



Ontogenetic dietary shifts in *Deinonychus antirrhopus* (Theropoda; Dromaeosauridae): Insights into the ecology and social behavior of raptorial dinosaurs through stable isotope analysis

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ABSTRACT

The image of the highly intelligent, pack-hunting raptor has become engrained in scientific literature and popular works alike. First proposed to explain the relatively common co-occurrence of the large-bodied iguanodontian *Tenontosaurus tilletti* and the wolf-sized *Deinonychus antirrhopus* from the Lower Cretaceous of North America, a canid-like social hunting structure has become the standard depiction of dromaeosaurs in popular works over the last three decades. This reconstruction is, however, problematic largely due to the fact that highly coordinated hunting strategies are rarely observed in modern archosaurs. This has led to the alternative hypothesis that *D. antirrhopus* was more analogous to agonistic reptilian carnivores, like the Komodo dragon (*Varanus komodoensis*). Among the many differences between these two analogs is how social and asocial organisms rear their young, producing a diagnostic pattern based on the presence or absence of ontogenetic dietary changes. In order to test for dietary changes through growth, stable carbon and oxygen isotope ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) analysis was performed on tooth carbonate from small (< 4.5 mm crown height) and large (> 9 mm crown height) *D. antirrhopus* specimens from two microsites from the Lower Cretaceous Cloverly (Montana) and Antlers (Oklahoma) formations. Teeth from goniopholidid crocodylians and *Tenontosaurus tilletti* from the Cloverly Formation were also tested for comparison. The results show that the Cloverly goniopholidids, like their modern counterparts, went through a distinct transition in diet as they grew. The smallest teeth were the relatively most enriched in ^{13}C (mean = -9.32‰ ; $n = 5$), the medium-sized teeth were the most-depleted in ^{13}C (mean = -10.56‰ ; $n = 5$), and the largest teeth were intermediate (mean = -10.12‰ ; $n = 6$). These factors are characteristic of the dietary shifts seen in modern asocial reptiles. *D. antirrhopus* showed this same pattern in tooth samples collected from both rock units, with small teeth being the more enriched in ^{13}C (mean = -8.99‰ ; $n = 10$) and the large teeth being more depleted in ^{13}C (mean = -10.38‰ ; $n = 10$). These differences suggest that juvenile and adult *D. antirrhopus* from both formations likely consumed different prey. Hypothetical food sources, such as *T. tilletti*, are close to the ^{13}C isotopic signal of adult *D. antirrhopus*, consistent with the hypothesized trophic relationship (predator-prey) between these two species. Juvenile *D. antirrhopus* had a diet more enriched in ^{13}C , likely composed of smaller-bodied, but trophically-higher species. Taken together, these data add to the growing evidence that *D. antirrhopus* was not a complex social hunter by modern mammalian standards.

1. Introduction

The perception of the pack-hunting raptor is one of the most prevalent speculative examples of social behavior in dinosaurs. This hypothesis was first proposed by Ostrom (1969), to explain the occurrence of multiple individuals of the dromaeosaur *Deinonychus antirrhopus* mixed with the larger hypothetical prey species, *Tenon-*

tosaurus tilletti in the YPM 64–75 quarry of the Lower Cretaceous Cloverly Formation of Montana. Although a trophic relationship between these two species seemed certain, Ostrom (1969, 1986) could not envision a single *D. antirrhopus*, weighing approximately 70 to 100 kg (Seebacher, 2001), being capable of dispatching a one-ton *Tenontosaurus* alone (Ostrom, 1969; Forster, 1984; Maxwell and Ostrom, 1995; Roach and Brinkman, 2007). Based on the taphonomic association of at least three individuals at YPM

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64–75, Ostrom proposed that *D. antirrhopus* was a pack hunter, similar to modern canids. Since then, dozens of sites have been discovered with associated *T. tilletti* and *D. antirrhopus* remains in both the Cloverly (Maxwell and Ostrom, 1995) and the contemporaneous Antlers Formations of Oklahoma (Brinkman et al., 1998). The prevalence of this association strongly suggests that *T. tilletti* was a chief food source for *D. antirrhopus* (Ostrom, 1969; Forster, 1984; Maxwell and Ostrom, 1995); however, the dynamics of *D. antirrhopus* hunting capabilities are still debated.

Ostrom's (1969, 1986) suggestion that *D. antirrhopus* had a canid-like pack-hunting strategy is rather intuitive. *D. antirrhopus* was morphologically similar to canids in some of its predatory adaptations; such as its cursorial, elongate limbs, specialized for speed and agility (Ostrom, 1969). Further, *D. antirrhopus* possessed a relatively large brain by dinosaurian standards (Balanoff et al., 2013), a necessary prerequisite for handling the cognitive challenges associated with complex social roles. Even Ostrom's (1969) original argument for pack hunting based on the *Deinonychus-Tenontosaurus* size differences is highly reasonable, as this predator/prey size disparity is not unlike that of many wild canids, including the African Wild Dog *Lycaon pictus*. These 20 to 25 kg predators work in small to medium-sized groups to capture and dispatch prey up to 200 kg in size, with preferred larger prey within the 120–140 kg range (Hayward et al., 2006). The social hunting strategies of this species are highly efficient, with a success rate of up to 85% in some populations, where group size is correlated with an increased success rate, shorter hunts, increased prey size, and increased prey yield. In addition to benefits related to hunting, larger groups increase the ability of the pack to steal carcasses from other predators as well as provide greater protection for their pups (Creel and Creel, 1995).

