Feeding traces attributable to juvenile *Tyrannosaurus rex* offer insight into ontogenetic dietary trends

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Abstract

Theropod dinosaur feeding traces and tooth marks yield paleobiological and paleoecological implications for social interactions, feeding behaviors, and direct evidence of cannibalism and attempted predation. However, ascertaining the taxonomic origin of a tooth mark is largely dependent on both the known regional biostratigraphy and the ontogenetic stage of the taxon. Currently, most recorded theropod feeding traces and bite marks are attributed to adult theropods, whereas juvenile and subadult tooth marks have been rarely reported in the literature. Here we describe feeding traces attributable to a late-stage juvenile *Tyrannosaurus rex* on a caudal vertebra of a hadrosaurid dinosaur. The dimensions and spacing of the traces were compared to the dentition of *Tyrannosaurus rex* maxillae and dentaries of different ontogenetic stages. These comparisons reveal that the tooth marks present on the vertebra closely match the maxillary teeth of a late-stage juvenile *Tyrannosaurus rex* specimen histologically determined to be 11-12 years of age. These results demonstrate that late-stage juvenile and subadult tyrannosaurs were already utilizing the same large-bodied food sources as adults despite lacking the bone-crushing abilities of adults. Further identification of tyrannosaur feeding traces coupled with experimental studies of the biomechanics of tyrannosaur bite forces from younger ontogenetic stages may reveal dynamic dietary trends and ecological roles of *Tyrannosaurus rex* throughout ontogeny.

Introduction

Bite marks and feeding traces attributable to theropods dinosaurs provide important insight on behavior, physiology, and paleobiology. Furthermore, bite and feeding traces on fossilized bone represents a valuable demonstration of paleoecology; the interaction between two organisms as preserved in both traces and body fossils. Bite marks and feeding traces are relatively common in the fossil record, and are widely reported for theropod dinosaurs. Such traces have provided evidence of gregariousness and social interactions (Tanke and Currie, 1998;

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Bell and Currie, 2009; Peterson et al., 2009; Currie and Eberth, 2010), feeding behaviors and bone utilization (Erickson and Olson, 1996; Chure et al., 1998; Hone and Watabe, 2010; Hone and Rauhut, 2010), direct evidence of attempted predation (Carpenter, 1998; Happ, 2008; DePalma et al., 2013), and cannibalism (Longrich et al., 2010; McLain et al., 2018).

Despite the abundant record of theropod tooth marks, ascertaining the origins of feeding traces and bite marks can be challenging; determining the species responsible for the marks and establishing whether tooth marks are the result of active predation or scavenging largely depends on the taphonomic setting of the skeletal elements, the presence of shed teeth, and the location of the traces on the specimen in question (Hunt et al, 1994; Bell and Currie, 2009; Hone and Rauhut, 2010). However, most recorded cases of theropod feeding or the presence of bite marks are attributed to adult theropods, leaving the presence of juvenile and subadult tooth marks largely absent from the literature and discussion.

Here we report on the presence of feeding traces on the caudal vertebra of a hadrosaurid (BMR P2007.4.1, "Constantine"). Based on the shape and orientation of the traces, and the known fauna of the Hell Creek Formation, they are interpreted to be feeding traces of a large theropod dinosaur, such as *Tyrannosaurus rex* (Erickson and Olson, 1996; Horner et al., 2011). By comparing the dimensions and spacing of the traces with the maxillae and dentaries of specimens of *Tyrannosaurus rex* of different ontogenetic stages, we interpret these tooth marks to be feeding traces from a juvenile *Tyrannosaurus rex* and discuss the insights the specimen provides for juvenile tyrannosaur feeding behavior.

Institutional Abbreviations - BHI, Black Hills Institute of Geologic Research, Hill City, SD, USA; **BMR**, Burpee Museum of Natural History, Rockford, IL, USA.

Geologic Setting

Specimen BMR P2007.4.1 ("Constantine") is a partial hadrosaurid skeleton collected from the Upper Cretaceous Hell Creek Formation of Carter County, southeastern Montana in the Powder River Basin (Figure 1). This specimen was collected on public lands under BLM Permit #M96842- 2007 issued to Northern Illinois University and is accessioned at the Burpee Museum of Natural History in Rockford, IL. Exact coordinates for the location are on file in the paleontology collections at the Burpee Museum of Natural History (BMR), where the specimen is reposited.

