Feeding behaviour and bone utilization by theropod dinosaurs

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LETHAIA

Examples of bone exploitation by carnivorous theropod dinosaurs are relatively rare, representing an apparent waste of both mineral and energetic resources. A review of the known incidences and possible ecological implications of theropod bone use concludes that there is currently no definitive evidence supporting the regular deliberate ingestion of bone by these predators. However, further investigation is required as the small bones of juvenile dinosaurs missing from the fossil record may be absent as a result of theropods preferentially hunting and consuming juveniles. We discuss implications for both hunting and feeding in theropods based on the existing data. We conclude that, like modern predators, theropods preferentially hunted and ate juvenile animals leading to the absence of small, and especially young, dinosaurs in the fossil record. The traditional view of large theropods hunting the adults of large or giant dinosaur species is therefore considered unlikely and such events rare. □ *Behaviour, carnivory, palaeoecology, predation, resource utilization.*

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Tetrapod bone can provide an important source of essential elements, such as calcium, phosphorus and potassium, and sustenance (due to their fat, blood and bone marrow content, Haynes 1980; Kardong 2002) for a predatory animal. Extant carnivorous mammals exploit bone extensively, even in situations where the prey item is large and provides energy-rich muscle and organ tissue (e.g. elephants, buffalo, Haynes 1980). Large- and small-bodied opportunists consume available bones (e.g. hyenas and jackals), as do primary carnivores (e.g. felids and hunting dogs, van Valkenburgh 1996). Extant crocodiles (Fisher 1981; Naju & Blumenschine 2006) and birds (Dodson & Wexler 1979) also regularly consume the bones of their prey.

Given both their large body sizes (up to 14 m in length and 6–7 tonnes in weight) and hypercarnivorous habits (Holtz & Osmolska 2004), it might be expected that at least some non-avian theropod dinosaurs would have actively utilized prey, or scavenged, bone. However, direct evidence for predator-damaged bones in the dinosaur fossil record is rare and such remains occur less frequently than in the mammal record (Fiorillo 1991). Moreover, most examples of theropod predation damage appear to represent accidental contact between teeth and bone rather than deliberate attempts to consume bone. Recovered dinosaur bones rarely exhibit the modifications associated with osteophagy in extant taxa (Chure *et al.*

2000): for example, they generally lack the spiral fractures, splintered long bones and deep tooth puncture marks that result from the attentions of living bone-eating taxa. This lack of evidence leads to the surprising conclusion that theropods either did not utilize bone in their diets or consumed bones and left no direct evidence of this behaviour (perhaps due to some feature of their digestive physiology; Mellett 1983).

Here, we intend to re-assess the evidence for osteophagy in non-avian carnivorous theropod dinosaurs and explore the possible ecological implications of this inferred behaviour (or lack thereof). Multiple lines of evidence are available, but, although most of these have been discussed separately with regard to theropods, they have not been evaluated collectively. Direct evidence is available from predator-damaged bones, preserved stomach contents and coprolites. Indirect evidence from craniodental morphology and the inferred ecology of theropod dinosaurs also contributes to our picture of theropod diets. Comparisons with extant analogues, including birds, crocodilians and mammals, are informative and help to constrain speculation on the digestive and functional morphological repertoires of their extinct relatives (the Extant Phylogenetic Bracket, Witmer 1995). We have focused on those theropods thought to have a strictly carnivorous diet: several theropod clades, such as Ornithomimosauria and Therizinosauroidea, were probably not

primarily carnivorous (Kobayashi and Lü 2003; Barrett 2005) and are therefore excluded from consideration.

Tyrannosaurs – the exceptions that prove the rule?

Tyrannosaurs deserve special mention in any paper dealing with theropod osteophagy. Large tyrannosaurs (e.g. *Tyrannosaurus*, *Albertosaurus* and *Daspletosaurus*) have repeatedly been interpreted as the only non-avian theropods capable of damaging large prey bones on the basis of direct evidence (tooth puncture marks, Erickson & Olson 1996), the gross morphology of the skull and post-cranium (Holtz 2004), biomechanical analyses of cranial strength and biting performance (Rayfield 2004) and direct evidence of bone consumption from coprolites (Chin 1997).

Throughout this paper, reference is made to large theropods. These often include animals of similar size to tyrannosaurs (e.g. *Carcharodontosaurus*, *Saurophaganax*, *Ceratosaurus*) and some might have actually been significantly larger (e.g. *Giganotosaurus*, *Spinosaurus*; see Dal Sasso *et al.* 2005). Size is therefore not a key component of bone crushing (although large bones can still be exploited by large animals by swallowing them whole) and instead we must focus on the apparent numerous adaptations of tyrannosaurs for bone crushing (Barrett & Rayfield 2006). However, the capability to damage and bite through bone should not be considered synonymous with the actual activity of consuming bone for nutritional reasons (i.e. ability does not necessarily equal behaviour). Bone may be consumed simply because it is easier than not doing so (i.e. an inability to separate bone from flesh on a carcass) or it may be consumed accidentally (e.g. when biting off the distal part of the tail). However, it is probably impossible to distinguish among these potential behavioural aspects of bone consumption and so instead we will focus on the consumption of bone by tyrannosaurids based on their apparent ability to crush and break even large bones or bone complexes (e.g. the sacrum; see Erickson & Olson 1996).

Direct evidence – bone modification

Bones that exhibit damage resulting from tooth–bone contact represent the primary evidence for osteophagy. Such damage is relatively easy to distinguish from 'trample' marks, transport-induced breaks and other taphonomic alterations (Fiorillo 1987).