The most substantial refutation of the *D. antirrhopus* pack-hunting hypothesis came from Roach and Brinkman (2007), who upon re-evaluation of YPM 64–75, found evidence that suggested at least one of the *D. antirrhopus* was killed by conspecifics. The authors go on to note that cooperative behavior in modern archosaurs is relatively rare and that a more suitable analog should be used to approximate *D. antirrhopus* behavior. Indeed, modern crocodylians show only the most rudimentary forms of cooperation during hunting (Pooley and Ross, 1989). In birds, group coordination is more common, yet pack hunting of large-bodied prey is almost non-existent. In the few notable species that do practice cooperative hunting, close kinship bonds and extreme environmental conditions may contribute to this atypical behavior (McIlhenny, 1939; Buckley, 1999; Roach and Brinkman, 2007). Given these differences, Roach and Brinkman (2007) hypothesized a lifestyle for *D. antirrhopus* more similar to that of the modern Komodo dragon *Varanus komodoensis*, a highly asocial species capable of hunting prey much larger than itself. Although multiple individuals congregating around a kill is common in this species, a strict hierarchical feeding structure is followed based largely on size. Smaller lizards must wait on the periphery, while the youngest individuals are excluded altogether and are forced to rely on a different food source (Auffenberg, 1981; Diamond, 1992). It is this pattern between the diet of young and old individuals of agonistic species that we believe holds the key to understanding *D. antirrhopus* social behavior.

Such ontogenetic dietary changes are widely documented in modern animals and are especially common in organisms that are gape-dependent feeders (Werner and Gilliam, 1984). For example, juvenile crocodylians are incapable of killing the larger prey species favored by adults, and scavenging is often too dangerous because older individuals will cannibalize the young (Grigg and Kirshner, 2015). Instead, young crocodylians go through a transition during ontogeny, initially consuming mostly invertebrates and gradually replacing this with a diet of fish, followed occasionally by an addi-

tional switch to large-bodied terrestrial or semiaquatic vertebrates (Blomberg, 1976; Wallace and Leslie, 2008). Conversely, pack-hunting social mammals do not show such diversity in diet through ontogeny. In these animals, such as the grey wolf (*Canis lupus*), the protection of the pack allows all members to feed upon similarly-sized prey items (Bryan et al., 2006). Although small deviations likely occur, the bulk diet of juveniles can be hypothesized to derive largely from the diet of the rest of the group. This can be visualized in ontogenetic studies of dietary-derived carbon isotopes in the social bottlenose dolphin *Tursiops truncatus*, in which, aside from a small enrichment while nursing, there is minimal variation throughout life (Knoff et al., 2008). Unfortunately, due to the unique lifestyle of marine mammals, many of the isotopic studies of diet and growth in social species are unsuitable for comparison with extinct terrestrial dinosaurs.

Isotopic studies of ontogenetic differences in birds are largely correlated with the parental feeding behavior and as a result are better suited for comparison. In some marine seabirds, such as some procellariiforms, adults feed their young a different diet than their own, leading to a unique isotopic dietary signal in the juveniles; however this observation is based on relatively small differences and is not seen in all seabirds (Kojadinovic et al., 2008). It should also be noted that this phase of life is relatively short-lived in modern birds, as most altricial young grow rapidly (Varricchio and Jackson, 2016). Conversely, non-avian dinosaurs likely had multi-year growth rates, increasing the potential for differing dietary signals with maturity. Even in fast-growing birds, however, these dietary differences can extend beyond the nestling phase and can be directly attributed to the hunting behavior differences between age classes. For example, the white-tailed eagle, *Haliaeetus albicilla* shows marked differences in the isotopic composition of immature, full size individuals as compared with mature adults. The difference is likely attributable to the better hunting experience, range defense, and dietary diversity in mature birds (Soutullo et al., 2006).

By investigating these ontogenetic dietary patterns, we believe a rough approximation of social behavior can be postulated for medium to large-bodied carnivorous vertebrates. In this framework, the canid-style pack hunting hypothesis of Ostrom (1969, 1986) is represented by an organism with a dietary pattern that is relatively unchanging between juveniles and adults, while the Komodo dragon-style asocial hypothesis of Roach and Brinkman (2007) is found in a species that changes abruptly between small and large individuals. Here, we use tooth carbonate stable isotope analysis as a proxy for diet to test for ontogenetic niche changes in *D. antirrhopus* teeth derived from two separate microsites in the Antlers Formation of Oklahoma and the Cloverly Formation of Montana.