The collection locality is composed of a 4m fine-grained, gray-tan lenticular sandstone within a larger surrounding blocky mudstone unit (Figure 2). The sandstone lacks bedforms, resulting from either a) rapid accumulation (resulting in a lack of sedimentary structures), or b) sedimentary structures that were obliterated by later currents or bioturbation, and is rich in rounded and weathered microvertebrate remains. The site is stratigraphically positioned approximately 44 m above the underlying Fox Hills – Hell Creek contact and overlies 0.5 m of siderite, which sits above a 5 m blocky mudstone. Grains are subrounded to subangular. Microvertebrate and fragmented macrovertebrate fossils are abundant and heavily rounded and abraded (Peterson et al., 2011). The fine-grained composition suggests a channel-fill deposit,

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99   overlying a floodplain deposit (Murphey et al., 2002; Peterson et al., 2011). The taphonomic
100 distribution of the elements and their stratigraphic position suggests the skeleton was subaerially
101 exposed on a floodplain for a considerable period of time prior to burial, allowing for
102 weathering, disarticulation, and removal of many skeletal elements.
103
104
105 **Materials & Methods**
106   Specimen BMR P2007.4.1 ("Constantine") consists of weathered pelvic elements
107 (sacrum, left and right ilia), three dorsal vertebrae, and two proximal caudal vertebrae (Figure 3,
108 Table 1). The dorsal vertebrae were too weathered for collection, though their dimensions and
109 relative locations within the quarry assemblage were measured and documented. Additionally, a
110 series of heavily-weathered bone fragments and a small shed theropod tooth (*Saurornithoides*
111 *sp.*) were also collected.
112   The ilium of BMR P2007.4.1 possesses a number of hadrosaurid characters such as 1) a
113 shallow morphology, 2) a ~23° preacetabular process in medial view relative to the main body,
114 and 3) a well-developed supra-acetabular process caudalm to the acetabulum. While these
115 characters are common among hadrosaurids, the stratigraphic position of BMR P2007.4.1
116 suggests it is attributable to the Late Cretaceous hadrosaurid *Edmontosaurus* (i.e. Brett-Surman
117 and Wagner, 2007; Campione, 2014).
118   The centra of the two caudal vertebrae lack any evidence for hemal arch attachments,
119 suggesting they are among the more cranial-positioned caudal vertebrae, such as C1-C4
120 (Campione, 2014). One of the caudal vertebra possesses three v-shaped indentations on the
121 ventral surface of the centrum (Figure 4A-E). These traces feature collapsed cortical bone within
122 the indentation, producing puncture marks (*sensu* Bindford, 1981). The punctures penetrate 5
123 mm deep, are spaced 68 mm apart from their apical centers, show no signs of healing, and are
124 inferred to have been created post-mortem as feeding traces (e.g. Noto et al., 2012; Hone and
125 Tanke, 2015; McLain et al., 2018). The v-shape preserved in each puncture indicates that the
126 original teeth would have possessed a prominent keel, though no striations from serration marks
127 are present in the traces.
128   The large size and shape of the punctures suggests that they were produced by a large- to
129 medium-bodied carnivore. Such carnivores from the Hell Creek Formation include tyrannosaurs
130 such as *Tyrannosaurus rex* (Erickson and Olson, 1996; Horner et al., 2011), medium-sized
131 dromaeosaurids such as *Dakotaraptor steini* (DePalma et al., 2015), and crocodilians such as
132 *Borealosuchus sternbergii*, *Brachychampsa montana*, and *Thoracosaurus neocesariensis*
133 (Matsumoto and Evans, 2010). By comparing the shape and orientation of the traces to the teeth
134 of these carnivores from the Hell Creek Formation, they are hypothesized to be bite marks from
135 a large theropod dinosaur, such as *Tyrannosaurus rex* (Erickson and Olson, 1996); crocodilian
136 teeth are circular in cross-section and too small, and dromaeosaurid teeth – even large
137 dromaeosaurids such as *D. steini* – are too small and laterally-compressed to have produced the
138 punctures observed on BMRP2007.4.1.