Theropod feeding traces typically consist of either tooth scratches on the bone surface (produced as the teeth are drawn across a bone to deflesh it or to remove the cortex) or puncture wounds (resulting from teeth piercing and entering the cortex). The length, depth and spacing of scratches can be used to attribute the marks to a potential trace maker (e.g. Chure *et al.* 2000). Similarly, the outlines of puncture wounds, or casts of moulds taken from within the wounds, reveal the dental morphology of the predator and thereby provide information on its identity (e.g. Erickson & Olson 1996; Carpenter *et al.* 2005; Fig. 1).

The rarity of bones that display obvious damage inflicted by theropod teeth implies that theropods were not habitually osteophagous (Chure *et al.* 2000). Known examples (Table 1) typically consist of one or more scratch marks or puncture wounds on a single element of a particular prey item. This observation also suggests that the few feeding traces available are primarily accidental in nature, with the predator/scavenger biting bone while feeding on the surrounding tissue or attempting to dismember the carcass. This is highlighted by the fact that most predator damage consists of scratches (created by tearing and pulling) rather than punctures (created by impact). Even where conspicuous puncture wounds are present, they usually represent isolated bites, rather than a pattern consistent with repeated feeding activity across an entire specimen (Jacobsen 1998). One exception to this is a *Triceratops* pelvis that bears numerous puncture wounds, presumably from the same attacker, which was most probably a *Tyrannosaurus* (Fig. 1, Table 1).

Studies on the occurrence of predator-damaged bones within accumulations, such as species-specific

Fig. 1. Triceratops sacrum with bite marks (black arrows) attributed to *Tyrannosaurus*. The lower right section has actually been bitten off. Moulds taken from the scores and punctures replicate the teeth of *Tyrannosaurus* (Erickson & Olson 1996). Image: copyright G.M. Erickson.

Table 1. Examples of notable injuries to dinosaur and other archosaur remains attributable to theropod dinosaurs.

Description	Attributed bite maker	Source
Triceratops pelvis exhibiting multiple tooth punctures	*Tyrannosaurus*	Erickson & Olson (1996)
Bitten off horn and scratch marks in a *Triceratops* skull	*Tyrannosaurus*	Happ (2008)
Healed bite mark on *Edmontosaurus* neural spine	*Tyrannosaurus*	Carpenter (2000)
Allosaurus pubic boot with one side bitten through	*Torvosaurus* or *Ceratosaurus*	Chure *et al.* (2000)
Stegosaurus cervical plate that has been bitten through	*Allosaurus*	Carpenter *et al.* (2005)
Camarasaurus ilium showing tooth drag marks	*Allosaurus*	Chure *et al.* (2000)
Hypacrosaurus fibula with a tooth embedded in it	*Tyrannosaurus*	Chin (1997)
Edmontosaurus phalanx with tooth punctures	*Tyrannosaurus*	Erickson & Olson (1996)
Damaged *Apatosaurus* bones	*Allosaurus*	Matthew (1908)
Various damaged sauropod bones (including long bones, sacra, etc.)	Various large Jurassic theropods	Hunt *et al.* (1994)
Various dinosaur bones including sauropods and *Majungasaurus*	*Majungasaurus*	Rogers *et al.* (2004)
Teeth scratch and puncture marks on skulls of *Sinraptor* and tyrannosaurids	*Sinraptor* and tyrannosaurids	Tanke & Currie (2000)
Pterosaur vertebra with tooth embedded in it	Spinosaurid	Buffetaut *et al.* (2004)
Pterosaur tibia with tooth embedded in it	Dromaeosaurid	Currie & Jacobsen (1995)

bone beds, suggest that while feeding traces are not common, they may be more frequent than generally realized. In some accumulations, approximately 4% of the elements have been modified by predators (Fiorillo 1991). A similar figure was obtained from a survey of multiple neoceratopsian bonebeds and up to 14% of bones are damaged in some hadrosaur accumulations (Jacobsen 1998). However, this last figure may have been inflated artificially by the presence of large tyrannosaurs inflicting more damage than would be normal compared with other large theropod communities (see below). The relative proportion of damaged bones seems to be higher in isolated bones than in mass assemblages (Fiorillo 1991). Mass death events may have isolated and buried the carcasses and thus prevented scavenging, or alternatively with the large number of bodies available, scavengers may have been capable of preferentially consuming meat and thus avoiding bones.

Broken, gnawed and tooth-marked bones are common in the mammalian fossil and sub-fossil record (Haynes 1980) suggesting common bone feeding behaviour; in fact, it is noticeable higher than seen for dinosaurs (Farlow 1976). Clearly, if this behaviour was frequent among theropods, it would be recorded with far greater frequency than is observed in extant mammalian predators (Carlson & Pickering 2003) and crocodiles (Naju & Blumenschine 2006). On the basis of direct bite-mark evidence, it can be concluded that theropods (with the possible exception of the larger tyrannosaurs) did not deliberately attack and consume bone (although the pattern may be obscured, see Erickson & Olson 1996).

Feeding apparatus

It has been suggested that the skulls and teeth of theropods were poorly adapted for trituration or crushing of bone and that the lack of evidence for osteophagy reflects the inability of these animals to process this food source (Fiorillo 1991). Theropods could not chew bones in a conventional mammalian manner with lateral jaw movements (although this is limited in many carnivores) but could presumably bite repeatedly on a bone in the jaws if they wished. The bone fragments seen in the coprolite referred to a tyrannosaur suggest the possibility of very high levels of oral processing (Andrews & Fernandez-Jalvo 1998) giving credibility to this interpretation (in tyrannosaurs at least). Clearly, theropods could also drag their teeth across bones without sustaining injury or damage to the teeth and this could be done repeatedly to weaken or damage bones (e.g. as with the *Camarasaurus* ilium, see Chure *et al.* 2000). However, apart from occasional scrape marks on bones there is no direct evidence for either of these behaviours.

