18, 0.3, -0.311	0.073, 0.039, 0.07
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.003, 0.007, 0.007
Digit III	1000	0.002	2.45	-0.048, 0.113, -0.206	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.17	176.849	-0.034, 1.361, -0.27	12.066, 4.054, 14.020
HAT	844.585	1.097	926.51	0.287, 1.837, 0	102.138, 1564.56, 1662.13
Whole Body	891.511	1.436	1280.21	0.198, 1.706, 0	-

Table 10. Results for the - 7.5% model of MOR 693 with enlarged (+ 15%) legs.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	33.484, 302.116, 334.996
Air sacs	0	0.0007	0	-	-
Neck	938.621	0.103	96.678	1.75, 2.1566, 0	16.896, 203.955, 219.999
Pharyngeal cavity	0	0.006	0	-	-
Thorax	695.372	0.444	308.745	0.91, 1.795, 0	18.802, 156.171, 174.624
Lungs	0	0.135	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.616, 32.422, 43.128
Tail	1000	0.272	271.764	-1.286, 1.651, 0	20.304, 844.849, 861.996
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	1.0348, 18.124, 18.24
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.075, 1.261, 1.302
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.183, 1.454, 1.606
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.069, 0.514, 0.571
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.361, 21.352, 21.72
Thigh	1000	0.193	193.347	0.004, 1.57, -0.283	19.299, 6.927, 22.623
Shank	1000	0.051	51.24	-0.171, 0.796, -0.295	1.771, 0.889, 2.084
Metatarsus	1000	0.012	12.074	-0.188, 0.303, -0.317	0.118, 0.079, 0.112
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.003, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.262	262.669	-0.039, 1.327, -0.288	14.536, 5.09, 16.898
HAT	866.831	1.097	950.914	0.307, 1.832, 0	105.828, 1582.22, 1678.18
Whole Body	911.789	1.621	1478.01	0.184, 1.654, 0	-

Table 11. Results for the + 7.5% best estimate model of MOR 693.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	34.807, 303.668, 337.871
Air sacs	0	0.0007	0	-	-
Neck	953.717	0.138	131.613	1.76, 2.159, 0	25.907, 284.315, 307.945
Pharyngeal cavity	0	0.006	0	-	-
Thorax	776.723	0.606	470.694	0.924, 1.795, 0	43.554, 252.364, 278.902
Lungs	0	0.135	0	-	-
Sacrum	1000	0.194	193.893	-0.046, 1.769, 0	14.171, 33.747, 44.833
Tail	1000	0.369	369.534	-1.297, 1.636, 0	31.342, 1156.42, 1182.02
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	0.978, 18.263, 18.322
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.069, 1.269, 1.304
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.174, 1.463, 1.607
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.066, 0.517, 0.572
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.287, 21.512, 21.805
Thigh	1000	0.163	162.792	0.001, 1.584, -0.273	15.125, 5.224, 17.607
Shank	1000	0.046	46.104	-0.16, 0.819, -0.295	1.716, 0.694, 1.959
Metatarsus	1000				0.106, 0.068, 0.101
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.003, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.03, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.226	225.488	-0.041, 1.328, -0.281	16.96, 6.038, 19.721
HAT	876.879	1.397	1255	0.301, 1.818, 0	152.357, 2073.53, 2195.18
Whole Body	922.644	1.849	1705.97	0.211, 1.689, 0	-

Table 12. Results for the + 11.25% best estimate model of MOR 693.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	Ixx Iyy Izz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	35.083, 304.004, 338.483
Air sacs	0	0.0007	0	-	-
Neck	961.571	0.147	141.351	1.767, 2.169, 0	29.656, 308.481, 335.552
Pharyngeal cavity	0	0.006	0	-	-
Thorax	792.739	0.651	516.073	0.924, 1.794, 0	51.79, 278.915, 308.219
Lungs	0	0.135	0	-	-
Sacrum	1000	0.204	203.635	-0.045, 1.767, 0	16.838, 34.931, 48.675
Tail	1000	0.395	394.485	-1.302, 1.632, 0	34.66, 1239.91, 1268.12
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	0.967, 18.293, 18.341
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.067, 1.271, 1.305
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.172, 1.465, 1.608
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.065, 0.518, 0.572
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.272, 21.547, 21.825
Thigh	1000	0.177	177.115	0.003, 1.583, -0.279	17.441, 5.896, 20.172
Shank	1000	0.049	48.712	-0.166, 0.806, -0.295	1.753, 0.786, 2.027
Metatarsus	1000	0.011	11.414	-0.181, 0.304, -0.316	0.118, 0.079, 0.112
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.003, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.03
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.243	243.249	-0.04, 1.331, -0.285	19.325, 6.812, 22.365
HAT	904.378	1.487	1344.81	0.3, 1.815, 0	170.574, 2209.33, 2342.7
Whole Body	928.18	1.973	1831.3	0.21, 1.687, 0	-