151   To test this hypothesis, the punctures on the caudal vertebra of BMR P2007.4.1 were first
152 coated in ReboundTM 25 platinum-cure silicone rubber (Smooth-On) in order to make a silicone
153 peel of the punctures in order to better visualize the morphology and dimensions of the teeth
154 responsible for the traces (Figure 5A-B). These "teeth" were then compared with the dental
155 dimensions and spacing of two *Tyrannosaurus* maxillae and dentaries. To approximate the
156 ontogenetic stage of the tyrannosaur, a late-stage juvenile specimen (BMR P2002.4.1, "Jane")
157 histologically determined to be approximately 11-12 years old at the time of death (Erickson et
158 al., 2006) that possesses laterally compressed, sharp crowns, and a mature specimen (BHI 3033,
159 "Stan") with robust, blunt crowns were utilized.
160   All specimens were digitized via triangulated laser texture scanning with a NextEngine
161 3D Laser Scanner, capturing data at seven scanning divisions in high-definition (2.0k points/in2).
162 The resulting digital models were built with the NextEngine ScanStudio HD Pro version 2.02,
163 and finalized as STL models (Supplemental Figures S1 and S2). Scanning was conducted at the
164 Department of Geology at the University of Wisconsin-Oshkosh in Oshkosh, WI.
165 The tooth spacing of both adult and late-stage juvenile tyrannosaur maxillae and dentaries were
166 measured for both immediately-adjacent teeth and teeth from alternating replacement positions
167 (i.e. *Zahnreihen*), and compared with the spacing of the punctures (Figure 6A-B). Furthermore,
168 the cross-sectional morphology of adult and late-stage juvenile tyrannosaur maxillae and
169 dentaries were measured labiolingually and mesiodistally at a 5 mm apical depth for each tooth
170 crown, and plotted with measurements from the punctures found on BMR P2007.4.1 (Figure 7).
171

Results

173   The mesiodistal width measurements from the silicone peel taken from BMR P2007.4.1
174 average 7.8 mm and the labiolingual depth average was 5.2 mm. Maxillary and dentary teeth of
175 the adult *Tyrannosaurus* (BHI 3033) were found to be too large and widely spaced to have
176 produced the punctures (Figures 7,8A,B; Table 2A-C). For BHI 3033, the average dentary tooth
177 crown mesiodistal width at 5 mm depth was 7.13 mm, and the average dentary tooth crown
178 labiolingual depth at 5 mm was 4.10 mm. The average maxillary crown mesiodistal width at 5
179 mm were 7.72 mm, and the average maxillary crown labiolingual depth at 5 mm averaged to
180 4.21 mm.
181   However, the teeth of BMR P2002.4.1 produced similarly shaped punctures at 5 mm
182 apical depth (Figure 7, 9; Table 2B-C). The puncture measurements taken from the peel, BMR
183 P2007.4.1 demonstrate a mesiodistal width and labiolingual depth consistent with the
184 measurements taken from the maxillary and dentary teeth of the late-stage juvenile
185 *Tyrannosaurus*. When plotted against the mesiodistal width and labiolingual depth of the
186 maxillary teeth, measurements from the peel taken from BMR P2007.4.1 fall well within the
187 cluster radius created by the late-stage juvenile *Tyrannosaurus*, BMR P2002.4.1 (Figure 7).
188 Furthermore, the inferred crown spacing of the punctures closely matched those of the late-stage
189 juvenile tyrannosaur maxilla (Table 3A-B).
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Discussion and Conclusions

While feeding traces and bite marks attributed to mature tyrannosaurids are well-documented in common Late Cretaceous taxa such as hadrosaurids and ceratopsians (i.e. Fiorillo, 1991; Erickson et al., 1996a,b; Jacobsen, 1998; Farlow and Holtz, 2002; Fowler and Sullivan, 2006; Peterson et al., 2009; Bell and Currie, 2010; Fowler et al., 2012; DePalma et al., 2013, Mclain et al., 2018), the identification of juvenile tyrannosaur feeding traces adds insight into the role of juvenile theropods in Cretaceous ecosystems. The dimensions and spacing of the punctures closely matches the maxillary teeth of BMR P2002.4.1, a late-stage juvenile (11-12 yr old) tyrannosaur which incidentally itself possesses morphologically similar craniofacial lesions previously interpreted as a conspecific bite (Peterson et al., 2009).

Longrich et al. (2010) reported on evidence of cannibalism in *T. rex* based on a number of bitten and scored remains of *Tyrannosaurus rex*, some attributed to juvenile or subadult individuals. However, many of these traces resemble the 'puncture and pull' bite marks that have previously been attributed to *T. rex* (Erickson et al., 1996a; Erickson et al., 1996b), and also include furrows and scores (*sensu* Binford, 1981).