2. Stable isotopes

Deinonychus antirrhopus teeth, like other vertebrates, are composed of a matrix of organic molecules surrounded by crystals made of bioapatite [$\text{Ca}_5(\text{PO}_4)_3(\text{OH}, \text{CO}_3)$] and adsorbed inclusions (e.g., Pb, Sr, Hg). Regarding paleoecology, the most commonly analyzed components of vertebrate teeth are carbon and oxygen isotopes, usually derived from carbonate or phosphate in the enamel (e.g., Fricke et al., 2008; Fricke et al., 2009; Fricke et al., 2011; Suarez et al., 2012). Carbonate (CO_3) is fairly abundant in teeth, readily substituting for the phosphate and hydroxyl in the bioapatite matrix. The carbon comes largely from an animal's diet, which can vary isotopically based on the type of vegetation consumed at the base of the food web. At each trophic level, the $\delta^{13}\text{C}$ ratio becomes more fractionated, usually enriching in the heavy isotope. In this way, animals with different $\delta^{13}\text{C}$ are likely sourcing their carbon from a different plant base or are feeding at different trophic levels. Oxygen isotopes in bioapatite are derived from in-

gested and atmospheric H₂O. Unlike carbon, oxygen isotopes reveal more about environmental preference and physiology, controlled by both kinetic and equilibrium reactions with body temperature, water source, climate, and geography dictating the ultimate $\delta^{18}\text{O}$ ratio. Because terrestrial animals derive most of their tissue oxygen from ingested water, the factors controlling the abundance of ^{18}O in local water sources are of primary importance (Koch, 2007).

3. Geologic background

Deinonychus antirrhopus specimens used in this study were recovered from two microsites, V706 and V1075, collected by field parties from the Sam Noble Oklahoma Museum of Natural History. V706 is in the Antlers Formation of SE Atoka County, Oklahoma. This microsite was found approximately 1.5 m beneath a layer containing abundant dinosaur remains, including the first definitive *D. antirrhopus* fossils found outside of Montana and Wyoming (Brinkman et al., 1998). The microsite was preserved in a mottled and nodule-rich mudstone, interpreted as an overbank fluvial lag. Geographically, the Antlers Formation represents a low-lying floodplain near the eastern shore of the encroaching gulf arm of the Western Interior Seaway. To date, thousands of specimens have been identified from this site, representing a highly diverse fauna, including freshwater fishes, sharks, amphibians, lizards, crocodylians, mammals, and dinosaurs (Cifelli et al., 1997). In total, 36 diagnostic *D. antirrhopus* teeth were recovered from this bonebed. V1075 is located in Ostrom's (1970) unit VII of the Cloverly Formation, roughly 36 km ESE of Pryor, Bighorn County, Montana. Unit VII is composed largely of sloped, colored mudstones and interbedded channel sandstones. Environmentally, unit VII represents a tropical-semitropical environment at the edge of the Arctic arm of the Western Interior Seaway (Nydam and Cifelli, 2002). Like the assemblage from the Antlers Formation, the Cloverly fauna is known from a robust fossil record. In total, 34 complete teeth were identified as *D. antirrhopus* from V1075.

4. Methods

Teeth from two roughly contemporaneous (Aptian-Albian, Lower Cretaceous) OMNH microsites, V706 from the Antlers Formation of southeastern Oklahoma and V1075 from the Cloverly Formation of southcentral Montana, were sorted for complete and diagnostic *D. antirrhopus* teeth. These teeth were identified based on their (1) lateral compression, (2) greatly enlarged posterior denticles (as compared to the anterior denticles), and (3) apically-curved denticles on the posterior margin. Specimens were measured using photographs and ImageJ software (Schneider et al., 2012) for crown height, basal length, and basal width. Between the populations, crown height was found to be significantly different using a *t*-test ($t = -2.97$; $p = .004$), with teeth from the Antlers Formation being larger (9.42 mm) on average than those from the Cloverly Formation (6.73 mm). Using images of *D. antirrhopus* and the closely-related *Velociraptor mongoliensis* from Ostrom (1969) and Norell et al. (2006), we determined that the tallest erupted tooth in a specimen is rarely more than 50% the height difference of the smallest fully-erupted tooth. The degree of crown curvature above the jaw was used as a proxy for tooth development (Table 1). Based on these results, a representative sample of 10 teeth was chosen composed of specimens falling equally into two bins, < 4.5 mm and > 9 mm in crown height (Fig. 1; Table 2). These size bins were chosen to ensure equal-sized samples based on the limited number of diagnostic small teeth. Though a modest sample size by standards of most isotopic analyses, the 10 samples from each site represents a destruction of 29% (V1075) and 28% (V706) of the identified *D. antirrhopus* material from the individual microsites. The specimens were cast prior to destructive sampling. (See Tables 3 and 4.)