Table 13. Results for the + 15% best estimate model of MOR 693.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	35.217, 302.97, 337.582
Air sacs	0	0.0007	0	-	-
Neck	963.593	0.162	156.102	1.771, 2.168, 0	33.557, 341.362, 371.429
Pharyngeal cavity	0	0.006	0	-	-
Thorax	807.59	0.702	566.928	0.928, 1.793, 0	61.81, 308.161, 340.201
Lungs	0	0.135	0	-	-
Sacrum	1000	0.217	216.678	-0.049, 1.775, 0	19.247, 38.594, 54.342
Tail	1000	0.424	423.864	-1.299, 1.63, 0	38.711, 1332.79, 1363.99
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	0.951, 18.19, 18.244
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.066, 1.265, 1.298
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.171, 1.458, 1.6
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.065, 0.516, 0.569
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.253, 21.428, 21.711
Thigh	1000	0.193	193.347	0.004, 1.57, -0.283	19.299, 6.927, 22.623
Shank	1000	0.051	51.24	-0.171, 0.796, -0.295	1.771, 0.889, 2.084
Metatarsus	1000	0.012	12.074	-0.188, 0.303, -0.317	0.118, 0.079, 0.112
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.003, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.03, 0.03
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.262	262.009	-0.039, 1.33, -0.288	21.201, 7.946, 24.872
HAT	910.865	1.595	1452.83	0.304, 1.814, 0	191.053, 2366.73, 2510.97
Whole Body	932.916	2.119	1976.85	0.213, 1.686, 0	-

Table 14. Results for the + 15% best estimate model with reduced respiratory structures.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	35.41, 299.543, 334.348
Air sacs	0	0.0007	0	-	-
Neck	973.099	0.162	157.642	1.771, 2.168, 0	34.055, 339.557, 369.857
Pharyngeal cavity	0	0.005	0	-	-
Thorax	842.692	0.702	591.57	0.928, 1.788, 0	64.303, 317.734, 335.933
Lungs	0	0.11	0	-	-
Sacrum	1000	0.217	216.678	-0.049, 1.775, 0	19.214, 40.461, 56.177
Tail	1000	0.424	423.864	-1.299, 1.63, 0	38.402, 1349.17, 1380.06
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	0.944, 17.885, 17.931
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.065, 1.246, 1.279
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.17, 1.437, 1.577
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.064, 0.508, 0.561
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.243, 21.075, 21.348
Thigh	1000	0.193	193.347	0.004, 1.57, -0.283	19.299, 6.927, 22.623
Shank	1000	0.051	51.24	-0.171, 0.796, -0.295	1.771, 0.889, 2.084
Metatarsus	1000	0.012	12.074	-0.188, 0.303, -0.317	0.118, 0.079, 0.112
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.003, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.03, 0.03
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.262	262.009	-0.039, 1.33, -0.288	21.201, 7.946, 24.872
HAT	927.279	1.595	1479.01	0.316, 1.811, 0	193.873, 2388.61, 2519.07
Whole Body	945.271	2.119	2003.03	0.223, 1.686, 0	-