Correlating traces in bone, such as tooth marks, to specific taxa and ontogenetic stages usually requires direct comparisons (e.g. Peterson et al., 2009; Fahlke, 2012). However, in cases where direct comparisons are not available, estimates can be made for tooth size, morphology, and spacing based on ontogenetic trajectories. While bite marks and feeding traces attributable to younger juvenile and hatchling tyrannosaurs have not yet been identified, the punctures present on the caudal vertebra of BMR P2007.4.1 provide direct evidence that late-stage juvenile *Tyrannosaurus rex* such as BMR P2002.4.1 possessed – at least in part – a similar diet as adults.

While bite marks resulting from active predation cannot easily be distinguished from postmortem feeding traces, the ventral position of the punctures in the caudal centrum of BMR P2007.4.1 suggests that the feeding was taking place postmortem with the hadrosaur already on its side (Chure et al., 1996). The afflicted vertebra is from the cranial-most part of the tail. Observations of the feeding behaviors of carnivoran mammals and birds indicate that in most cases, consumption of the axial skeleton occurs after limbs and viscera have been consumed (e.g. Hill and Behrensmeyer, 1980; Haglund, 1997; Carson et al., 2000; and Behrensmeyer et al., 2003). Hadrosaur tails had substantial muscles such as m. ilio-ischiocaudalis and m. caudofemoralis longus (Persons and Currie 2014) that might be a target of early stage consumption. However, the ventral bite traces on BMR P2007.4.1 suggest that the tyrannosaur was feeding after the haemal complexes and most of the superficial hypaxial muscles and m. caudofemoralis longus had been removed. As such the punctures on BMR P2007.4.1 suggest later-stage carcass consumption and postmortem feeding behaviors.

The identification of penetrating bite marks attributable to not only *Tyrannosaurus rex*, but an individual of 11-12 years of age can potentially allow for the determination of the ontogeny of bite force in *Tyrannosaurus rex* and for comparison with other theropods (e.g. Barrett and Rayfield, 2006, Gignac et al., 2010; Bates and Falkingham, 2012). Studies on the estimated bite forces of an adult *Tyrannosaurus rex* have yielded a wide range of results.

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Comment [ES4]: True, although most recently-dead non-avian dinosaurs had substantial tail muscles unlike those of any terrestrial mammal (or bird) carcass. The tail might be counted as a limb in the scavenging sequence. However, the ventral position of the bite marks may strengthen the late-stage interpretation. A sentence is suggested.

Estimates based on muscle volume proposed bite forces between 8,526—34,522 N, coupled with tooth pressures of 718—2,974 MPa, and a unique tooth morphology and arrangement to promote fine fragmentation of bone during osteophagy (Gignac and Erickson, 2017). However, estimates incorporating likely muscle fiber length produced results over 64,000 N for adult *T. rex* (Bates and Falkingham, 2018). Juvenile *T. rex* such as BMR P2002.4.1 have much narrower and blade-like tooth morphologies and were unlikely to have been able to withstand similar bite forces at this ontogenetic stage. Bates and Falkingham (2012) estimated a maximum bite force for BMR P2002.4.1 at 2,400-3,850 N, and hypothesized that an increase in bite force during growth could indicate a change in feeding behavior and dietary partitioning while approaching adulthood.

Observation on extant crocodilians have documented a wide variety of dietary partitioning during ontogeny (e.g. Tucker et al., 1996; Platt et al., 2006; Platt et al., 2013). In the American Crocodile (*Crocodylus acutus*), hatchling and small juveniles have a dietary overlap of over 80%, commonly feeding upon insects and crustaceans (Platt et al., 2013). Alternatively, larger juveniles, subadults, and adults possess a dietary overlap of over 75%, consisting of more birds, mammals, fish, and other reptiles (Platt et al., 2013). Comparable ontogenetic dietary partitions were also observed in Morelet's Crocodile (*Crocodylus moreletii*) (Platt et al., 2006), and in Australian freshwater crocodiles (*Crocodylus johnstoni*) (Tucker et al., 1996). However, crocodilians are less discriminant of food sources when scavenging (e.g. Antunes, 2017). While the punctures present on BMR P2007.4.1 are likely from post-mortem scavenging behaviors of a juvenile tyrannosaur, the degree of dietary overlap or partitioning between juvenile and adult tyrannosaurs remains unresolved.