Table 1

Relative crown height difference for fully-erupted upper and lower teeth in two velociraptorine dinosaurs. Data from Norell et al. (2006) and Ostrom (1970).

Genus	Velociraptor			Deinonychus
Specimen #	AMNH FR 6516	IGM 100/25	IGM 100/982	YPM 5205
Upper: Lower tooth count	5:5	5:1	6:0	7:3
Max upper jaw difference	35.56%	34.71%	29.21%	43.01%
Max lower jaw difference	24.19%	n/a	n/a	42.07%
Max upper and lower jaw difference	48.15%	34.71%	29.21%	49.02%

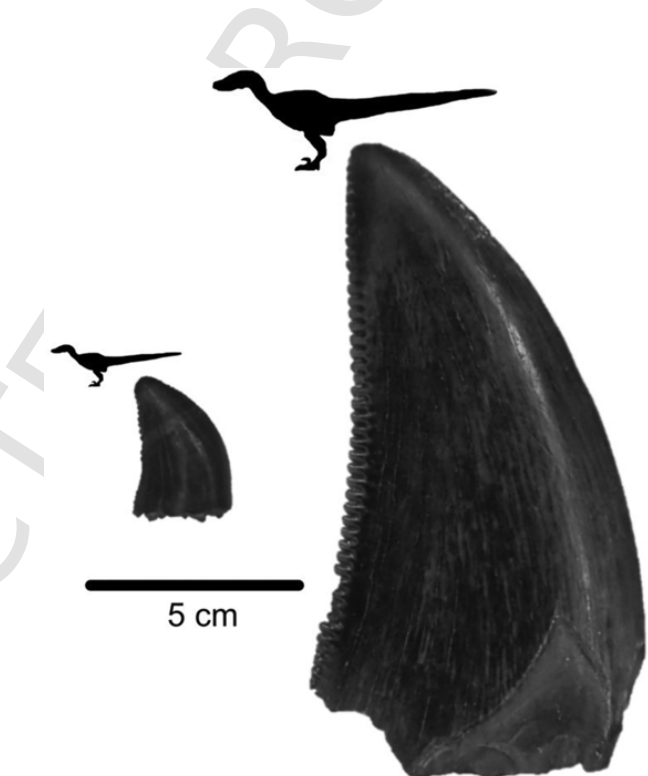


Fig. 1. two representative (left, OMNH 34031; right, OMNH 34115) *Deinonychus antirrhopus* teeth from V706 in the Antlers Formation.

Comparisons were made to a similar sample of goniopholidid teeth from V1075 (three bins of < 5 mm, 5.1–10 mm, and > 10.1 mm; V706 did not have a represented sample of teeth in the three tooth height categories). The size bins were chosen to closely approximate the two bins used for the *D. antirrhopus* sample and to best represent the sampled population. Goniopholidid teeth from V1075 were substantially more abundant than those of *D. antirrhopus* which allowed for the inclusion of a middle size bin and is comparable to modern isotopic studies (see Radloff et al., 2012 discussed below). Further, diversity of goniopholidids from the Cloverly Formation is still unknown making it difficult to constrain this sample based on intraspecific tooth heterogeneity as was done for *D. antirrhopus*. However, these neognathosuchians presumably went through ontogenetic dietary shifts similar to modern crocodylians, thus making them the best available control for the isotopic analysis.

For comparison of carbon isotope values in a potential prey species (*Tenontosaurus tilletti*), two specimens (OMNH 10144 and 10,132) were sampled for enamel carbonate in two teeth each.

Table 2

Full dataset summary statistics for *D. antirrhopus* teeth from two localities in different rock formations vs. the sampled data set for isotopic analysis (small <4.5 mm and large >9 mm).

Formation	Data set	n	Mean Crown height (cm)	SD	Min – Max (cm)
Antlers	All V706	36	0.942	0.436	0.170–1.933
	Small	6	0.287	0.091	0.170–0.407
	Large	20	1.258	0.265	0.972–1.933
	Sampled	10	0.839	0.607	0.192–1.933
	Small	5	0.310	0.796	0.192–0.407
	Large	5	1.368	0.353	0.990–1.933
Cloverly	All V1075	34	0.673	0.308	0.235–1.292
	Small	13	0.371	0.074	0.235–0.486
	Large	9	1.087	0.146	0.924–1.292
	Sampled	10	0.701	0.396	0.304–1.277
	Small	5	0.336	0.029	0.304–0.372
	Large	5	1.067	0.139	0.924–1.277

Table 3

Measurements for Cretaceous goniopholidid teeth from V1075, Cloverly Formation, Montana.