Smaller bones (e.g. distal caudal vertebrae and phalanges) could probably have been swallowed whole by many theropods. Some medium-sized bones (e.g. vertebrae and ribs) could be bitten through or at least have parts removed relatively easily (e.g. neural arches) by large theropods. Even those genera that do not appear to be well adapted to biting on bone could probably have broken a neural spine that was only a few millimetres thick.

It has been suggested that the feeding strategy of theropods involved careful avoidance of any tooth–bone contact (Chure *et al.* 2000) and may have been aimed at avoiding damage to the teeth. Teeth in most theropods probably represented important tools for prey capture as well as feeding, and thus significant damage or loss might have severely impeded their survival. While this may well have been true for small theropods with fine, fragile teeth (e.g. dromaeosaurids) and these could also be more delicate in their feeding on larger bones, it seems doubtful for the larger carnivores. Even so, there are scrape marks and

even a tooth embedded in bone attributable to dromaeosaurid predators (Currie & Jacobsen 1995) showing that even these animals produced strong tooth–bone contacts and even broke teeth during feeding.

The 'carnosaurs' with relatively thin teeth (e.g. carcharodontosaurids) might have risked damage to their teeth if they impacted on bone, and the slightly curved or sinusoidal shape of their crowns (see Fig. 2) leaves them vulnerable to bending forces during heavy compressive pressure compared with a straight tooth. However, these teeth were still relatively robust (compared with those of smaller theropods, in addition to being absolutely more robust), and although not molariform, they are much bigger in absolute size than the teeth of many mammals capable of bone-cracking behaviour. Thus, the risk is unlikely to be as high as might otherwise be inferred compared with mammals capable of cracking large bones. Furthermore, biting in these animals was probably strictly orthal, in which case the bite force is transmitted directly from the tip of the tooth to the base, so that the lateral flattening of the tooth plays only a minor role. Indeed, biomechanical studies have shown both the ability of theropod skulls (Rayfield *et al.* 2001; Rayfield 2005) and teeth (Mazzetta *et al.* 2004) to withstand large bite forces. In addition, the constant replacement of teeth in theropods means that there is overall relatively little

harm to an individual in losing or breaking a few teeth if this leads to gaining a vital meal. Even modern and recently extinct mammals that cannot replace teeth can show high incidences of broken canines and carnassials (van Valkenburgh 1988, 2009) that would presumably have more serious consequences for them than for a theropod that could replace its damaged teeth.

At least some large non-tyrannosaur theropods were capable of exerting bone-crunching bites on bones (presumably without tooth damage) as observed by the bitten-through *Allosaurus* pubic boot and *Stegosaurus* armour plate (see Table 1). There are also records of theropods inflicting significant damage on conspecifics through cranio-facial biting behaviours in both tyrannosaurids and allosauroids (Tanke & Currie 2000). Clearly, theropods were willing to engage in behaviour that risked damage to their own teeth, jaws and skull in circumstances that would presumably involve more risk than static feeding on a corpse.

While some theropod teeth were dislodged by biting bone (e.g. *Hypacrosaurus* fibula with embedded tooth, see Fig. 3), this may represent the loss of loose or old teeth in which the root was already partially or fully resorbed (wear on theropod teeth is actually not uncommon but has mainly been described for tyrannosaurs; see Farlow & Brinkman 1994; Schubert &

Fig. 2. Theropod lateral tooth, *Carcharodontosaurus* sp., mid-Cretaceous, Kem Kem, Morocco; BSPG 1993 IX 1, in mesial (left), (?) lingual (middle) and distal (right) views. Note the slight sinusoidal curve of the tooth in distal view. Note the small wear facet at the tip, especially visible in mesial view. Scale bar with 10- and 1-mm divisions.
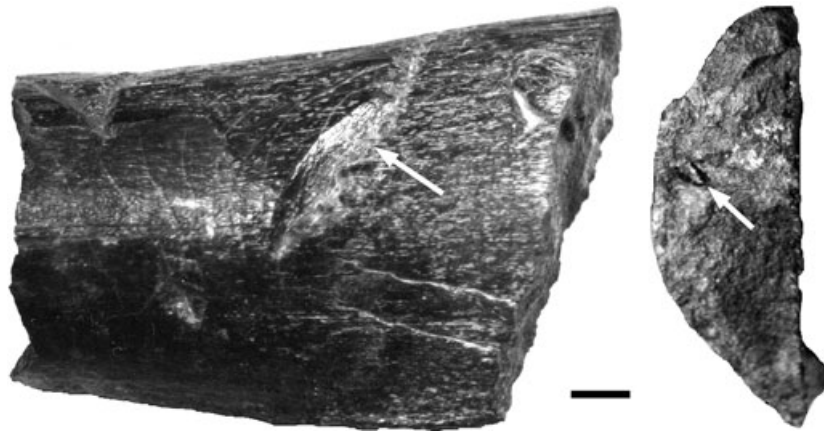
Fig. 3. A partial *Hypacrosaurus* fibula (MOR 549) in lateral view (left) and in cross-section (right). It shows a deep tooth score mark (left, indicated by white arrow) and an embedded partial tyrannosaur tooth (right, indicated by white arrow). Scale bar is 10 mm. For details, see Chin (1997).

