

Estimating maximum bite performance in *Tyrannosaurus rex* using multi-body dynamics

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Bite mechanics and feeding behaviour in *Tyrannosaurus rex* are controversial. Some contend that a modest bite mechanically limited *T. rex* to scavenging, while others argue that high bite forces facilitated a predatory mode of life. We use dynamic musculoskeletal models to simulate maximal biting in *T. rex*. Models predict that adult *T. rex* generated sustained bite forces of 35 000–57 000 N at a single posterior tooth, by far the highest bite forces estimated for any terrestrial animal. Scaling analyses suggest that adult *T. rex* had a strong bite for its body size, and that bite performance increased allometrically during ontogeny. Positive allometry in bite performance during growth may have facilitated an ontogenetic change in feeding behaviour in *T. rex*, associated with an expansion of prey range in adults to include the largest contemporaneous animals.

Keywords: *Tyrannosaurus*; bite performance; modelling; ontogeny

1. INTRODUCTION

Attaining quantitative measures of mechanical performance for extinct animals is notoriously difficult and involves numerous assumptions, particularly when a close living analogue is lacking. This has frustrated attempts to definitely assess the feeding strategies of large carnivorous dinosaurs, particularly one of the largest and best-known taxa, *Tyrannosaurus rex* [1–4]. Some studies contend that a modest bite limited *T. rex* to scavenging [3], while others have argued that high ‘bone-crushing bite’ forces facilitated a ‘puncture–pull’ mode of predation [1,2,4]. Resolving this issue would not only enhance understanding of the palaeobiology of *T. rex*, but would also provide a clearer understanding of trophic ecology in dinosaurian ecosystems.

Addressing this issue directly requires a model to be constructed that makes explicit assumptions about musculoskeletal geometry, mass and inertia, together with muscle properties in *T. rex* (figure 1). These factors have a determinate effect on mechanical performance [5–8] and such a model would provide reasonable estimates of the quantitative data required to test

hypotheses regarding bite performance, facilitating meaningful comparisons between *T. rex* and other taxa, both living and extinct. Here, we use the computational engineering technique multi-body dynamic analysis (MDA) to investigate bite performance in *T. rex*. Specifically, we test the hypotheses that *T. rex* had an extremely (i) high absolute and (ii) relative bite force, and (iii) that bite performance increased in relative terms during ontogeny.

2. MATERIAL AND METHODS

A Z&F 5600i laser scanner was used to digitize skulls of an adult *Alligator mississippiensis* (skull length 0.53 m), *Allosaurus* (SMA0005), and near-complete juvenile (BMRP2002.4.1) and adult (BHI3033) *T. rex*. A juvenile *Alligator* (skull length 0.188 m) and adult human model were derived from computer tomography data. Volumetric reconstructions of the upper and lower jaw segments were produced in MAYA to provide inertial properties ([9], figure 1a). Upper and lower jaw segments were joined by a single hinge joint, orientated perpendicular to the cranial–caudal axis of the skull (figure 1). We reconstructed the main jaw-closing musculature in *Alligator* and the dinosaurs using simplified functional groups ([2]; figure 1). The temporalis, masseter and pterygoideus muscles were reconstructed in the human model.

To investigate bite performance, we used the MDA package Gait-Sym. Models required physiological cross-sectional area (PCSA), fibre length (FL), maximum contraction velocity (V_{\max}) and force per unit area (FPUA) to be specified for each muscle. FPUA was initially set to 300 000 N m² [10,11] and V_{\max} to 8 s⁻¹ to represent mixed slow–fast twitch fibre types [10,11]. For our human and juvenile *Alligator* models, all subsequent input data were available in the literature [6,12]. Quantitative muscle data were unavailable for adult *Alligator* and parameters were estimated in the same manner as for the dinosaurs. FLs of jaw-closing muscles in our human model ranged between 10 and 40 per cent of maximum muscle length across the range of joint motion investigated. We therefore set FLs in our adult *Alligator* and dinosaur models to 25 per cent maximum length over the same range of joint motion, testing 10–40% maximum lengths in our sensitivity analysis (table 1). Muscle PCSAs were calculated by dividing a volume for each muscle by its FL. Initial muscle volumes were derived by reconstructing three-dimensional volumes within the skull models in MAYA (figure 1). Repeating this approach with our human and juvenile *Alligator* models resulted in volumes with 5–12% error in most muscles, but a 22 per cent overestimation in the human medial pterygoid muscle relative to measured values [6,12]. We therefore tested muscle volumes $\pm 20\%$ initial estimates for the dinosaurs and adult *Alligator* (table 1). Pennation effects were tested in two ways: first we produced models in which PCSAs were increased by 6.04 per cent, equivalent to that expected from 20° pennation angle (3° greater than the maximum angle reported in *Alligator* [12]). Second, we produced models with both increased PCSAs and shorter FLs to mimic the expected contractile effects of pennation angle [10,11]. We varied V_{\max} between 4 and 12 s⁻¹, consistent with the range found in the literature ([10,11]; table 1). For biting simulations, the jaws in each model were opened to 45° and all jaw-closing muscles activated maximally for 1 s. Forces were measured in stiff springs (stiffness 2 000 000 N m²) positioned on the teeth.