ID (OMNH)	Height (cm)	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
SC1	0.3	–11.09	–12.38
SC5	0.3	–8.18	–13.1
SC2	0.4	–7.92	–11.45
SC3	0.4	–10.23	–13.83
SC4	0.4	–9.18	–13.42
61317A	0.7	–10.25	–12.56
61299B	0.8	–11.64	–14.16
61317C	0.8	–10.33	–13.63
61317B	0.9	–11.86	–12.84
61297B	1	–11.92	–14.63
61299A	1.3	–11.39	–13.31
BC2	1.3	–10.14	–13.46
61297A	1.4	–8.56	–9.84
61,298	1.5	–11.16	–13.22
BC1	1.6	–8.8	–12.48
60,442	3.1	–10.68	–14.08

OMNH 10144 is one of the smallest specimens of *T. tilletti* known. This specimen is actually composed of at least four similarly-sized individuals that were found together in association with the much larger OMNH 10132 from the OMNH's V184 bonebed in the Cloverly Formation of Big Horn County, Montana (Forster, 1990). Two teeth from each specimen (OMNH 10144 and 10,132) were separated into approximately equal occlusal and basal halves, representing assumed different times of tooth development. Tooth carbonate samples (the complete tooth for the goniopholidid and *D. antirrhopus*, half of the tooth for *T. tilletti*) were treated following a modified technique of Koch et al. (Koch et al., 1997; see Frederickson et al., 2018) and measured following the exact procedure of Frederickson et al. (2018). All specimen stable isotope values are reported relative to VPDB (Vienna Pee Dee Belemnite), with comparisons made for all three species using non-parametric statistical tests (Mann-Whitney or Kruskal-Wallis) in the software package PAST3 (Hammer et al., 2008).

5. Results

Cretaceous goniopholidid crocodylians, like their modern counterparts, show a distinct transition in diet with growth (Fig. 2). Teeth smaller than 5 mm in height are relatively enriched in $\delta^{13}\text{C}$ (mean = -9.32 , SD = 1.35, $n = 5$), with only one specimen having a value that falls within the range of the next size class. The medium-sized teeth (5.1–10 mm in height) are more depleted (mean = -11.20 , SD = 0.84, $n = 5$) and show lower variance than the other two size classes ($V = 0.701$). The largest class (10.1+ mm crown height, $n = 6$) is intermediate in ^{13}C values between the previous two classes (mean = -10.12 , SD = 1.20). Comparison of all three size classes is just above the statistical threshold ($p = .054$), though individual comparison of the values between the smallest and medium-sized classes are significantly different ($p = .04$). Unsurprisingly, measurements of $\delta^{18}\text{O}$ showed less difference between groups ($p = .41$), though the middle size-class are on average slightly more depleted in $\delta^{18}\text{O}$ (mean = -13.56 , SD = 0.870) than the small or large classes (mean = -12.84 , -12.73 and SD = 0.939, 1.51). Since we assume these animals were living in close proximity and likely in aquatic to near-aquatic environments, the small differences in $\delta^{18}\text{O}$ will not be discussed further.

Deinonychus antirrhopus teeth show a significant difference between size classes in the carbon isotopic data for the Antlers Formation ($p = .02$) (large mean = -10.96% , SD = 0.572; small mean = -9.38% , SD = 0.814). Cloverly Formation size-classes are not statistically different ($p = .40$) (large mean = -9.80% , SD = 1.74; small mean = -8.6% , SD = 1.244), but do show a similar pattern as seen in the Antlers Formation specimens, with juveniles more enriched on average than the adults (Fig. 2). As in the Antlers Formation, small teeth from the Cloverly do not generally have $\delta^{13}\text{C}$ values below -10% . Adults can far exceed this depletion, with individuals reaching -11.45 and -11.71% in the Antlers and Cloverly, respectively. As in the goniopholidids, $\delta^{18}\text{O}$ in *D. antirrhopus* show no significant difference between size classes in either the Antlers ($p = .53$; large mean = -6.95% , SD = 3.245; small mean = -6.30% , SD = 0.761) or Cloverly formation ($p = .67$; large mean = -12.52% , SD = 0.564; small mean = -11.32% , SD = 2.787), implying a similar source of ingested water for both size classes. The difference in $\delta^{18}\text{O}$ between the Antlers and Cloverly samples may represent a latitudinal gradient, as the Cloverly Formation is about 10 to 15° of latitude north of the Antlers Formation (Werning, 2012), or the difference could represent a more depleted source of water (such as montane meltwater) for the more northern theropods than the southern ones.

The Cloverly and Antlers formations' dominant terrestrial herbivore is *Tenontosaurus tilletti*. Isotopic studies of tenontosaurus teeth from the Cloverly Formation are relatively depleted in ^{13}C (mean = -12.97% ; $n = 8$; SD = 0.670) as compared to the predatory taxa. Unlike goniopholidids and *D. antirrhopus*, young *T. tilletti* show no statistical difference from their adult counterparts (Fig. 3; $p = .19$; adult mean = -12.69% , SD = 0.34, $n = 4$; yearling mean = -13.25% , SD = 0.85, $n = 4$). This result, however, is based on teeth from only two individuals and should be viewed with restraint. Predictably, the *T. tilletti* isotope levels are significantly lower than those recorded for the predatory taxa from the Cloverly ($p < .01$). In both the goniopholidids and *D. antirrhopus* the presumed adult teeth are closer to the relatively depleted signature of *T. tilletti* teeth than their conspecific juveniles. However, caution should be taken while making direct comparisons as the tenontosaurus come from a different bonebed than the goniopholidids and theropods tested here.

