

Tyrannosaurus en pointe: allometry minimized rotational inertia of large carnivorous dinosaurs

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Theropod dinosaurs attained the largest body sizes among terrestrial predators, and were also unique in being exclusively bipedal. With only two limbs for propulsion and balance, theropods would have been greatly constrained in their locomotor performance at large body size. Using three-dimensional restorations of the axial bodies and limbs of 12 theropod dinosaurs, and determining their rotational inertias (RIs) about a vertical axis, we show that these animals expressed a pattern of phyletic size increase that minimized the increase in RI associated with increases in body size. By contrast, the RI of six quadrupedal, carnivorous archosaurs exhibited changes in body proportions that were closer to those predicted by isometry. Correlations of low RI with high agility in lizards suggest that large theropods, with low relative RI, could engage in activities requiring higher agility than would be possible with isometric scaling.

Keywords: biomechanics; theropods; archosaurs; rotational inertia; turning performance

1. INTRODUCTION

Non-avian theropod dinosaurs were the dominant terrestrial predators for over 130 Myr, until their extinction 65 Myr ago (Currie 1997). A notable feature of these animals is that their body masses spanned four orders of magnitude, yet they were all strictly bipedal animals. With just two limbs to effect and control body rotation, theropod turning performance would have been greatly limited in absolute terms as they became extremely large (Carrier *et al.* 2001). Their relative turning performance, however, was contingent on how their bodies scaled as theropods grew and evolved. Scaling of animal body size affects many aspects of physiology and adaptation, including metabolism, energetics, growth and biomechanics (Schmidt-Nielsen 1984). We examined the effects of body scaling on the turning performance of theropod dinosaurs by investigating how their potential agility would be affected as they attained body masses of several tonnes.

To modify its body orientation in order to adopt the new direction of travel, an animal must pivot about its point of support (e.g. stance foot of a biped), and the effort required to turn will be directly proportional to its

rotational inertia (RI). The RI of any object is a function of both its mass and its shape, and is expressed as

$$RI = \sum_i m_i r_i^2, \quad (1.1)$$

where m_i is an element of mass, and r_i is its distance from the axis of rotation. Turning ability, measured here as the magnitude of angular acceleration (α) that can be imparted to a body, is related to the body's RI by the following expression:

$$\alpha = \frac{\tau}{RI}, \quad (1.2)$$

where τ is the torque, or couple, applied to the body by the muscles and gravity. From equation (1.2) it can be seen that by minimizing RI, the angular acceleration for a given torque can be maximized.

If body proportions were to vary isometrically with growth, two animals of the same species, but of different size, would be geometrically similar (Alexander 1985). This leads to the prediction that the linear dimensions of geometrically similar animals will be proportional to the cube roots of their mass:

$$L \propto M^{1/3}. \quad (1.3)$$

RI is proportional to the product of mass and the square of the characteristic length, L , and can be written as

$$RI \propto M \times L^2. \quad (1.4)$$

By combining equations (1.3) and (1.4), geometric similarity predicts that the relationship between an animal's mass and its RI would be expressed as

$$RI \propto M^{5/3}. \quad (1.5)$$

If theropod RI scaled with an exponent less than that predicted by geometric similarity, the turning ability of large theropods would be augmented substantially over that expected if they were geometrically similar to smaller individuals. This possibility suggests the following proposals: either RI in theropods scaled to the 5/3 exponent predicted by geometric similarity, or it scaled with some lower exponent.

We also tested whether theropod RI was linked to their bipedality, by comparisons with ecologically similar quadrupeds. The prevalence of quadrupedal, non-dinosaurian, carnivorous archosaurs during the Triassic (248–206 Myr ago; Benton 1997) provides a natural experiment for examining this issue. The masses of our sample of theropods span four orders of magnitude, but the lower range of theropod masses is overlapped for an interval of three orders of magnitude with those of non-dinosaurian archosaurs. If RI scaling were the same for all carnivorous archosaurs, the connection between bipedality and non-isometric RI scaling would be weakened. By comparing RI scaling of the quadrupedal archosaurs and theropods, we can test the theory that RI in both quadrupedal and bipedal carnivorous archosaurs scaled identically.