Table 15. Results for the + 15% best estimate model of MOR 693 with reduced (- 7.5%) legs.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	Ixx Iyy Izz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	35.217, 302.97, 337.582
Air sacs	0	0.0007	0	-	-
Neck	963.593	0.162	156.102	1.771, 2.168, 0	33.557, 341.362, 371.429
Pharyngeal cavity	0	0.006	0	-	-
Thorax	807.59	0.702	566.928	0.928, 1.793, 0	61.81, 308.161, 340.201
Lungs	0	0.135	0	-	-
Sacrum	1000	0.217	216.678	-0.049, 1.775, 0	19.247, 38.594, 54.342
Tail	1000	0.424	423.864	-1.299, 1.63, 0	38.711, 1332.79, 1363.99
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	0.951, 18.19, 18.244
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.066, 1.265, 1.298
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.171, 1.458, 1.6
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.065, 0.516, 0.569
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.253, 21.428, 21.711
Thigh	1000	0.127	126.54	0.006, 1.631, -0.259	10.353, 3.543, 12.109
Shank	1000	0.036	36.393	-0.144, 0.859, -0.292	1.626, 0.422, 1.787
Metatarsus	1000	0.00079	7.908	-0.18, 0.3, -0.311	0.073, 0.039, 0.07
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.003, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.03, 0.03
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.17	176.849	-0.034, 1.361, -0.27	12.066, 4.054, 14.020
HAT	910.865	1.595	1452.83	0.304, 1.814, 0	191.053, 2366.73, 2510.97
Whole Body	852.539	2.119	1806.53	0.238, 1.725, 0	-

Table 16. Results for best estimate model of MOR 693 with + 15% tail and - 7.5% neck and thorax.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	36.674, 369.545, 405.615
Air sacs	0	0.0007	0	-	-
Neck	938.621	0.103	96.678	1.75, 2.157, 0	19.082, 271.325, 289.554
Pharyngeal cavity	0	0.006	0	-	-
Thorax	695.372	0.444	308.745	0.91, 1.795, 0	18.383, 255.038, 273.072
Lungs	0	0.135	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13, 12.614, 22.706
Tail	1000	0.424	423.864	-1.299, 1.63, 0	36.47, 1053.25, 1082.22
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	0.9066, 24.29, 24.278
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.06, 1.628, 1.654
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.163, 1.887, 2.02
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.062, 0.672, 0.723
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.191, 28.477, 28.674
Thigh	1000	0.146	146.198	0.002, 1.606, -0.268	12.752, 4.44, 14.88
Shank	1000	0.041	41.352	-0.152, 0.839, -0.293	1.682, 0.546, 1.879
Metatarsus	1000	0.009	9.214	-0.18, 0.301, -0.313	0.089, 0.052, 0.086
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.008, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.202	202.772	-0.039, 1.346, -0.277	14.536, 5.09, 16.898
HAT	886.29	1.248	1106.09	0.083, 1.799, 0	126.701, 1816.05, 1923.72
Whole Body	915.03	1.652	1511.63	0.05, 1.677, 0	-

Table 17. Results for best estimate model of MOR 693 with - 7.5% tail and + 15% neck and thorax.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	32.735, 199.988, 232.119
Air sacs	0	0.0007	0	-	-
Neck	963.593	0.162	156.102	1.771, 2.168, 0	30.765, 183.923, 211.201
Pharyngeal cavity	0	0.006	0	-	-
Thorax	807.59	0.702	566.928	0.928, 1.793, 0	62.825, 116.165, 149.228
Lungs	0	0.135	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.827, 66.166, 77.083
Tail	1000	0.272	271.764	-1.286, 1.651, 0	21.109, 1029.57, 1047.53
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	1.069, 13.382, 13.532
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.079, 0.73, 0.775
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.188, 1.113, 1.271
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.071, 0.39, 0.45
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.406, 15.858, 16.27
Thigh	1000	0.146	146.198	0.002, 1.606, -0.268	12.752, 4.44, 14.88
Shank	1000	0.041	41.352	-0.152, 0.839, -0.293	1.682, 0.546, 1.879
Metatarsus	1000	0.009	9.214	-0.18, 0.301, -0.313	0.089, 0.052, 0.086
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.008, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.202	202.772	-0.039, 1.346, -0.277	14.536, 5.09, 16.898
HAT	899.929	1.413	1271.6	0.508, 1.84, 0	164.075, 1816.89, 1939.05
Whole Body	923.027	1.817	1677.14	0.375, 1.721, 0	-