Table 4
Measurements for *D. antirrhopus* teeth used in this experiment.

ID (OMNH)	Bonebed	Class	Length (cm)	Width (cm)	Height (cm)	Gum angle	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
34972	706	Small	0.137	0.085	0.192	54.74	-9.91	-6.66
32427	706	Small	0.146	0.088	0.285	64.63	-10.28	-5.85
34032	706	Small	0.19	0.093	0.32	68.43	-8.15	-6.36
34033	706	Small	0.216	0.086	0.346	64.99	-9.16	-5.33
34879	706	Small	0.25	0.102	0.407	54.71	-9.38	-7.32
34205	706	Large	0.466	0.235	0.99	59.68	-11.45	-6.4
52711	706	Large	0.656	0.314	1.198	50.9	-11.34	-5.38
49412	706	Large	0.735	0.352	1.304	52.4	-10.86	-5.19
34115	706	Large	0.742	0.381	1.413	59.2	-10.02	-5.1
17709	706	Large	0.913	0.446	1.933	62.44	-11.14	-12.68
69433	1075	Small	0.19	0.076	0.304	61.7	-6.94	-12.45
69431	1075	Small	0.232	0.087	0.312	64.6	-7.69	-13.05
69432	1075	Small	0.232	0.089	0.336	57.8	-9.73	-6.36
69430	1075	Small	0.259	0.1	0.356	61.8	-9	-12.43
69434	1075	Small	0.274	0.108	0.372	50.6	-9.68	-12.3
60396	1075	Large	0.567	0.328	0.924	51.4	-11.19	-13.18
60397	1075	Large	n/a	n/a	1	n/a	-11.71	-12.94
60393	1075	Large	0.622	0.285	1	51.9	-9.5	-12.45
60400	1075	Large	0.679	0.275	1.131	56.3	-9.3	-12.3
60392	1075	Large	0.755	0.371	1.277	62.69	-7.3	-11.74