There are no precise extant analogues of non-avian theropods with which to test more extensively theories about their agility. Unlike non-avian theropods, birds have markedly flexed knees and lack tail-based propulsion (Gatesy & Middleton 1997), whereas mammals with hind-limb kinematics such as those of non-avian theropods are quadrupedal (Carrano 1999). For these reasons, we opted to develop a series of digital models to investigate the

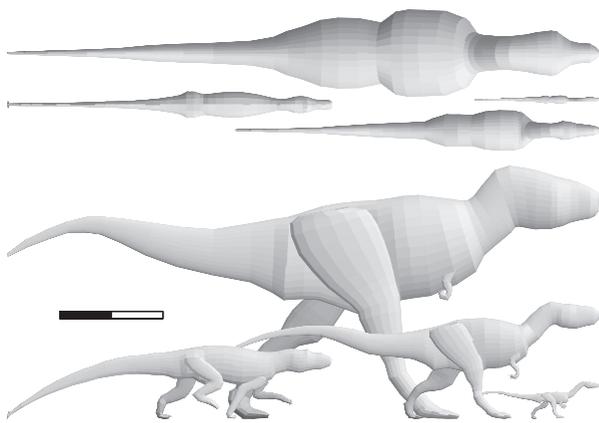


Figure 1. Dorsal and lateral 3D views of carnivorous archosaur body models. The theropods *Coelophysis*, *Allosaurus* and *Tyrannosaurus* (bottom to top, at right) span three orders of magnitude in body mass, and exhibit increasing concentration of body mass about the hips and trunk regions with increasing body size. The quadrupedal rauisuchian *Saurosuchus* (lower left) has a narrow, shallow body, and only half the axial body mass of the comparably long *Allosaurus* (table 1). These differences in body shape have important consequences for RI and agility. Scale bar, 2 m.

dynamics of body shape and mass of extinct animals (figure 1). Although extant morphological analogies are inexact, we tested our assumption that agility will correlate with low RI by computing RI for four lizards with different modes of life.

2. MATERIAL AND METHODS

(a) Modelling of body size and rotational inertia

Fossil taxa were selected for the degree of completeness of their remains to enable accurate body shape restoration, and to ensure that as wide a range of body masses as possible could be spanned by the data (figure 1). Table 1 lists the various sources used for producing the restorations. Coordinates defining the limb and body shapes were collected from digitized published restorations using a 'slicing' technique (Henderson 1999). The initial density of the entire post-cervical region was set to that of water (1000 g l^{-1}). Lungs and air sacs were then modelled as hollow cavities in the anterodorsal thoracic regions and set to a volume equal to 10% of the axial body, as has been observed in extant crocodylians (Gans & Clark 1976) and lizards (Tenney & Tenney 1970). Using 10% as a lung volume is conservative when applied to more derived theropods, as theropods have highly pneumatized skeletons that correlate with air sacs in birds (Britt 1997). The presence of air sacs in extinct theropods would substantially reduce their density and RI. We conservatively set cranio-cervical densities at 900 g l^{-1} in light of the pneumatization seen in theropods and other archosaurs (Witmer 1997). Determination of each axial body's RI, with respect to a vertical axis through its centre of mass (CM), was done using the methods of Henderson (2003). Henderson (2003) demonstrated precise correspondences between analytic and experimental results with extant crocodylians. The positions and masses of the limbs were also incorporated into the final computation of RI. The extant lizard body forms were obtained from the isometric lateral and dorsal views in Smith (1946), and modelled using the same techniques as for fossil forms. To correct for size differences, the lizard body sizes were normalized to unit length by dividing the linear dimensions of each lizard by the body length.

(b) Sensitivity of RI results to model accuracy

The lateral profiles of extinct archosaurs are well constrained by skull lengths, the axial skeletal length, the tips of the neural spines and gastralia. The main uncertainty concerns the transverse dimensions of the body and the consequent frontal profile, as many fossils are flattened laterally when found. To investigate the possible effects

of variation in estimates of the transverse dimensions, additional estimates of mass and RI were determined with the widths of all the models increased and decreased by 10%.