Despite not yet possessing the same feeding mechanisms of an adult *Tyrannosaurus rex* (i.e. bone-crushing and osteophagy), the punctures present on BMR P2007.4.1 demonstrate that late-stage juvenile and subadult tyrannosaurs were already biomechanically capable of puncturing bone during feeding, and were doing so without the large, blunt dental crowns of adults. Further identification of tyrannosaur feeding traces from different ontogenetic stages coupled with experimental studies of the biomechanics of tyrannosaur bite forces may reveal more insight into dynamic dietary trends and ecological role of *Tyrannosaurus rex* throughout ontogeny.

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The dimensions and spacing of the punctures closely matches the maxillary teeth of BMR P2002.4.1, a late-stage juvenile (11-12 yr old) tyrannosaur which incidentally itself possesses morphologically similar craniofacial lesions previously interpreted as a conspecific bite (Peterson et al., 2009). While bite marks resulting from active predation cannot easily be distinguished from postmortem feeding traces, the ventral position of the punctures on the caudal centrum of BMR P2007.4.1 suggests that the feeding was taking place postmortem with the hadrosaur already on its side (Chure et al., 1996). The afflicted vertebra is from the cranial-most caudal sequence where a significant muscle mass would have been associated en vivo, suggesting relatively early-stage carcass consumption and reflecting postmortem feeding behaviors.

While feeding traces and bite marks attributed to mature tyrannosaurids are well-documented in common Late Cretaceous taxa such as hadrosaurids and ceratopsians (i.e. Fiorillo, 1991; Erickson et al., 1996a,b; Jacobsen, 1998; Farlow and Holtz, 2002; Fowler and Sullivan, 2006; Peterson et al., 2009; Bell and Currie, 2010; Longrich et al., 2010; Fowler et al., 2012; DePalma et al., 2013, Mclain et al., 2018), the first identification of juvenile tyrannosaur feeding traces adds insight into the role of juvenile theropods in Cretaceous ecosystems. The identification of penetrating bite marks attributable to not only *Tyrannosaurus rex*, but an individual of 11-12 years of age can potentially allow for the determination of the ontogeny of bite force in *Tyrannosaurus rex* and for comparison with other theropods (e.g. Barrett and Rayfield, 2006, Gignac et al., 2010; Bates and Falkingham, 2012).

The bite forces of an adult *Tyrannosaurus rex* have been estimated to have been between 8,526—34,522 N, coupled with tooth pressures of 718—2,974 MPa, and a unique tooth morphology and arrangement to promote fine fragmentation of bone during osteophagy (Gignac and Erickson, 2017). However, juvenile *T. rex*, such as BMR P2002.4.1 have much narrower and blade-like tooth morphologies and were unlikely to have been able to withstand similar bite forces at this ontogenetic stage. Bates and Falkingham (2012) estimate a maximum bite force for BMR P2002.4.1 at 2,400-3,850 N, and suggest that an increase in bite force during growth could indicate a change in feeding behavior and diet while approaching adulthood.

Observation on extant crocodilians have documented a wide variety of dietary partitioning during ontogeny (e.g. Tucker et al., 1996; Platt et al., 2006; Platt et al., 2013). In the American Crocodile (*Crocodylus acutus*), hatchling and small juveniles have a dietary overlap of over 80%, commonly feeding upon insects and crustaceans (Platt et al., 2013). Alternatively, larger juveniles, subadults, and adults possess a dietary overlap of over 75%, consisting of more birds, mammals, fish, and other reptiles (Platt et al., 2013). Comparable ontogenetic dietary partitions were also observed in Morelet's Crocodile (*Crocodylus moreletii*) (Platt et al., 2006), and in Australian freshwater crocodiles (*Crocodylus johnstoni*) (Tucker et al., 1996).

While bite marks and feeding traces attributable to younger juvenile and hatchling tyrannosaurs have not yet been identified, the punctures present on the caudal vertebra of BMR P2007.4.1 provide direct evidence that late-stage juvenile *Tyrannosaurus rex* such as BMR

P2002.4.1 possessed a similar diet as adults. Despite not yet possessing the same feeding mechanisms of an adult *Tyrannosaurus rex* (i.e. bone-crushing and osteophagy), the punctures present on BMR P2007.4.1 demonstrate that late-stage juvenile and subadult tyrannosaurs were already biomechanically capable of puncturing bone during feeding, and were doing so without the large, blunt dental crowns of adults. Further identification of tyrannosaur feeding traces from different ontogenetic stages coupled with experimental studies of the biomechanics of tyrannosaur bite forces may reveal more insight into dynamic dietary partitioning and ecological role of *Tyrannosaurus rex* throughout ontogeny.