To assess our scaling hypotheses, we isometrically scaled (i.e. length $\propto \text{mass}^{1/3}$, areas $\propto \text{mass}^{2/3}$) all our MDA models to the mass of the adult *T. rex* model and repeated our analysis. This allows direct comparison of size-normalized bite performance, and consideration of soft tissue uncertainties when testing scaling hypotheses.

3. RESULTS

Initial simulations produced the bite forces shown in figure 2 and summarized in table 2. Muscle FL and V_{\max} had little effect on sustained bite force ($\pm 5\%$ initial models) across a large range of input values tested. However, both parameters did have a considerable impact on bite velocities (figure 2b). PCSA had a significant effect on absolute bite force; $\pm 20\%$ PCSA yielding forces 18–25% higher and lower than initial models (figure 2b). Increasing PCSA to mimic the effects of a 20° pennation angle increased bite force by approximately 6 per cent in any given model

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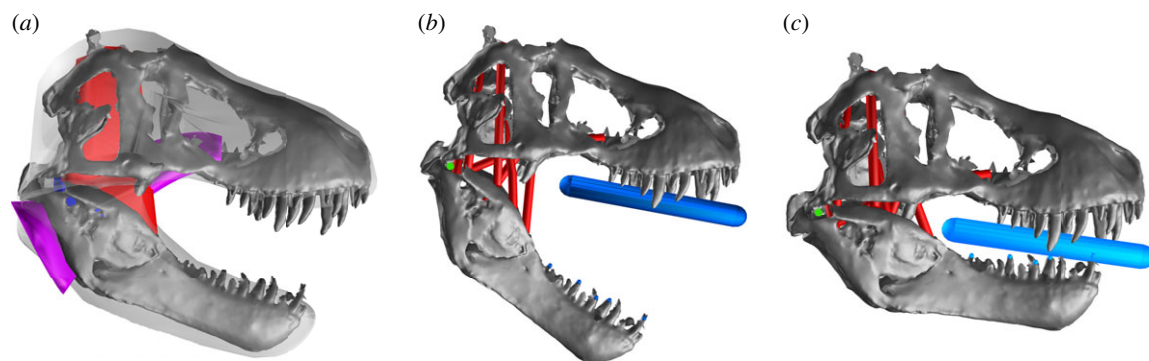


Figure 1. MDA model of adult *T. rex*. (a) Three-dimensional digitized skull with soft tissues reconstructed for mass and muscle properties (red, adductor mandibulae externus group; blue, adductor mandibulae posterior group; purple, pterygoideus group). (b) MDA model with joint centres (green circle), muscles (red cylinders), and ‘contact’ springs (blue spheres and cylinder) on the teeth in the initial simulation starting pose. (c) MDA model during sustained biting.

Table 1. Outline of the sensitivity analysis carried out on the adult *Alligator* and dinosaur MDA models.

input parameter	initial model	range tested
muscle mass/PCSA	best estimate volumetric reconstruction of muscles	$\pm 20\%$ based on error in estimates of muscle volume reconstruction in living taxa
maximum contraction velocity (V_{\max})	8 s^{-1}	$4\text{--}12 \text{ s}^{-1}$ [10,11]
muscle fibre length (FL)	25% maximum muscle length (average value in muscles in the human model)	10–40% maximum muscle length (range of values for muscles in the human model)
fibre pennation angle	zero pennation	— increase in PCSA expected from 20° pennation angle (max pennation measured in <i>Alligator</i> 17° [13]) — increase in PCSA expected from 20° pennation angle and shortest FLs (i.e. 10% maximum muscle length)

(figure 2b). Increasing PCSA and decreasing FL produced increasingly forceful but lower velocity bites, respectively (figure 2b). Overall this yielded a range of maximum bite forces at posterior tooth positions of 2565–4012 N and 35 640–57 158 N for the juvenile and adult *T. rex* models, respectively (figure 2).

