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Bite-force estimation for *Tyrannosaurus rex* from tooth-marked bones

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WHETHER tyrannosaurs occupied predatory or scavenging niches has been debated for nearly a century[1-5]. Palaeontologists have turned to the study of dental morphology to address this question, but the results have been highly disparate. Some contend that the tyrannosaur dentition was very strong and well suited for engaging and killing herbivorous dinosaurs[6,7]. Others posit that tyrannosaurs ate carrion, because their teeth and/or jaws would fail during struggles with prey[2,3]. The discovery of skeletal remains with bite marks from *Tyrannosaurus rex*[8] makes it possible to estimate, through indentation simulations on bovine ilia, the bite forces produced by *T. rex* during feeding. The estimates (6,410 to 13,400 N) rival the largest bite forces determined for any taxon to date and suggest that *T. rex* had very strong, impact-resistant teeth. Although these data do not prove that *T. rex* was predominantly predacious, they indicate that its dentition could probably withstand the stresses associated with prey capture.

A recently unearthed *Triceratops* sp. pelvis from the Hell Creek Formation of Montana (USA) bears dozens of large bite marks (Fig. 1)[8]. Casts of some of the deeper punctures show that an adult *T. rex* produced the marks using its longer anterior caniniform

teeth[8]. The bitten bones are predominantly composed of cancellous bone tissue, capped only by a thin layer of dense cortical bone[8]. On the basis of these marks, it is difficult to gauge whether the teeth that produced the bite marks were particularly robust. We attempted to quantify the forces that the tyrannosaur dentition absorbed when biting the *Triceratops* ilium, by using laboratory simulations. We contrasted the results with those for extant taxa to place them in a comparative context, and assessed the functional and behavioural implications of these comparisons.

Using histological examination we determined that extant bovine ilia exhibit comparable microstructure to *Triceratops* ilia. Consequently, bovine ilia were used to model the bitten *Triceratops* bones. Sections of ilia with cortices of varying thickness were penetrated with a *T. rex* tooth replica to a depth of 11.5 mm (the depth of the deepest ilium bite mark[8]) using a servohydraulic mechanical loading frame. The forces produced throughout these simulations were recorded. When indented, the bovine ilia exhibited localized crushing as the only mode of failure, and the punctures produced were comparable in morphology to the *T. rex* bite marks. The forces during testing increased with increasing penetration depths (Fig. 2). Peak forces ranged from 1,900 to 15,100 N (Fig. 3). A positive correlation between peak penetration force and cortical thickness was found (Fig. 3).

A bone sample removed from the bitten *Triceratops* ilium within 2 cm of the deepest bite mark (11.5 mm) revealed a cortical thickness of 2.5 mm. From a linear regression of our data (Fig. 3), we determined that roughly 6,410 N of force was required to produce the bite mark. Estimates as great as 13,400 N for posterior teeth were obtained when biting velocity, energy absorption by flesh, and the mechanical advantage of posterior teeth relative to more anterior teeth were taken into consideration (Fig. 3).

These bite-force estimates make it possible to evaluate speculations on tyrannosaur tooth strength and potential behaviours using comparisons with extant taxa. The largest maximum bite force measurements or estimates for extant vertebrates at posterior tooth positions are: 550 N for labrador dogs[9], 749 N for humans[10], 1,412 N for wolves[11], 1,446 N for dusky sharks (location of force measurement within jaw not given)[12], 1,712 N for orangutans[13], 4,168 for lions[11], and 13,300 N for American alligators[14] (K. A. Vliet, personal communication). Using bite force as a relative indicator of dental strength, the results suggest that *T. rex* teeth were as strong as, or in most cases substantially stronger than, those of any extant taxa tested to date. Consequently,
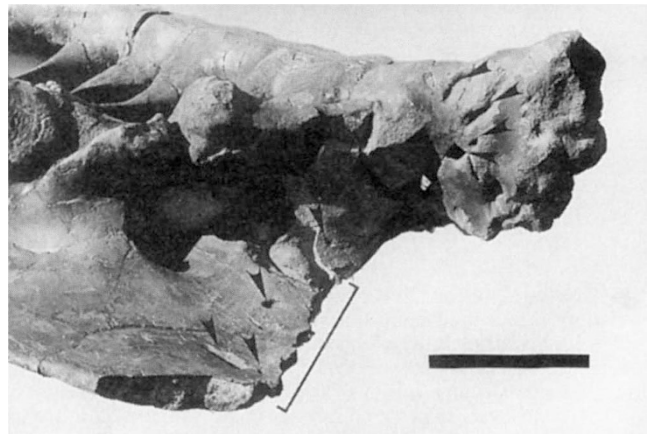