3. RESULTS

(a) RI scaling of theropods and quadrupedal carnivorous archosaurs

Least-squares regression of log-transformed data (table 1) indicates that theropod RI scaled to mass with an exponent of 1.546 and an intercept of -1.630 , whereas in the quadrupedal forms RI scaled to mass with an exponent and intercept of 1.624 and -1.630 , respectively. These slopes are significantly different (t -test, $p < 0.016$), and that of the quadrupedal archosaurs is closer to the value of 1.667 predicted from geometric similarity. Plotting RI against body mass (figure 2) highlights the reduction of RI at large body size in theropods, despite the apparently small difference in their scaling coefficient from that of non-dinosaurian forms. Dramatically, the 5.7 tonnes (t) *Acrocanthosaurus atokensis* has only 43% of the RI predicted from isometric scaling, and this diminishes to 36% in the 10 t *Tyrannosaurus rex*. This 10 t estimate is greater than those for other specimens of *T. rex* (Henderson 1999), but because mass is proportional to the cube of length, the greater length of Field Museum of Natural History specimen FMNH PR2081 (we measured it at 12.01 m) results in a substantially larger body mass. As *Tyrannosaurus* is almost twice the mass of the next heaviest animal, *Acrocanthosaurus*, *T. rex* could potentially act as an outlier and distort the identified scaling relationship. However, exclusion of *T. rex* from the regression analysis resulted in trivial changes in the slope and intercept values (to 1.545 and -1.629 , respectively).

(b) Sensitivity of RI results to model accuracy

Altering body widths by $\pm 10\%$ changed the axial body masses by *ca.* 10% in all cases, but the changes were slightly greater for larger forms. For example, the high and low mass estimates for *Acrocanthosaurus* are 6171 kg and 5173 kg, respectively, which reflect changes in axial mass of 10.37% and -10.28% , whereas the changes in the larger *Tyrannosaurus* are 10.58% and -10.44% . As RI is proportional to body mass via equation (1.4), the RI of the models also changed by *ca.* 10% in each case. Even with these varied mass and RI estimates, there is a clear separation between the RI scaling plots for bipedal and quadrupedal archosaurs, and the basic trends and scaling relationships still hold. This suggests that the pattern observed is real, and not an artefact of a particular choice of body width.

(c) Correlation of RI and lifestyle in lizards

Fast, predaceous lizards (Smith 1946), such as race runners (*Cnemidophorus*) and leopard lizards (*Gambelia*), have compact bodies, slender tails and low RIs (table 1). By contrast, less agile lizards like the chuckwalla (*Sauromalus*) and the Gila monster (*Heloderma*) have high RIs. Herbivorous chuckwallas wedge themselves into crevices rather than flee predators, and the stumpy armoured Gila monster feeds on slow or stationary prey and defends itself with a strong toxic bite. This correlation between low RI and agility in lizards suggests that theropods with comparatively low RI would have exhibited high relative agility.

Table 1. Biomechanical results for taxa used in this study.
 (See electronic Appendix A (available on The Royal Society's Publications Web site) for full citations of illustration sources.)