Bite force remained lower than adult *T. rex* in all taxa when MDA models were isometrically scaled to the same mass (figure 2d,e). However, uncertainties in muscle PCSA means error bars show considerable overlap with *Allosaurus* and slight overlap with adult *Alligator* (figure 2d,e). Large error bars on bite velocity predictions mean all taxa show considerable overlap (figure 2d).

4. DISCUSSION

(a) Validation

Predicted bite force in our human and *Alligator* models closely match previous values (figure 2a,f). Our human bite forces (700–1020 N) overlap experimental values of 730–749 N [5,6] and lie within estimates in earlier modelling studies of 678–1080 N [7,8], with variability across studies attributed to significant variation in muscle size between individuals and the level of muscle activation associated with different biting activities [5–8]. Erickson *et al.* [13] reported peak forces of 500–765 N and 9000–11 125 N in alligators of equivalent size to our models. Peak forces in the initial biting impact overlap these values (figure 2a,f; juvenile 601–801 N, adult 9800–13 135 N). Sustained bite

force in the juvenile model (202–266 N) overlaps the higher end values of Porro *et al.* ([12]; 120–215 N), and shows even closer agreement (148–209 N) if we use the lower value for FPUA ($250\,000 \text{ N m}^{-2}$) preferred by these authors.

(b) Bite performance in *Tyrannosaurus rex*

We are aware of two previous quantitative estimates of bite force in *T. rex*. Indentation experiments, which estimate the force required to replicate a fossilized bite mark, produced values of 6400–13 400 N for a single posterior tooth [4]. Meers [1] used allometric scaling arguments to suggest that *T. rex* could have generated on average 7600–9800 N at a single tooth. Even with more conservative estimates for muscle mass our model suggests that these earlier analyses significantly underestimated bite performance in adult *T. rex*. Even the lowest forces predicted at the most anterior teeth in our model are nearly double that predicted by indentation simulations [4], while forces at posterior teeth are three times higher. Adult *T. rex* magnitudes are 8–10 times greater than those predicted for *Alligator*, *Allosaurus* and juvenile *T. rex*, and consequently are significantly higher than values measured or predicted for any terrestrial animal (figure 2f).

(c) Scaling bite performance

Uncertainty in muscle properties means we are unable to reject the hypothesis that *T. rex* had a relatively high