FIG. 1 *Triceratops* sp. pelvis in ventrolateral view bearing bite marks from an adult *Tyrannosaurus rex*. The sacrum and left ilium (Museum of the Rockies specimen MOR 799, Montana State University, Bozeman, MT) have 58 definitive bite marks attributable to 'puncture and pull' biting behaviour by the feeding tyrannosaur(s)[8]. Arrows denote some of the more conspicuous bite marks. Brackets bound a region where the tyrannosaur(s) removed approximately one-sixth of the anterior portion of the ilium by means of repetitive biting. Scale bar, 25 cm.
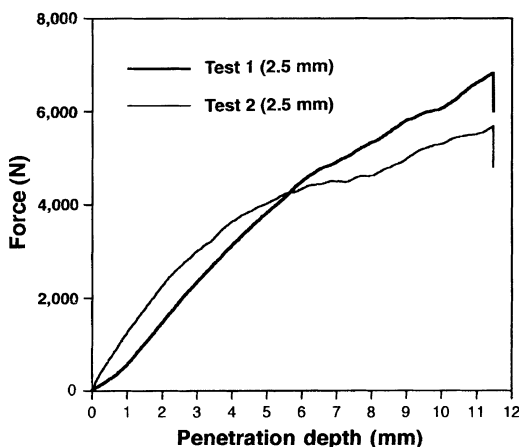
FIG. 2 Typical force against penetration curves produced during the penetration of bovine ilia by an adult *Tyrannosaurus rex* tooth replica. The two curves represent simulations conducted on samples with 2.5-mm thick cortices.

METHODS. Bovine ilia were used in the simulations because their histological structure (a fibrolamellar cortex overlying cancellous bone[26]) was found to match that of the *Triceratops* ilium. Bone sections $10 \times 50 \times \sim 3.0$ cm with cortices ranging from 0.5 to 5.5 mm in depth (the range of initial cortical-thickness estimates based on gross morphology) were mounted on a servohydraulic mechanical loading frame (MTS Bionix, Minneapolis) and penetrated with an aluminium–bronze *T. rex* tooth replica. The replica was cast from an actual adult *T. rex* maxillary tooth, after casts made from some of the deeper bite marks revealed the size and shape of the teeth that had impacted the pelvis[8]. The replica was penetrated into the ilia sections at $1\,\mathrm{mm\,s^{-1}}$ to a depth of 11.5 mm, equivalent to the maximum depth of the deepest ilium bite mark[8]. Forces were measured with an MTS 25 N strain-gauge-based axial load cell accurate to 0.2%. The forces increased with increasing penetration depth even after the cortical layer had been perforated and the underlying cancellous bone was being crushed. The increase in force with penetration depth is attributed to a greater cortical surface area coming into contact with the semi-conical penetrator tooth as it descended through the ilia.
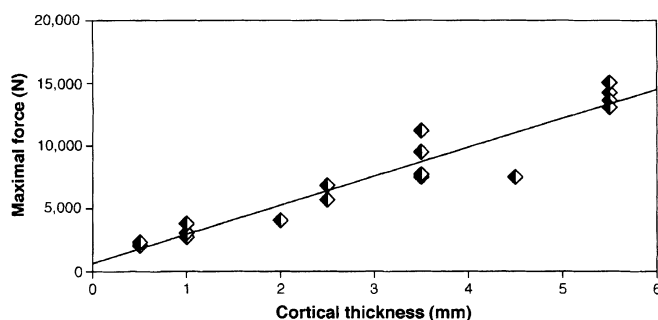

FIG. 3 Maximum penetration force values for an adult *Tyrannosaurus rex* tooth replica impacted through bovine ilia with varying cortical thickness. Peak penetration forces increased with increasing cortical thickness ($y = 2305.402x + 646.634$, $r^2 = 0.91$).