Ungar 2005) and is not necessarily an indication of habitually loosely socketed teeth in theropods. In fact, tooth roots in theropods are actually quite strong, being typically at least twice as long as the crowns and somewhat expanded; so, the teeth were not loosely attached in a living animal (O.W.M.R., personal observation). Tooth loss in many fossil theropod skulls is thus the result of the degradation of the soft tissues holding the teeth in place after the death of the animal, which is also seen in modern crocodiles and many mammals (O.W.M.R., personal observation). When alive, theropod teeth were weakened in their sockets by the development of replacement teeth and the roots of the tooth in the mouth having already been reabsorbed and thus weakly held in the jaw, and easily dislodged. Coyotes and foxes are capable of leaving gnaw marks on large *Bos* and *Bison* bones (Fiorillo 1991); so, it is reasonable to expect an allosaur to be capable of grating on some large bones without losing fully functional teeth.

Teeth may also have been shed during hunting or feeding regardless of tooth–bone contact. Once the root has been resorbed, theropod teeth seem to be shed with remarkable ease and this may have been a habitual (or at least very frequent) part of feeding. Shed teeth are found with great frequency and are often unworn (Fiorillo & Currie 1994), suggesting that they were shed or lost without having gone through much use before their replacement (or were not subjected to heavy wear). The classic *Tenontosaurus/Deinonychus* associations (Maxwell & Ostrom 1995), amongst others (e.g. Buffetaut & Suteethorn 1989; Ryan *et al.* 1998), show very high numbers of shed teeth, suggesting that this was a common occurrence. A distinction should be made, however, between teeth that are being shed anyway (because it is simply their time to be replaced) and are shed during feeding, and

those teeth that become unusable due to extensive damage. The implications are that teeth were not subjected to much wear but rather were lost regularly as a result of feeding but without significant tooth–bone contact. The latter is common in theropods that have constant tooth replacement and simply depends on replacement rates and only secondarily on the forces exerted on the tooth (as the root is already reabsorbed when they are lost). Thus, the potential loss of teeth cannot account for theropods avoiding tooth–bone contact as it is unlikely that it would have had any significant detrimental effect on the animal or its health.

Stomach contents

There are a number of well-preserved and articulated large theropod specimens that are known from around the world (e.g. *Allosaurus*, *Albertosaurus* and *Tarbosaurus*). It is rare for both large and small theropods to be preserved with bony stomach contents of previous meals, although a few are known, and in these, bones of considerably smaller prey than the predator seem to have been swallowed whole (e.g. *Baryonyx*, *Compsognathus* and *Sinosauropteryx*). Some tyrannosaurids have been found with juvenile ornithischians as part of the stomach contents (Varricchio 2001) and bone was found in coprolites attributed to tyrannosaurs (Chin 1997, and see below). Therefore, if theropods were regularly consuming large pieces of bone, one would expect to find many more specimens (especially the tyrannosaurs) with preserved bone mass in their chest cavities.

In large living crocodiles at least (that habitually consume large quantities of unprocessed bone), the effect of stomach acids is such that no recognizable bone fragments are passed from the body (Andrews &

Fernandez-Jalvo 1998). This is also true of some other ectothermic animals, such as large amphibians (Mellett 1983). Even if consumed bones were subjected to considerable oral processing and were maintained in the high-acid environment of the stomach for extended periods of time, one would expect to see some bone preserved occasionally when an animal died soon after feeding before the process of digestion had acted fully on the consumed bone. Even a large tyrannosaurs feeding on the bones of a juvenile animal (with probably incomplete ossification) with extensive oral processing and a long digestion time (again assumed based on the size of the animal) identifiable pieces can be identified from the coprolites resulting from this; so, stomach contents should be recovered on occasion, especially for individually large bones or bone pieces if ingested. The quality of preservation of some complete specimens is such that even small bone fragments in the stomach should be recovered occasionally.

However, even in largely articulated specimens, the ribcage is often broken open and prey bone fragments might have been scattered outside the ribcage. Thus, they may simply have gone unnoticed or unreported in the past as unrecognizable and undiagnostic bone fragments, if collected at all, are often not studied in any detail during the study of a fossil. Intensive search for acid-etched or tooth-marked bone fragments in museum collections of material excavated at theropod sites might thus reveal additional evidence for bone consumption by theropods, but such a survey is beyond the scope of this paper.

The abilities of birds (Dodson & Wexler 1979; Housten & Copsey 1994), crocodiles (Fisher 1981) and large varanids that can digest heavy bone loads effectively (Auffenberg 1981) suggest that if theropods were consuming very large amounts of bone, or very large pieces of bones, then some should still survive long enough to be found in stomach contents (as indeed they survive to be recovered in coprolites at least on some occasions). In crocodiles, little survives the digestive process and even enamel can be stripped from teeth, although bones and bone fragments can be passed out in faeces (Fisher 1981). Crocodiles typically break bones prior to ingestion, including those that are not ultimately consumed (Naju & Blumenschine 2006) a process that leaves distinctive marks, which cannot be confused with mammalian bite and break traces (Naju & Blumenschine 2006). In birds, little is known outside of studies of owls, which habitually consume small mammals whole and then regurgitate undigested material. Nevertheless, they are capable of digesting more than 50% of the bones consumed (Dodson & Wexler 1979) and this points to a strong digestion despite minimal oral processing and reduced time in the digestive tract. A similar figure of 50% for bone digestion was also found for the bearded vulture after consuming ribs from large mammals without any form of mechanical processing (Housten & Copsey 1994).