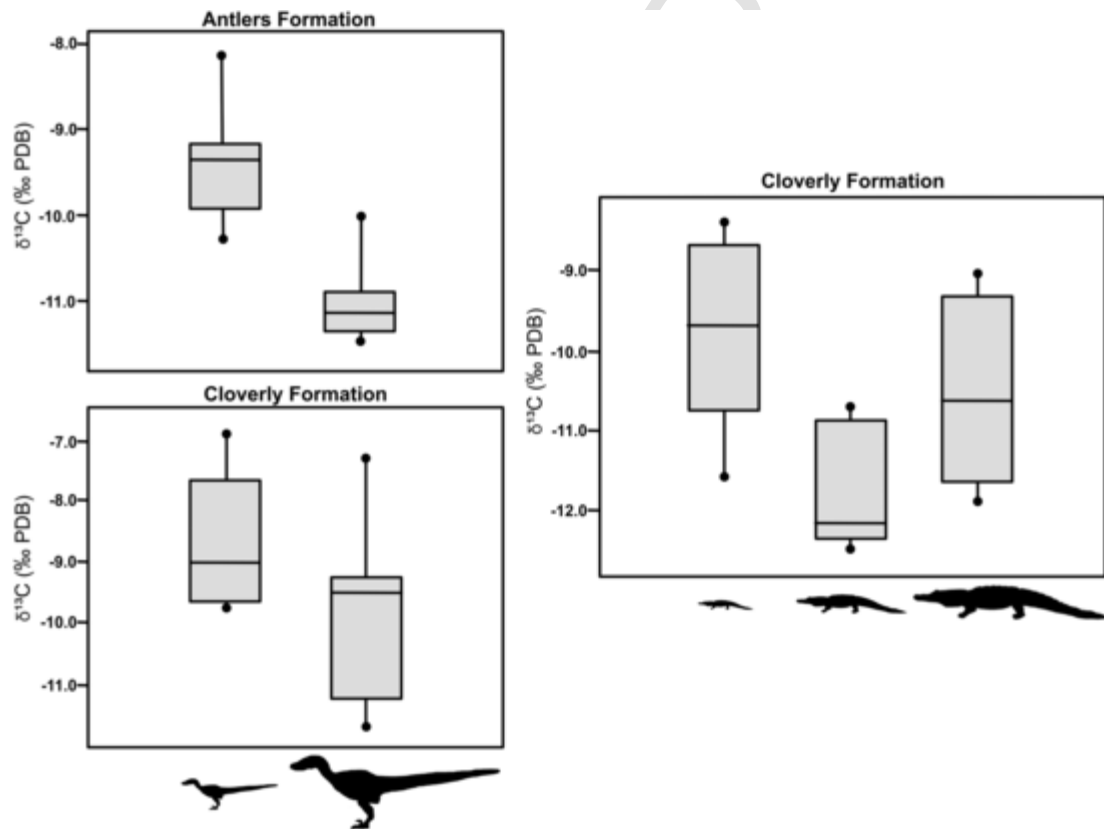


Fig. 2. Left, $\delta^{13}\text{C}$ for small (<4.5 mm crown height, $n = 5$) and large (>9 mm crown height, $n = 5$) *D. antirrhopus* teeth from the Antlers (upper) and Cloverly (lower) formations, Oklahoma and Montana. Right, $\delta^{13}\text{C}$ analysis for small (left, <5 mm crown height, $n = 5$), medium (middle, 5 to 10 mm crown height, $n = 5$), and large (right, 11+ mm crown height, $n = 6$) goniopholidid teeth from the Cloverly Formation, Montana.

6. Discussion

6.1. Niche partitioning in goniopholidids

Our $\delta^{13}\text{C}$ results for Cretaceous goniopholidids from Montana match well with observed dietary patterns of modern crocodylians.

Analyses based on gut contents show a clear transition in diet in multiple modern species. Platt et al. (2006) found that insects and arachnids make up a large portion (97.1 to 95.1%) of the diet in hatchling and small juvenile Morelet's crocodile (*Crocodylus moreletii*), while in adults these prey items made up a substantially smaller portion of the dietary intake (12.5%). Instead, adult individ-

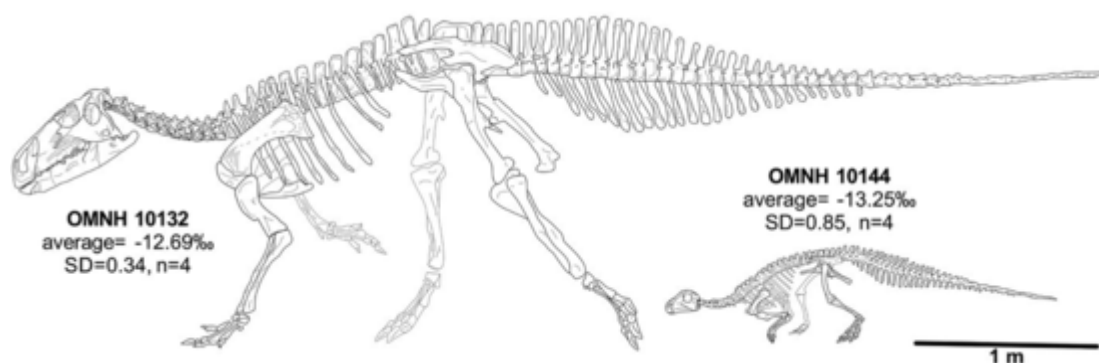


Fig. 3. : Stable carbon isotope analysis of two associated *Tenontosaurus tilletti* specimens from the Cloverly Formation. The sampled enamel shows no statistical difference between the juvenile and adult teeth ($n = 8$; $p = .19$). Reconstructions based upon mounted skeletons at the OMNH.

uals rely on gastropods, fish, and crustaceans (70.8%, 31.2%, and 20.8% respectively) as the mainstay of their diets. Similarly, the Australian freshwater crocodile (*Crocodylus johnstoni*) begins post-hatching life with a diet largely comprised of insects and spiders, before steadily transitioning to a diet of more fish and even terrestrial vertebrates in the largest individuals (Tucker et al., 1996). This change in resource utilization has morphological correlates beyond increase in body size. In a study of American alligators (*Alligator mississippiensis*), for example, Erickson et al. (2003) found that bite force increases with positive allometry relative to body size, which is hypothesized to compensate for the larger, more durable, and stronger prey items favored by adults.

In the Nile crocodile (*Crocodylus niloticus*) these same body-size/diet transitions in $\delta^{13}\text{C}$ occur at approximately 130 cm SVL (the tip of the snout to the first scale row after the cloaca) and 240 cm SVL (Radloff et al., 2012). Small *C. niloticus* transition between a diet composed of insects to a more fish-based diet with increasing size. The largest individuals have a relatively enriched $\delta^{13}\text{C}$ signature, largely the result of a diet based in significant part on C4 grass-feeding animals. These same changes in the diet appear to be manifested in the Cretaceous goniopholidid $\delta^{13}\text{C}$ record presented here, albeit for different reasons. The smallest teeth are enriched in ^{13}C , similar to the smallest individuals documented by Radloff et al. (2012). There is also a similar decline in the middle size class, in which a distinct dietary transition occurred in *C. niloticus*. Surprisingly, the largest individual tooth (length of 31 mm) is more depleted in ^{13}C (-10.68‰) than was observed in the modern crocodile study. A possible explanation lies in composition and diet of large terrestrial herbivorous prey, which varies between the modern and ancient environments. Incorporation of the isotopically-depleted *Tenontosaurus* into the diet of large size-class goniopholidids could produce the relatively lower ^{13}C values in these individuals. This is directly opposed to the more enriched-C4 herbivores present in the diet of modern large *C. niloticus*.