METHODS Because of the 7-fold range of peak force values in the simulations, it was necessary to obtain precise measurements of the cortical depths penetrated by the *T. rex* teeth. A bone sample taken adjacent to the deepest bite mark revealed a 2.5 mm cortical thickness. From the regression equation, approximately 6,410 N of force was required to produce the bite mark. This bite mark was made by one of the tyrannosaur's longer caniniform teeth[8], probably a tooth between the fourth and seventh maxillary positions (based upon American Museum of Natural History specimen AMNH 5027, New York). To account for the relative mechanical advantage of more posteriorly positioned teeth[27], moment calculations were used to calculate the simultaneous forces produced at the most posterior tooth positions. Values ranging from 7,870–10,300 N were projected, assuming 6,410 N of force were produced simultaneously by teeth from the fourth to seventh tooth positions. Because bone strength increases with strain rate[28] and the penetration rate of the tooth replica was just $1\,\mathrm{mm\,s^{-1}}$, it is likely that the simulation force values underestimated actual forces. A tooth-impact velocity of $10\,\mathrm{mm\,s^{-1}}$ for a biting tyrannosaur (based on extant large reptile feeding; G.M.E., personal observations) would have required $\sim$20% more bite force[28]. Adhering flesh[8] may have absorbed another 10% (or more) of the initial bite force[29]. These considerations suggest that bite forces as high as 13,400 N could have been produced by an adult *T. rex* during feeding. Greater forces may have been possible during snapping bites or those involving bodily inertia to augment tooth penetration. Such biting is characteristically used when prey are seized initially (G.M.E., personal observations of reptilian feeding). Taphonomic interpretations suggest that the bite marks on the *Triceratops* ilium were not the result of this behaviour[8]. Additionally, if the tyrannosaur's contralateral teeth were used when the deepest bite mark was made, greater bite forces may have been generated than those we estimated[13,30]. This is indeterminable from MOR 799.

speculations that their dentition was mechanically weak were not supported.

Peak bite-force estimates for large American alligators (*Alligator mississipiensis*) are within the range we calculated for a feeding *T. rex*. This taxon shares many dental attributes with *T. rex* (including thecodont implantation[15,16], stout semi-sharp caniniform teeth that are transversely rounded[6,7,16], and nearly identical histological structures[17,18]). These morphological similarities imply similarity in function[19]. Alligators use their teeth to procure large prey and to engage conspecifics during confrontations[20]. Both activities demand teeth that can sustain large compression and bending forces, particularly because impacts with bones are frequent[20]. The bite-force estimates and tooth mark evidence show that *T. rex* teeth could similarly withstand large bite forces and sustain repetitive bone impacts. Therefore, it is not unreasonable to suspect that the *T. rex* dentition could be used in behaviours similar to those of alligators, and with some mechanical safety[21]. Physical evidence supports this reasoning. Bony calli on adult tyrannosaur crania attest to biting injuries during intraspecific aggression[22,23], and a healed hadrosaur tail injury has been attributed to biting by a *T. rex* during a failed predation attempt[5].

Although our data suggest that *T. rex* could produce enormous bite forces and possessed a dentition that could endure stresses associated with prey struggles, they by no means prove that *T. rex* was predacious. Indeed it could be argued that these characteristics enhanced their utilization of scavenged carcasses. Nevertheless, these results refute assertions that *T. rex* was mechanically limited by its dentition to scavenging carrion. We contend that if *T. rex* could consistently manoeuvre into a position to engage prey with its dentition, it could have exploited a predatory niche.

It has been shown recently that theropod bite marks are much more common in the fossil record that was once suspected[8,24,25]. Consequently, the methods used here could be used to assess bite-force estimates for other tyrannosaur individuals, as well as for many theropod species. Such data would greatly augment our understanding of dinosaur tooth form and function, the physical capacities of their teeth and jaws (ontogenetically and interspecifically), and provide new insight into the musculoskeletal biomechanics of dinosaur crania.   □

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Tracking the evolution of warning signals

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EVOLUTIONARY studies are hampered by a lack of experimental ways in which to test past events such as the origination of aposematism[1-7], whereby unpalatable or poisonous prey signal their unprofitability, often by being warningly coloured. Inexperienced predators do learn to avoid unpalatable prey as a result of such signals[8-10], but in addition there may be an inherited cautiousness about attacking when common or conspicuous warning signals are evident[11-16]. As current predators are not naive in the evolutionary sense, it is still not resolved[3-7,17,18] whether aposematism originated only in aggregations of prey[19,20] or among solitary prey as well[21-23]. Here we explore this controversy in evolutionarily naive predators by creating a novel world with warning signals not found in the environment. Initially, the aggregation of prey favoured the warning signals supporting Fisher's view[24] of kin aggregations as the evolutionary starting point of aposematism. However, once predators had experienced warning signals, pre-existing avoidance seemed to facilitate evolution of Müllerian mimicry complexes[25] with similar types of signals even among solitary prey.