In the theropod *Baryonyx* stomach contents included scales attributed to the fish *Lepidotes* (Charig & Milner 1997), which have a very thick layer of ganoin and should thus be very resistant to acid wear. These scales, however, show serious acid damage (P.M. Barrett, personal communication), and this provides evidence that theropods had very acidic stomach environments. Large theropods would have had long digestion times due to the length of their gut, and there is evidence that at least in the stomach there was a highly destructive acid environment (Chin *et al.* 1998; Varricchio 2001). While this might permit them to digest large pieces of bone effectively, the presence of fragments of bones from juvenile animals in the coprolites of even the largest tyrannosaurs (Chin *et al.* 1998; Varricchio 2001) suggest that complete elimination of large bones would be very difficult.

Coprolites

If theropods were consuming bone regularly, their coprolites should be common (Bradley 1946), but instead they are rare (Chin 1997), although this is true of coprolites of terrestrial vertebrates in general. The low number of theropod coprolites could be a result of unfavourable conditions for preservation, behavioural factors (e.g. defecation in water) or they may be hard to diagnose, with or without high bone content. However, the basic observation is that theropod coprolites of any kind are rare. Coprolites attributable to herbivores are also infrequent and, although these would be far less favoured for preservation over a mineral-rich bone-based coprolite, the sheer size and number of herbivorous dinosaurs should produce many more coprolites than are currently known. Thus, the apparent rarity of theropod coprolites may simply be due to preservational or collection bias and should be considered as equivocal evidence with respect to bone consumption by theropods. Furthermore, as with crocodiles (see above) consumed bone may simply have been degraded and digested to the point where even bone fragments are absent from faeces (which seems unlikely as discussed above), although the additional minerals should still be present which would enhance the chances of preservation.

Overall, the lack of any form of bone fragments in the stomach contents of well-preserved specimens (see above), the rarity of coprolites, and the presence of

fragments of bones from juveniles in the few coprolites suggest three possible explanations:

1. theropods selectively consumed meat and were careful to avoid any contact with bones during feeding;
2. theropods habitually consumed medium- or even large-sized bones (with or without oral processing) and these were rapidly and totally digested and thus left no traces; or
3. theropods consumed only small bones (in comparison with the predator's body size; e.g. from juvenile animals, which would also be less mineralized) and these were digested fully leaving little or no trace.

Each explanation has arguments in its favour as described above, but only the third alternative has good supporting evidence from the fossil record (stomach contents and coprolites contain the remains of juveniles, not adults). Furthermore, the first and second alternatives both conflict with available evidence – there are signs of damage on fossil bones from feeding, suggesting that tooth–bone contact was not avoided, and while admittedly negative evidence, there is no suggestion of large quantities of partly digested bones from adults known in either stomach contents or coprolites.

Discussion

The fundamental conclusion of the above review is that although the apparent extent of bone exploitation by large theropods remains low, its true extent remains unknown. However, we are still in a position to make a number of predictions about both hunting and feeding behaviours based on the available evidence, and comparisons with extant taxa, both within the extant phylogenetic bracket and with other large-bodied carnivores. Future analyses or discoveries may tip the balance towards or away from bone use, and this will favour one or the other of the following predictions which may then become open to further testing and analysis.

Feeding habits

Although their gross morphology is unlike anything alive today, one can assume that theropods hunted in a broadly similar manner to modern predators. Prey would have been pursued until it was tired and/or injured through numerous small wounds, or would have suffered a devastating injury through a single wound inflicted from an ambush (McDonald 1994).

The large size and presumed relatively slow speed of many adult dinosaurian herbivores would have made a mammalian style 'pursuit and trip' exceptionally difficult for theropods to perform, although it remains a possible tactic for animals hunting smaller ornithopods or juveniles. (A 'trip' approach would be problematic against large and heavy prey, and it would be difficult for a bipedal theropod to try and trip a quadrupedal prey species with a relatively higher instability of the former when trying to perform such a manoeuvre, and large graviportal quadrupeds would be hard to trip). In large theropods, the risk of injury (e.g. Farlow *et al.* 1995) and relatively slow maximum speeds (e.g. Hutchinson & Garcia 2002) make an ambush tactic most likely, in which a crippling bite is inflicted after a short run. Such a behavioural pattern has already been proposed by Paul (1987) and Molnar & Farlow (1990), and is consistent with skull biomechanics (Rayfield *et al.* 2001; Rayfield 2004) and the little direct evidence there is for predatory behaviour (Carpenter 2000). Although there is some evidence for frontal encounters between tyrannosaurids and ceratopsians (Happ 2008), this was probably the exception rather than the rule (see also Holtz 2008).

Both modern predators and scavengers eat quickly as they risk being displaced from the kill by larger competitors or groups of competitors. Only some solitary cats (e.g. tigers and leopards) that can remove the kill to a place of safety have the luxury of time to process the food without any form of competition (from other species or conspecifics). Even pack hunters will face competition for food from other group members despite tight social hierarchies.