Table 18. Results for best estimate model of MOR 693 with + 11.25% tail and - 7.5% neck and thorax.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	36.129, 358.069, 393.594
Air sacs	0	0.0007	0	-	-
Neck	938.621	0.103	96.678	1.75, 2.157, 0	18.7, 259.665, 277.512
Pharyngeal cavity	0	0.006	0	-	-
Thorax	695.372	0.444	308.745	0.91, 1.795, 0	18.406, 236.783, 254.84
Lungs	0	0.135	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.077, 14.562, 24.729
Tail	1000	0.395	394.485	-1.302, 1.632, 0	33.151, 1024.25, 1050.96
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	0.927, 23.221, 23.229
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.0626, 1.565, 1.594
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.166, 1.812, 1.948
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.063, 0.644, 0.696
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.218, 27.242, 27.466
Thigh	1000	0.146	146.198	0.002, 1.606, -0.268	12.752, 4.44, 14.88
Shank	1000	0.041	41.352	-0.152, 0.839, -0.293	1.682, 0.546, 1.879
Metatarsus	1000	0.009	9.214	-0.18, 0.301, -0.313	0.089, 0.052, 0.086
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.008, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.202	202.772	-0.039, 1.346, -0.277	14.536, 5.09, 16.898
HAT	883.273	1.219	1076.71	0.119, 1.8, 0	121.901, 1947.81, 2056.57
Whole Body	913.284	1.623	1482.26	0.076, 1.679, 0	-

Table 19. Results for best estimate model of MOR 693 with - 7.5% tail and + 11.25% neck and thorax.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	Ixx Iyy Izz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	32.867, 256.754, 289.018
Air sacs	0	0.0007	0	-	-
Neck	961.571	0.147	141.351	1.766, 2.169, 0	27.391, 241.404, 266.21
Pharyngeal cavity	0	0.006	0	-	-
Thorax	792.739	0.651	516.073	0.924, 1.794, 0	52.592, 183.439, 213.546
Lungs	0	0.135	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.788, 59.105, 69.983
Tail	1000	0.272	271.764	-1.286, 1.651, 0	20.963, 995.348, 1013.15
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	1.063, 14.166, 14.31
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.078, 1.02, 1.065
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.187, 1.17, 1.336
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.071, 0.411, 0.47
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.398, 16.767, 17.171
Thigh	1000	0.146	146.198	0.002, 1.606, -0.268	12.752, 4.44, 14.88
Shank	1000	0.041	41.352	-0.152, 0.839, -0.293	1.682, 0.546, 1.879
Metatarsus	1000	0.009	9.214	-0.18, 0.301, -0.313	0.089, 0.052, 0.086
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.008, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.202	202.772	-0.039, 1.346, -0.277	14.536, 5.09, 16.898
HAT	895.316	1.347	1205.99	0.472, 1.839, 0	150.4, 1769.58, 1886.25
Whole Body	920.354	1.751	1611.54	0.344, 1.715, 0	-

Table 20. Results for the best estimate model of MOR 693 with an enlarged rib cage.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	34.208, 290.461, 324.065
Air sacs	0	0.0007	0	-	-
Neck	946.09	0.121	114.477	1.758, 2.160, 0	21.572, 230.902, 250.968
Pharyngeal cavity	0	0.006	0	-	-
Thorax	717.914	0.627	450.132	0.934, 1.796, 0	40.085, 235.364, 234.717
Lungs	0	0.178	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.438, 38.114, 48.642
Tail	1000	0.317	317.484	-0.193, 1.644, 0	25.077, 1036.63, 1057.47
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	1.003, 17.091, 17.175
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.072, 1.198, 1.236
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.178, 1.38, 1.528
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.067, 0.487, 0.543
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.329, 20.156, 20.482
Thigh	1000	0.146	146.198	0.002, 1.606, -0.268	12.752, 4.44, 14.88
Shank	1000	0.041	41.352	-0.152, 0.839, -0.293	1.682, 0.546, 1.879
Metatarsus	1000	0.009	9.214	-0.18, 0.301, -0.313	0.089, 0.052, 0.086
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.008, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.202	202.772	-0.039, 1.346, -0.277	14.536, 5.09, 16.898
HAT	885.5	1.343	1158.9	0.348, 1.824, 0	137.022, 1871.78, 1956.82
Whole Body	933.983	1.713	1564.44	0.248, 1.7, 0	-