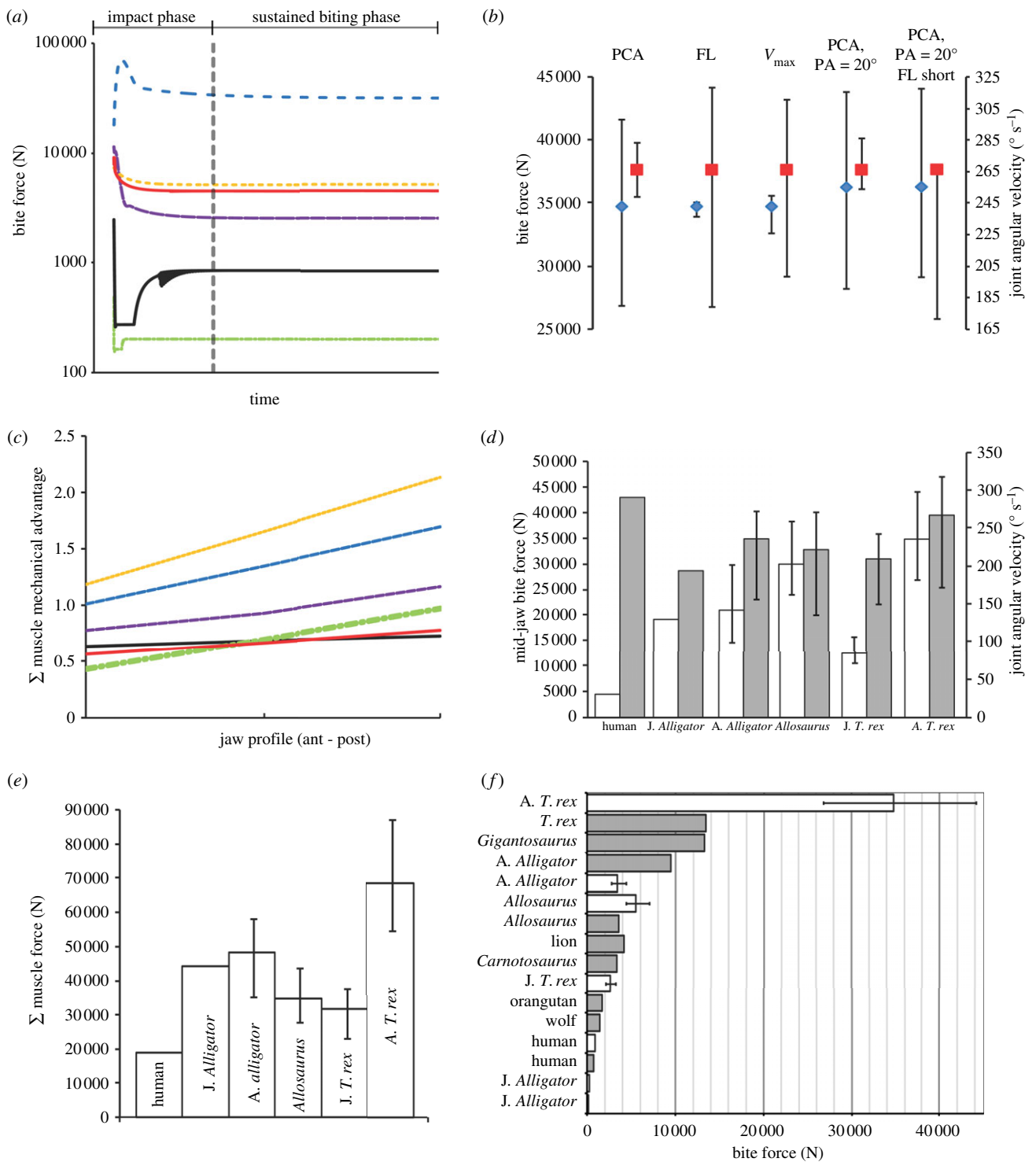


Figure 2. (a) Bite force versus time for mid-jaw positions in the MDA models, showing an initial force peak representing the bite impact, before levelling off to record the sustained bite force (time normalized across models so that initiation of biting coincides). (b) Range in bite performance predictions for adult *T. rex* about the initial model for each parameter in the sensitivity analysis. Blue diamonds, initial model force; red squares, initial model velocity. (c) Mechanical advantage of jaw-closing muscles in the models. (d) Results of isometrically scaling all models to the mass of adult *T. rex*. White bars, force; grey bars, velocity. (e) Summed muscle force in the isometrically scaled models. (f) Comparison of biting forces predicted in this study with some of the largest values in the literature for terrestrial vertebrates ([4–8,12,13], grey bars are values from previous studies; white bars are from this analysis). (a,c) Lines: black, human; green, juvenile *Alligator*; red, adult *Alligator*; yellow, *Allosaurus*; blue, adult *T. rex*; purple, juvenile *T. rex*.

bite performance for its body size. Considerable overlap in error bars with *Allosaurus*, owing largely to the latter's high mechanical advantage (figure 2c), perhaps suggests that large-bodied theropods in general were capable of generating proportionally high bite forces.

Our initial adult *T. rex* reconstruction has a higher proportion of muscle mass (6.89% skull mass, versus 1.2–5.64% in other models), consistent with anatomical studies that have postulated relatively large jaw-closing muscles, based on lateral expansion of

Table 2. Summary of initial, minimum and maximum bite force results.

	initial model		MIN bite force PCA – 20%		MAX bite force PCA +20% FL shortest	
	anterior teeth	posterior teeth	anterior teeth	posterior teeth	anterior teeth	posterior teeth
human	700	1020	—	—	—	—
juvenile <i>Alligator</i>	202	266	—	—	—	—
adult <i>Alligator</i>	2325	4476	1860	3580	2996	5761
<i>Allosaurus</i>	4179	6809	3342	5449	5345	8724
juvenile <i>T. rex</i>	2010	3210	1600	2565	2450	4012
adult <i>T. rex</i>	24 575	44 940	18 065	35 640	31 086	57 158
human scaledup	3750	5221	—	—	—	—
juvenile <i>Alligator</i> scaledup	10 580	27 466	—	—	—	—
adult <i>Alligator</i> scaledup	11 839	29 896	12 509	16 649	20 250	39 427
<i>Allosaurus</i> scaledup	20 698	39 029	16 652	31 284	26 452	50 096
juvenile <i>T. rex</i> scaledup	10 145	14 480	8065	13 020	12 792	18 780

the temporal box and parietal crests, deepening of the posterior mandible and overall massive skull construction [1,2]. Our prediction of relatively higher muscle mass in our adult *T. rex* model appears insensitive to the scaling metric used; for example, PSCA remains considerably higher in adult *T. rex* if linear skull dimensions, rather than mass, are used to derive scaling exponents (electronic supplementary material, table S14). Slight overlap in bite force error bars with the adult *Alligator* model (figure 2d) offers weak support for a proportionally higher bite performance relative to living carnivorous archosaurs. Muscle data for adult *Alligator* would refine this prediction.