This is an important point as an animal which is rapidly trying to consume as much food as possible in the shortest time is unlikely to show a delicate touch in avoiding contacting bone with its teeth (the more delicate felids still break their teeth during hunting or feeding; van Valkenburgh 2009). This is especially so with theropods, which do not have the range of motion in the jaw (especially laterally) that mammals can demonstrate, nor the specialized carnassials of most carnivorans for processing meat. Therefore, unless large amounts of meat were ordinarily available for theropods, or their overall population density was very low, it is very unlikely that theropods could have afforded to have been fussy eaters and taken extreme care to avoid biting on bone while feeding on the surrounding tissue. Bite marks, while rare, show that tooth–bone contact did occur and we do see some relatively robust bones bitten through at least on occasion (see Table 1). The objective of a carnivore or scavenger at a kill is generally to consume the maximum amount of food in the shortest possible time.

However, this assumes that theropods were bringing down prey, which represented a significant fraction of their mass (i.e. greater than half). Most adult herbivorous dinosaurs were of similar or substantially greater mass than individual theropods that probably preyed on them. In the case of diplodocoid sauropods for example, if a small pack of allosauroids killed an adult, the latter would probably weigh more than the whole group combined. In this case, there would be a very large quantity of meat available, and avoiding bone would neither be particularly difficult, nor costly in terms of time or effort. This scenario, despite its aesthetic appeal is, however, unlikely. Theropods would almost certainly have avoided healthy adults completely and instead targeted easier prey – juveniles (Farlow & Holtz 2002; see also Hummel & Clauss 2008).

While there is, of course, significant variation present in extant organisms, few modern predators make active selection of prey that is potentially difficult or dangerous to handle. Predators select for the young, the old and the weak or injured (Palmqvist *et al.* 1996), or at least their presence greatly enhances the ability of predators to hunt successfully (Temple 1987). Modern and recent mammalian predators (Krüger *et al.* 1999; Husseman *et al.* 2003; Steele 2004) and birds (Donazar & Ceballos 1989; Boshoff *et al.* 1994; Rohner & Krebs 1996) certainly prefer these kinds of sub-optimal fitness prey. Small prey of a given species is also typically preferred over larger individuals by such diverse predators as leopards (Hayward *et al.* 2006), hunting dogs (Fuller & Kat 1993), bluefish (Scharf *et al.* 1998) and several invertebrates (Barbeau & Scheibling 1994) or simply small prey in general (e.g. Webb *et al.* 1991; Gotmark & Post 1996; Turesson *et al.* 2002).

The huge infant mortality seen in almost all vertebrate taxa (as described above) would also suggest that this is indeed normal for just about all predator/prey systems that have been studied. The requirements of growth in juveniles and their inexperience at foraging necessitates that they forage for longer periods (Carey & Moore 1986; Marchetti & Price 1989; Weathers & Sullivan 1989; Arenz & Leger 2000) and it has been shown in a variety of vertebrate taxa that foraging makes individuals more vulnerable to predation (Carey & Moore 1986; Krause & Godin 1996), and that predators will preferentially attack foraging or unwary prey (Krause & Godin 1996), thus making juveniles a preferred target of predators for multiple overlapping reasons. Finally, learned anti-predator responses are common in vertebrates after predatory encounters (Fuiman 1993; Kelley & Magurran 2003; Quinn & Cresswell 2004), which highlights the vulnerability of juveniles which are naive with respect to predators.

(Note that the citations above are limited by the nature of laboratory studies, which tend to focus on small species and especially fish, and wild studies that tend to focus on birds).

Active predators are vulnerable to starvation following an injury and will not pursue a prey individual (or species) that is easily capable of escaping the predator or causing it serious injury if an easier alternative is available. Given the large size of adult dinosaurs and their apparent longevity, there may have been a strong numerical and therefore biomass bias towards healthy adults in a dinosaurian population (Paul 1994; Erickson *et al.* 2001; Hummel & Clauss 2008). However, specimens of young dinosaurs are notably rare except in mass death assemblages (Richmond 1965). This is not likely to be a size or collection bias as many large dinosaur-bearing formations are replete with bones of small tetrapods (pterosaurs, crocodilians, squamates, etc.), yet juvenile remains are still rare. Furthermore, although juvenile bones are less mineralized and therefore less likely to fossilize, some very young dinosaurs and embryos are known from nests (Carpenter 1999) suggesting that their rarity cannot entirely be explained by this factor and that they may genuinely be rare. Other biases may exist (juveniles may avoid areas favourable to preservation or suffer from destruction or damage during sorting) and ultimately these may be hard, if not impossible, to separate from selective feeding by theropods (and clearly both may be important factors).

The obvious conclusion is that like vertebrates today, many juvenile dinosaurs, without the protection of large size, adults, herds and/or experience, were especially vulnerable to predation by theropods. If we assume that juvenile dinosaurs were vulnerable in the same way for the same reason, this may explain the apparent crèche behaviour of some dinosaur species (Zhao *et al.* 2007; Varricchio *et al.* 2008) even where adults are thought to be solitary (Mathews *et al.* 2009) as a way of providing the natural protection of a group, reducing the change of a given individual being attacked and providing additional animals to look for danger.

Dinosaurs tended to lay eggs in large numbers relative to their body size (Janis & Carrano 1992; Paul 1994) and thus produced large numbers of offspring, yet the adult populations of many dinosaurs would have been limited due to their large size (e.g. Burness *et al.* 2001), indicating very high rates of infant mortality. Modern tetrapods also reflect this pattern of population structure with large numbers of very young juveniles (i.e. between 1 and 2 years of age), low numbers of more mature juveniles and subadults and then a large standing population of adults. The juvenile part of this population is, of course, transient

as they age and become subadults and adults and are replaced by new births. The subadult population is low and thus despite the high number of births, few juveniles make it to subadulthood or adulthood – juveniles obviously suffer from very high mortality rates, and this is especially as a result of predation (e.g. see Anders *et al.* 1997). This pattern has been shown in animals as diverse as lions (Creel & Creel 1997), passerines (Sullivan 1989), various African herbivores (Galliard *et al.* 1998), seals (Baker & Thompson 2007), and crocodiles (Webb *et al.* 2000) and so it can be concluded that theropods habitually ate juvenile dinosaurs and that this is at least partly reflected in the fossil record. It has already been noted that at least some herbivores suffered very high juvenile mortality as deduced from their population structure of mass mortality events (e.g. Varricchio *et al.* 2008 and references therein).