Table 21. Results for the best estimate model of MOR 693 with a contracted rib cage.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m2)
Head	990.536	0.069	68.347	2.397, 2.52, 0	33.721, 317.266, 350.384
Air sacs	0	0.0007	0	-	-
Neck	946.09	0.121	114.477	1.758, 2.160, 0	21.18, 262.108, 281.782
Pharyngeal cavity	0	0.006	0	-	-
Thorax	743.227	0.401	298.034	0.917, 1.8, 0	18.67, 170.957, 192.489
Lungs	0	0.103	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.555, 26.106, 36.751
Tail	1000	0.317	317.484	-0.193, 1.644, 0	25.673, 941.929, 963.367
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	1.024, 19.483, 19.589
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.074, 1.342, 1.383
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	0.181, 1.55, 1.7
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.068, 0.549, 0.606
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	1.348, 22.924, 23.278
Thigh	1000	0.146	146.198	0.002, 1.606, -0.268	12.752, 4.44, 14.88
Shank	1000	0.041	41.352	-0.152, 0.839, -0.293	1.682, 0.546, 1.879
Metatarsus	1000	0.009	9.214	-0.18, 0.301, -0.313	0.089, 0.052, 0.086
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.008, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.202	202.772	-0.039, 1.346, -0.277	14.536, 5.09, 16.898
HAT	901.343	1.117	1006.8	0.254, 1.829, 0	115.497, 1764.21, 1871.33
Whole Body	949.792	1.487	1412.34	0.17, 1.691, 0	-

Table 22. Results for the best estimate model of MOR 693 with increased inter-vertebral separation.

Segment	Net Density (kg m-3)	Volume (m3)	Mass (kg)	CM (x,y,z) (m)	lxx lyy lzz (kg m2)
Head	990.536	0.069	68.347	2.502, 2.52, 0	34.188, 327.892, 361.477
Air sacs	0	0.0007	0	-	-
Neck	957.357	0.126	120.627	1.846, 2.162, 0	22.808, 283.439, 304.644
Pharyngeal cavity	0	0.006	0	-	-
Thorax	731.951	0.552	404.037	0.953, 1.794, 0	29.803, 224.474, 249.715
Lungs	0	0.147	0	-	-
Sacrum	1000	0.188	187.543	-0.041, 1.766, 0	13.441, 34.66, 45.19
Tail	1000	0.331	330.726	-0.137, 1.644, 0	26.208, 1120.62, 1142.46
Arm	1000	0.009	9.2	1.691, 1.605, -0.217	1.003, 19.668, 19.753
Digit I	1000	0.0005	0.475	1.92, 1.34, -0.188	0.072, 1.352, 1.391
Digit II	1000	0.0006	0.569	1.896, 1.293, -0.154	1.507, 2.881, 1.7
Digit III	1000	0.0002	0.213	1.851, 1.289, -0.159	0.067, 0.553, 0.609
Total Fore limb	1000	0.01	10.457	1.716, 1.57, -0.211	2.650, 24.455, 23.454
Thigh	1000	0.146	146.198	0.002, 1.606, -0.268	12.752, 4.44, 14.88
Shank	1000	0.041	41.352	-0.152, 0.839, -0.293	1.682, 0.546, 1.879
Metatarsus	1000	0.009	9.214	-0.18, 0.301, -0.313	0.089, 0.052, 0.086
Digit I	1000	0.0002	0.213	-0.137, 0.135, -0.158	0.0002, 0.0002, 0.0001
Digit II	1000	0.001	1.427	-0.048, 0.113, -0.206	0.008, 0.007, 0.007
Digit III	1000	0.002	2.45	0.009, 0.091, -0.32	0.006, 0.031, 0.034
Digit IV	1000	0.002	1.89	-0.042, 0.107, -0.413	0.004, 0.013, 0.012
Pes	1000	0.006	6.008	-0.026, 0.103, -0.316	0.013, 0.051, 0.054
Hind limb	1000	0.202	202.772	-0.039, 1.346, -0.277	14.536, 5.09, 16.898
HAT	885.908	1.278	1132.19	0.324, 1.824, 0	131.751, 2039.99, 2150.39
Whole Body	928.021	1.657	1537.73	0.228, 1.698, 0	-

Table 23. Summary of results for mixed HAT segments sensitivity analysis.