Our models provide strong support for the hypothesis that bite performance experienced a large absolute and relative increase during tyrannosaur ontogeny. Juvenile *T. rex* possessed a lower, longer snouted skull than adult *T. rex*. Deepening of the rostrum and expansion of the posterior skull with maturity potentially provided greater volume for jaw-closing musculature and increased moment arms (figure 2). Relative shortening of anterior elements brought the tooth row closer to the jaw joint, further increasing mechanical advantage (figure 2).

The age of BMR P2002.4.1 has been estimated at 11 years indicating that this animal died at the beginning of the exponential growth phase [9]. Tyrannosaur body proportions changed appreciably during ontogeny, and biomechanical analyses have provided strong evidence that young individuals were more athletic than adults [9]. With bite forces comparable to *Alligator* and lions (figure 2g), combined with relatively long forelimbs and cursorial hindlimbs, juvenile *T. rex* appears well equipped to pursue and dispatch small to medium-sized prey. Forelimbs became significantly reduced (approx. 3% body mass in BMR P2002.4.1, approx. 0.1–0.4% in adults [9]), and our results strongly suggest increasing importance of the skull in food procurement as compensation.

In living carnivores, such as *Alligator*, strong positive allometry in bite performance is typically associated with an ontogenetic shift in feeding ecology [13]. Enhancement of an already highly competent biting apparatus during the exponential growth phase may be indicative of a change in feeding behaviour as

T. rex reached adulthood. Living carnivores preying on large animals have relatively high bite forces, while carnivores preying on small prey have more moderate bite forces for their size, suggesting that bite force represents an important adaptation to differing feeding ecologies, at least throughout carnivoran evolution [14]. Attaining adult body sizes, combined with specialized craniofacial anatomy underpinning high mechanical performance, may have allowed adult *T. rex* to function as a ‘large prey specialist’, alleviating direct competition from smaller, more agile carnivores, including juvenile *T. rex*.

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Correction

Correction to 'Estimating maximum bite performance in *Tyrannosaurus rex* using multi-body dynamics'

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Owing to an error in our muscle physiological cross-sectional area calculations, the range of bite force estimates for four models in our original analysis (maximum and minimum values presented in table 2 of [1]) are approximately 6% too high. This relates specifically to error in our calculation of the effect of a 20° pennation angle on muscle physiological cross-sectional area in the sensitivity analysis carried out on our adult *Alligator*, *Allosaurus*, juvenile and adult *Tyrannosaurus* models. Because the error is consistent across models, none of the conclusions of the paper have changed. A corrected version of table 2 of [1] is as follows:

Table 2. Corrected summary of initial, minimum and maximum bite force results.

	initial model		MIN bite force PCA — 20% and 20° pennation		MAX bite force PCA	
	anterior teeth	posterior teeth	anterior teeth	posterior teeth	anterior teeth	posterior teeth
human	700	1020	—	—	—	—
<i>J. Alligator</i>	202	266	—	—	—	—
<i>A. Alligator</i>	2325	4476	1754	3376	2790	5370
<i>Allosaurus</i>	4179	6809	3166	5149	5013	8163
<i>J. T. rex</i>	2010	3210	1544	2426	2400	3850
<i>A. T. rex</i>	24 575	44 940	17 073	33 123	29 510	53 735
human scaledup	3750	5221	—	—	—	—
<i>J. Alligator</i> scaledup	10 580	27 466	—	—	—	—
<i>A. Alligator</i> scaledup	11 839	29 896	11 800	15 833	14 983	35 906
<i>Allosaurus</i> scaledup	20 698	39 029	15 754	29 519	24 861	46 792
<i>J. T. rex</i> scaledup	10 145	14 480	7 575	12 295	12 020	16 600

Reference

1. Bates KT, Falkingham PL. 2012 Estimating maximum bite performance in *Tyrannosaurus rex* using multi-body dynamics. *Biol. Lett.* **8**, 660–664. (doi:10.1098/rsbl.2012.0056)