In those K-selected taxa (e.g. elephants) with a low birth rate, long development times and a high investment in offspring (typically large-bodied taxa) juvenile mortality is obviously lower. However, dinosaurs were both large and r-selected as egg layers (Janis & Carrano 1992; Paul 1994) and parental care would have been limited beyond the nest (Horner 2002). Certainly some dinosaurs hatched precocial young (Horner 2002). Thus, dinosaurs, despite the large size of many species, would have contributed very large numbers of juveniles to the population providing prey for populations of very large theropods at a rate beyond that seen in comparable faunas consisting of large mammals. Indeed, r-strategy in combination with large adult size might have been one of the secrets of the success of dinosaurs (Janis & Carrano 1992).

As juveniles had both smaller bones (in terms of absolute size) and these were probably weaker (less ossified, and not fused at, e.g. the sacrum and neural arches) their bones would have been far easier for theropods to both bite and consume. They would also have been easier to digest, and probably left less traces in the stomach contents or coprolites due to the lower mineral content and lower absolute volume of bone, and they would have been easier to break up during feeding than large adult bones. Therefore, between preferential feeding on juveniles and their increased ability to both consume and digest bones of juveniles, theropods were perhaps capable of preventing the vast majority of juvenile dinosaurs from entering in the fossil record just as is seen in modern vertebrates. This may also explain the apparent unwillingness of theropods to exploit large bones of killed or scavenged adult carcasses: there would have been sufficient bone in their diets already from juveniles consumed whole, and the opportunity to feed on large adults may have generally been a relatively rare event.

The little direct evidence there is from stomach or coprolite contents is consistent with this idea. The small theropods *Compsognathus* and *Sinosauropteryx* are known with remains of much smaller prey items in their stomach region, which were obviously swallowed whole, including the bones. Concerning large theropods, remains of a juvenile *Iguanodon* have been found in the rib cage of the type specimen of *Baryonyx* (Charig & Milner 1997). The fact that bones of all regions of the skeleton were found (see Charig & Milner 1997, appendix B) indicates that most of the prey was probably swallowed whole. Likewise, Varricchio (2001) reported remains of a juvenile hadrosaur as stomach contents of a *Daspletosaurus*, and bone remains of juvenile dinosaurs were also found in a coprolite attributed to *Tyrannosaurus* (Chin *et al.* 1998). Thus, there is some direct evidence that small or juvenile animals might have constituted an important part of a theropod's diet. If these smaller prey items were swallowed whole or in larger chunks, little tooth-inflicted damage to bone would be expected. This does not necessarily mean that bone might not have been physically damaged prior to digestion, as there is some evidence for the presence of a muscular gizzard in theropods (Varricchio 2001), and stomach stones were reported in at least one large theropod dinosaur (Mateus 1998).

Smaller theropods (or juveniles of large species) would have been unable to kill large adult prey species but, by scavenging on the kills made by larger predators, would presumably attempt to exploit any available nutrition and thus leave traces of their activities on fossil bones (as with Fiorillo 1991). As previously suggested, juvenile theropods might have had diets completely different from those of adults and could have fed on even smaller, non-dinosaurian prey or even insects as a form of niche partitioning such as is practiced by crocodiles (Tucker *et al.* 1996). However, small bones could be consumed whole and small individuals could be more delicate in their feeding actions and may simply have lacked the jaw power, or tooth strength to tackle bones and so no marks would be left (and small animals would simply not be capable of tackling large bones). Most, if not all, traces are attributed to larger (and presumably) adult theropods, but no analysis has yet attempted to correlate bone marks with likely trace maker size.

This does not rule out attacks by theropods on large adult animals. There are at least some records of these attacks having occurred (e.g. Carpenter 2000; Happ 2008), although we maintain that these would be rare. These attacks could have been made by young and inexperienced theropods themselves and may not be representative of 'normal' adult predation behaviour. This is supported by the fact that both of these

reported instances were obviously unsuccessful, as the bite marks show signs of healing, despite the injuries received by the victims. The very fact that unsuccessful attacks occur on adults may thus reflect that adults were a difficult animal to attack relative to juveniles (though age or illness would have made even large adults a target for predators).

Future research

While this paper is intended as a review of the available evidence and the theoretical implications of theropod feeding behaviour, the possibilities for testing these ideas should at least be discussed here. Testing the possible extent of theropod bone use is difficult – as described above there are numerous plausible factors or combinations of factors that can explain both heavy and light bone exploitation by theropods based on the limited evidence available. The complete destruction of bone through oral processing and stomach acids may mean that theropods habitually exploited some bone but left little or no trace of having done so. Equally, however, the lack or traces may result from a simple lack of use, or from theropods lacking access to the majority of skeletons recovered if they were buried before scavenging could occur.