	mass ^a (kg)	length (m)	RI ^a (kg m ⁻²)	illustration source
theropod dinosaurs				
<i>Acrocanthosaurus atokensis</i>	5672	11.84	1.846×10^4	Currie & Carpenter (2000)
<i>Allosaurus fragilis</i>	1092	7.260	1198	Paul (1988) and Currie (1997)
<i>Ceratosaurus nasicornis</i>	647.5	5.903	591.8	Paul (1988) and Currie (1997)
<i>Coelophysis bauri</i>	12.14	2.522	1.161	Paul (1988) and Currie (1997)
<i>Compsognathus longipes</i>	0.3180	0.8019	4.066×10^{-3}	Ostrom (1978) and Paul (1988)
<i>Daspletosaurus torosus</i>	3844	9.474	6678	Russell (1970) and Paul (1988)
<i>Dilophosaurus wetherilli</i>	355.2	6.277	276.7	Welles (1984) and Paul (1988)
<i>Herrerasaurus ischigualastensis</i>	64.33	2.774	9.217	Novas (1993)
<i>Gorgosaurus libratus</i> (adult)	2795	9.068	4777	Paul (1988) and Currie (1997)
<i>Gorgosaurus libratus</i> (juvenile)	463.6	5.264	212.4	Paul (1988)
<i>Sinraptor dongi</i>	1154	7.339	1420	Currie & Zhao (1993)
<i>Tyrannosaurus rex</i>	1.02×10^4	12.01	3.515×10^4	Paul (1988) and Currie (1997)
quadrupedal archosaurs				
<i>Euparkeria capensis</i>	0.6135	0.6898	1.115×10^{-12}	Paul (1987)
<i>Postosuchus kirkepatricki</i>	57.90	3.083	15.83	Parrish (1986)
<i>Riojasuchus tenuisiceps</i>	13.77	1.875	1.532	Parrish (1986)
<i>Saurosuchus galilei</i>	590.4	6.518	736.4	Paul (1987)
<i>Ticinosuchus ferox</i>	26.42	2.584	4.429	Krebs (1965)
<i>Vjushkovia triplocostata</i>	86.73	3.455	39.25	Parrish (1986)
lizards ^b				
<i>Cnemidophorus tesselatus</i>	0.5562	1.0	1.317×10^{-2}	Smith (1946)
<i>Gambelia wislizenii</i>	0.8000	1.0	1.311×10^{-2}	Smith (1946)
<i>Heloderma suspectum</i>	5.487	1.0	2.443×10^{-1}	Smith (1946)
<i>Sauromalus obesus</i>	5.620	1.0	1.731×10^{-1}	Smith (1946)

^a Mass and rotational inertia estimates include the axial body and both pairs of limbs. Mass determinations done with the digital volumetric method of Henderson (1999).

^b See electronic Appendix B for lizard body shape comparison, showing the large body volume/mass differences when lizards are normalized to unit length.

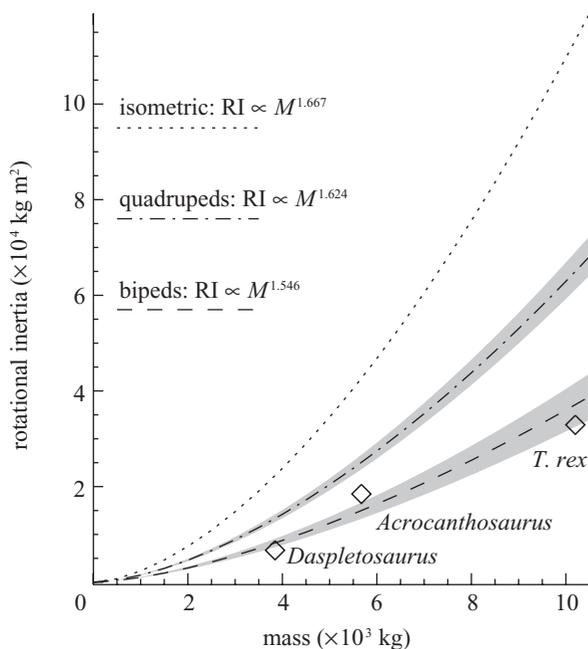


Figure 2. RI versus body mass in carnivorous archosaurs. Grey bands indicate the range of changes in RI magnitudes when computed with body widths that were 110% and 90% of the original models.

4. DISCUSSION

Given that theropod body shapes change with increasing size in a way that deviates from geometric similarity, we propose that these shape changes are the result of an allometric strategy that minimized relative RI, and thus the effort required to turn at large size. This strategy ensures that the added mass associated with evolving larger body size is positioned close to the centre of the body, thus reducing the distance of the added mass from the centre of rotation. Quadrupedal forms, with pairs of limbs posterior and anterior to their CM, have more options on how to effect a turn of the body. From our sample of quadrupedal archosaurs, minimization of axial body RI does not appear to be a guiding factor during a phylogenetic increase in body size. Theropods, with just two limbs for controlling body orientation and effecting turning forces, have a much more limited range of possibilities, and minimizing RI would appear to be a viable strategy to maintain relative agility. This minimization is analogous to that seen in the limbs of cursorial mammals, where musculature is concentrated towards the proximal ends, thus reducing RI and enabling the muscles to impart a high acceleration to the limbs' distal parts (Hildebrand 1986).