Thorax/neck	Tail	HAT CM		Whole body CM	
		Coordinates (x,y) (m)	Relative to hip joint (x,y) (m)	Coordinates (x,y) (m)	Relative to hip joint (x,y) (m)
Best estimate	Best estimate	0.3081, 1.826	0.278, -0.011	0.214, 1.696	0.184, -0.141
Best estimate*	Best estimate	0.291, 1.83	0.261, -0.007	0.2, 1.697	0.17, -0.14
Best estimate**	Best estimate	0.324, 1.823	0.294, -0.014	0.228, 1.696	0.198, -0.141
Best estimate†	Best estimate	0.299, 1.83	0.269, -0.007	0.207, 1.698	0.177, -0.131
- 7.5%	- 7.5%	0.307, 1.832	0.277, -0.005	0.215, 1.704	0.185, -0.133
+ 7.5%	+ 7.5%	0.301, 1.818	0.271, -0.019	0.211, 1.689	0.181, -0.148
+ 11.25%	+ 11.25%	0.3, 1.815	0.27, -0.022	0.21, 1.687	0.18, -0.15
+ 15%	+ 15%	0.304, 1.814	0.27, -0.023	0.213, 1.686	0.183, -0.151
+ 15%	- 7.5%	0.508, 1.84	0.478, 0.003	0.375, 1.721	0.345, -0.116
- 7.5%	+ 7.5%	0.083, 1.799	0.053, -0.038	0.05, 1.677	0.02, -0.16
Best estimate enlarged rib cage	Best estimate	0.348, 1.824	0.318, -0.013	0.248, 1.7	0.218, -0.137
Best estimate contracted rib cage	Best estimate	0.254, 1.829	0.224, -0.008	0.17, 1.691	0.14, -0.146
Vertebrae spacing +0.005m		0.324, 1.824	0.294, -0.013	0.228, 1.698	0.198, -0.139

*Best estimate thoracic and neck volumes with enlarged thoracic and pharyngeal air sacs.

**Best estimate thoracic and neck volumes with reduced thoracic and pharyngeal air sacs.

†Best estimate thoracic and neck volumes and air sacs with an abdominal air sac.

Table 24. Predicted hind limb mass proportions expressed as percentage of total body mass for models of each specimen.

HAT	Legs	% hind limb mass
Best estimate	Best estimate	13.51
+ 15%	+ 15%	13.29
+ 11.25%	+ 11.25%	13.28
+ 7.5%	+ 7.5%	13.22
- 7.5%	- 7.5%	15.52
+ 15%	- 7.5%	8.95
- 7.5%	+ 15%	17.79
Best estimate	+ 15%	16.21
Best estimate	- 7.5%	12.21

Table 25. Percentage volume contribution of respiratory structure in selected models.

Model	Lungs	HAT Vol	Body vol	Lung vol	%total body vol	%trunk vol
Best estimate	Best estimate	1.237	1.607	0.1417	8.818	11.455
Best estimate	Big Lungs	1.237	1.607	0.1687	10.498	13.638
Best estimate	Small Lungs	1.237	1.607	0.1157	7.200	9.353
+ 15%	Small Lungs	1.595	2.119	0.1157	5.460	7.254
- 7.5%	Big Lungs	1.097	1.436	0.1687	11.748	15.378

Table 26. Measurements between centra, taken on lateral surface at middle of centra for a selection of vertebrae in the mounted cast of MOR 693 at the University of Wyoming Geological Museum. Not every vertebral spacing was measured, but sequential measurements for most vertebrae in the dorsal and caudal series are provided, starting anteriorly from the first dorsal and caudal vertebrae and moving posteriorly.

Dorsal Spacing in mm: 9, 9,12,12, 20, 20,10,10.

Caudal Spacing in mm: 20, 20, 15, 15, 6, 12, 6, 5, 5, 7, 10, 7, 5, 12, 5, 8, 5, 6, 7, 5, 8, 11, 7, 7, 8, 9, 6, 5, 5, 4, 3, 5, 5, 3, 3, 2, 2, 5, 3, 5, 4, 5, 5, 4, 3, 2, 2, 4, 3, 2, 2, 1