As mentioned above, a possible test of the idea that theropods consumed but not necessarily broke bone prior to consumption (although possibly through the use of a gastric mill after ingestion) might be a careful survey of unidentifiable bone fragments found in association with skeletal remains of theropod dinosaurs, and including careful searches for acid-etched bone when excavating or preparing theropod dinosaur specimens. Even in less-than-perfect conditions, it might thus be possible to tell just a fragmented bone of the specimen at hand from a possible partially digested bone by looking for traces of chemical decomposition due to stomach acids (e.g. Charig & Milner 1997; Varricchio 2001). Further study of signs of stomach acids on bone in recent predators would be very helpful in order to provide a series of comparisons.

Another, related test would be to determine if theropods exploited only small bones, i.e. if they consumed those small enough to swallow with minimal or no oral processing. This is difficult to determine as few fossil specimens would be suitable for analysis, and maximal bone size to be swallowed whole, of course, depends on the size of the predator. In most cases, it would be virtually impossible to tell the absence of small bones due to predation from the absence due to taphonomic processes, such as hydraulic sorting or preferential preservation of large elements. Complete, articulated specimens that were presumably buried soon after death and not subjected to any form of feeding must be excluded. Those animals (apparently) buried as a result of flooding or similar 'instant' mortality situations must also be disregarded – completely disarticulated specimens or those with much missing cannot be assessed without the assumption that small missing parts are a result of taphonomy or mechanical action on the carcass before burial/preservation (and or subsequent erosion). Poorly preserved fossil bone will also be hard to assess for possible damage. Mass mortality graves are also unsuitable as these would either have not been available for predators to feed on or, if they remained exposed before burial, have supplied so much meat that bones could be avoided if desired. Suitable specimens are those that either show obvious damage or are relatively complete, articulated and well preserved. The absence of evidence is, however, not evidence of absence. Small bones might be consumed without any form of oral processing, but also their small size would make them prone to disarticulation during scavenging by smaller theropods, or they might not preserve at all even if they were present. Even modern herbivores and omnivores (including small rodents) occasionally exploit bone for mineral content and leave observable damage.

Even allowing for the conditions of death and burial, possible damage through mechanical action, erosion and quality of preservation (given the very large number bones available), if bones were regularly exploited by theropods of any size, there would be far more evidence of damage to them and large bones present in stomach contents, or evidence of adult bones in coprolites, and perhaps far more damaged theropod teeth known. There are large numbers of tooth-damaged bones known from the mammalian fossil record; so, despite these heavy constraints, evidence should be available if dinosaur bones were regularly used (Fiorillo 1991) and would be significantly higher than the current typical figures of around 5% that are observed (Jacobsen 1998).

However, analysis of multiple large bone beds might still reveal patterns of bone use by theropods beyond the base counts of bone damage by Fiorillo (1991) and others. Bones can be graded by absolute size with the assumption that smaller bones will be exploited more easily and therefore more often than larger ones. Despite the possible taphonomic bias against smaller bones, if theropods were actively consuming bones whole, this should be detectable by careful statistical analyses of several localities. Environments suitable for preserving small tetrapods and fragile bones such as skulls and gastralia should not be biased against ribs and tarsals; so, if certain elements are consistently underrepresented in the samples, their

preferential ingestion by predators would be a probable explanation. Multitaxon bonebeds might be especially suited for such an analysis, as they usually represent attritional mortality rather than catastrophic death events and thus presumably give a variety of predators more opportunity to feed on the carcasses.

The theropods themselves might also provide additional data. Both shed teeth and those still in place in the jaws can be examined for wear, breakages and microwear that may indicate their use on bones (as seen in carnivorans – van Valkenburgh 2009). In the jaws especially, if theropods were attempting to break bones, they would use the posterior teeth most often as this provides the best concentration of force during biting and thus these teeth should most often show breaks or damage.

Conclusions

The current evidence on bone consumption by theropods is equivocal and no one available hypothesis can be especially favoured. Previous analyses of tooth-marked bones strongly indicate that bone crushing and break-up was much less common in theropods than it is in modern mammalian and crocodilian predators. However, preferential consumption of small and/or juvenile prey and ingestion and subsequent digestion of whole bones is consistent with the available evidence and might explain the scarcity of juvenile dinosaurs in the fossil record. Although this idea is supported by the little direct evidence there is from stomach and coprolite contents, it should be noted that it is currently largely based on negative evidence. Further detailed analysis of both theropod feeding mechanics and a review of possibly exploited skeletons (especially of non-adults) might yet shed light on how theropods fed on available carcasses. Extensive work is already being carried out on the former by several research groups worldwide with impressive results, and on the basis of our interpretations here we would appeal to researchers to be vigilant when preparing new theropod finds in looking for possible stomach contents. Analyses of existing collections from dinosaur bearing horizons combined with studies of the effects of acid on bones in extant taxa can provide corroborating evidence for the ideas proposed here and so, while the conclusions of this paper are somewhat equivocal, there is a strong foundation for further work that can elucidate much about theropod feeding and digestion.

It must be considered a strong probability that although living biomass of dinosaurs was biased towards large adults, juvenile animals may have been systematically the primary prey of choice for the

Fig. 4. A complete theropod tooth (*Tyrannosaurus rex*) showing the crown and large root. Total length of the tooth is 300 mm, of which approximately 100 mm is crown and 200 mm is root. The relative proportions are typical of theropod teeth.

majority of theropods (see Hummel & Clauss 2008). This is backed up by both the fossil record of juvenile dinosaurs and the population structure of modern tetrapods and the behaviour of predators. This factor should be considered in subsequent analyses of dinosaurian population ecology and is an important, and so far ignored, component of hypothesized theropod hunting and feeding behaviour.

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