Fossil evidence suggests adaptations for theropod agility beyond considerations of body scaling. Tyrannosaurids display the elongate yet strong arctometatarsalian foot (Holtz 1995) whose complex dynamics probably augmented agility (Snively & Russell 2003). Healed bite marks (Carpenter 2000) and bone fragments found in a coprolite (Chin *et al.* 1998) indicate that *T. rex*, the largest theropod in this study, preyed on adult and juvenile orni-

thischian dinosaurs. Assuming that they were not raiding nests, *T. rex* would have had to turn quickly enough to catch young herbivorous dinosaurs that were presumably more agile than their adult counterparts. We suggest that the compaction of theropod body shape with increasing size imparted a sufficiently low RI for active predatory activities.

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- Alexander, R. McN. 1985 Body support, scaling, and allometry. In *Functional vertebrate morphology* (ed. D. Bramble, K. Liem & D. B. Wake), pp. 26–37. Cambridge, MA: Harvard University Press.
- Benton, M. J. 1997 *Vertebrate paleontology*, 2nd edn. London: Unwin & Hyman.
- Britt, B. B. 1997 Postcranial pneumaticity. In *The encyclopedia of dinosaurs* (ed. P. J. Currie & K. Padian), pp. 590–593. San Diego, CA: Academic.
- Carpenter, K. 2000 Evidence of predatory behavior by carnivorous dinosaurs. *Gaia* 15, 135–144.
- Carrano, M. T. 1999 What, if anything, is a cursor? Categories versus continua for determining locomotor habit in mammals and dinosaurs. *J. Zool. Lond.* 247, 29–42.
- Carrier, D. R., Walter, R. M. & Lee, D. V. 2001 Influence of rotational inertia on turning performance of theropod dinosaurs: clues from humans with increased rotational inertia. *J. Exp. Biol.* 204, 3917–3926.
- Chin, K., Tokaryk, T. T., Erickson, G. M. & Calk, L. C. 1998 A king-sized theropod coprolite. *Nature* 393, 680–682.
- Currie, P. J. 1997 Theropods. In *The complete dinosaur* (ed. J. O. Farlow & M. K. Brett-Surman), pp. 216–233. Indianapolis, IN: Indiana University Press.
- Gans, C. & Clark, B. 1976 Studies on the ventilation of *Caiman crocodylus* (Crocodylia: Reptilia). *Resp. Physiol.* 26, 285–301.
- Gatesy, S. M. & Middleton, K. M. 1997 Bipedalism, flight, and the evolution of theropod locomotor diversity. *J. Vert. Paleobiol.* 17, 308–329.
- Henderson, D. M. 1999 Estimating the mass and centers of mass of extinct animals by 3-D mathematical slicing. *Paleobiology* 25, 88–106.
- Henderson, D. M. 2003 Effects of stomach stones on the buoyancy and equilibrium of a floating crocodylian: a computational analysis. *Can. J. Zool.* 81, 1346–1357.
- Hildebrand, M. 1986 *Analysis of vertebrate structure*, 3rd edn. New York: Wiley.
- Holtz Jr, T. R. 1995 The arctometatarsalian pes, an unusual structure of the metatarsus of Cretaceous Theropoda. *J. Vert. Paleontol.* 14, 480–519.
- Ostrom, J. H. 1978 The osteology of *Compsognathus longipes*. *Zitteliana* 4, 73–118.
- Schmidt-Nielsen, K. 1984 *Scaling, why is animal size so important?* Cambridge University Press.
- Smith, H. M. 1946 *Handbook of lizards*. Ithaca, NY: Comstock Publishing Associates.
- Snively, E. & Russell, A. P. 2003 Kinematic model of tyrannosaurid (Dinosauria: Theropoda) arctometatarsus function. *J. Morphol.* 255, 215–227.
- Tenney, S. M. & Tenney, J. B. 1970 Quantitative morphology of cold-blooded lungs: Amphibia and Reptilia. *Resp. Physiol.* 9, 197–215.
- Witmer, L. M. 1997 The evolution of the antorbital cavity of archosaurs. A study of soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Soc. Vert. Paleontol. Mem.* 3.

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