On the basis of the fact that hand-reared predators with no experience of aposematic prey are not naive in the evolutionary sense, we created a world in which there were two types of symbols (crosses and filled squares) that were switched to form the background or the warning signal. As the symbols were not present during the evolutionary history of the predators, we assume that the experiments illustrate the initial conditions experienced by the first aposematic prey individuals. We started from the situation in which an unpalatable prey evolves a warning signal, then continued to test conditions for the evolution of similar signals in other unpalatable prey items (Müllerian mimicry)[25]. We used great tits (*Parus major*) caught in the wild as predators. To enhance the image of a novel world, all prey items were artificial. As initial prey we used items made of a piece of rye straw (a hollow stem of dead cultivated rye) filled with animal fat. White paper 'wings' at each end of the straw piece had either a cryptic signal similar to the background or a warning signal different from the

background. To make the items unpalatable we added chloroquine to the fat. As secondary prey, we used pieces of almond with the symbol glued on the slice.

In the 'initial origin' experiment, the prey were either dispersed as single items or aggregated with four similar items clumped close together (Fig. 1). As the idea was to determine how the warning signal initially enhances the survival probability of prey that have just acquired unpalatability[19,20], we had three types of randomly distributed prey: palatable controls with the cryptic symbol (16 items), unpalatable prey with the cryptic symbol (8 items), and unpalatable prey with the symbol differing from that of the background as the aposematic prey (8 items). Each individual tit had been trained to eat straw items with the cryptic symbol, and they were allowed to search for one hour in the test room. The procedure was repeated on three consecutive days (trials I–III). Conspicuousness or the type of signal itself did not influence the innate preferences between the two types of signals. Another set of eight tits were presented with two prey items (only 2 cm apart) and the same choice situation was repeated four times. The birds did not prefer any of the symbols (first choices for squares, 15, and crosses, 17; binomial test, $P = 0.86$) or the symbol conspicuous-
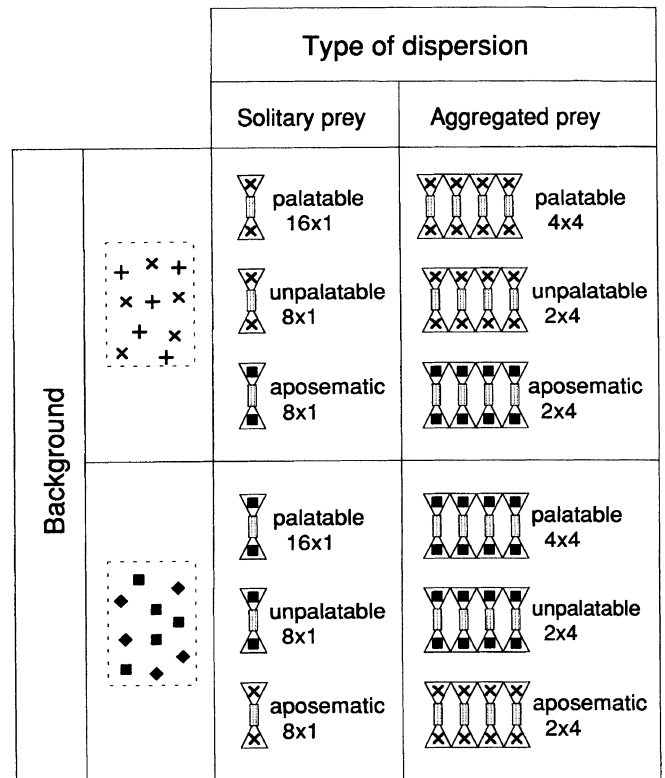

FIG. 1 The experimental set-up to test the origin of warning signals among straw prey. Each individual great tit was randomly assigned to one of the four treatments shown. The background was either a cross or a square and the prey were presented either solitarily or in aggregation. In each case, there were 16 palatable cryptic prey, 8 unpalatable cryptic prey and 8 unpalatable signalling prey (aposematic). Palatable items consisted of animal fat in a 6-mm rye straw with paper wings. Unpalatable items had a 12% concentration of chloroquine. Prey items were randomly placed on a 2 × 2 m floor of an aviary, where there were 6 × 6 = 36 pieces of white A4 paper (21 × 30 cm) with symbols as the background. To train the tits to use their cryptic items, they were offered two palatable pieces of straw filled with fat on two consecutive days. Before the trials, the tits were not allowed to feed for two hours, and each trial lasted one hour. We used only the 12 first items in the analyses, but in the first trials only the 6 first items were included to obtain the initial predation risks before birds could learn the signals. In the second experiment, almond slices were reduced to ~ 6 × 6 mm, with symbols glued to each slice with non-toxic glue. Unpalatable slices were dipped in a 40% solution of chloroquine.