6.2. Niche partitioning in *Deinonychus*

Based on carbon isotope data, juvenile and adult *D. antirrhopus* likely consumed different prey regardless of where they lived. The isotopic differences reported here is closer to the ontogenetic dietary pattern of the Komodo dragon, as observed by Roach and Brinkman (2007) than to the canid pattern proposed by Ostrom (1969, 1986). Though we lack skeletal evidence that juvenile and adult *D. antirrhopus* occupied the same environments, isolated teeth from individuals varying widely in size are found in close proximity, suggesting that the young and old were not physically separated. Given that gregariousness, even among different-sized individuals, is

not rare in theropods (Currie and Eberth, 2010), there is little reason to assume that *D. antirrhopus* would not also demonstrate a level of social tolerance at least as advanced as that seen in crocodylians. Because individuals of all sizes likely occupied the same environment, young animals must have behaved differently than adults, at least with respect to food preferences. We can presume, based on the taphonomic association of *D. antirrhopus* teeth with *Tenontosaurus* remains (see Forster, 1984; Maxwell and Ostrom, 1995; Brinkman et al., 1998) and the close average dental $\delta^{13}\text{C}$, that adult *D. antirrhopus* were feeding upon *Tenontosaurus* to some degree. However, some large-crowned *D. antirrhopus* teeth from the Cloverly also show a more enriched $\delta^{13}\text{C}$ signature (-7.3 to -9.5‰), overlapping with the range of values for smaller individuals, implying that adults were not monophagous.

The varying adult diet of *D. antirrhopus* is indicative of a dynamic and opportunistic hunter. Unsurprisingly, this breadth is reminiscent of modern large-bodied carnivores, where prey preference falls largely into an optimum size range, but other organisms will be consumed when available (e.g., adult African lions *Panthera leo* prefer prey weighing around 350 kg but will feed on elephants, mice, and various prey of intermediate sizes; Hayward and Kerley, 2005; Davidson et al., 2013). Greater variation between large-crowned teeth in the Cloverly than in the Antlers samples imply a geographical difference in diet, possibly correlated with availability of food supply (e.g., Fryxell et al., 1988). In their reinterpretation of dromaeosaur pedal morphology, Fowler et al. (2011) proposed the Raptor Prey Restraint (RPR) model which envisioned winged, adult *D. antirrhopus* acting more similar to modern accipitrids, using the large, recurved D-II pedal phalanx for small-prey immobilization, supplemented by wing-flapping to maintain stability. For larger prey, such as subadult *Tenontosaurus*, D-II may have acted more as a crampon for sustained “prey-riding”. A climbing, rather than a slashing function for the D-II foot claw was also proposed by Manning et al. (2006) as a result of robotic modeling.

Alternatively, juveniles might have been much more limited in their trophic abilities. Their enamel $\delta^{13}\text{C}$ signature is relatively more enriched in both formations than the larger individuals, including more than 4‰ increase on average compared to *T. tilletti* from the Cloverly Formation. Hunting juvenile *tenontosaurus* seems unlikely, as small *tenontosaurus* are isotopically similar to the adults (albeit from a very limited sample). Further, the juvenile *T. tilletti* (OMNH 10144) tested here was found in association with the adult individual (OMNH 10132; Forster, 1990), suggesting that hunting such animals would be a dangerous task for a small *D. antirrhopus*. Based on the $\delta^{13}\text{C}$ values, it seems far more likely that these juvenile *D. antirrhopus* ate a diet consisting of smaller, but likely trophically-higher prey than the adults.

6.3. A better analog

The life history of non-avian dinosaurs is imperfectly preserved in the fossil record. Based on the evidence at hand, all dinosaurs are currently viewed as being oviparous and most likely exhibited some form of parental care of their young, as is inferred for the common ancestor of Crocodylia and Aves (Tullberg et al., 2002). Most species grew over a multi-year period before reaching sexual maturity and possibly congregated in juvenile or mixed-aged groupings (Varricchio, 2011). The degree of parental care and social behavior in *D. antirrhopus* are relatively ambiguous. Parental care can only be assumed based on the evidence from other species, while social interactions are largely supported by bonebed composition. The evidence presented here shows that small, presumably young *D. antirrhopus* did not have the same diet as the adults, implying that parental feeding, if present, had concluded before the offspring were large enough to sustain a typical adult diet.

In their reevaluation of social behavior in *D. antirrhopus*, Roach and Brinkman (2007) used examples of high levels of intraspecific aggression and cannibalism in modern archosaurs and Cretaceous theropods as evidence against higher social coordination, though the complete validity of this argument did not go unchallenged (Currie and Eberth, 2010). In modern cannibalistic species lacking parental care, juveniles actively avoid their adult predators by seeking out adult-free environmental zones (Foster et al., 1988; Werner et al., 1983; Keren-Rotem et al., 2006). Beyond providing safety from larger conspecifics, these separate habitats often provide a higher availability of more-ideal sized prey. Both of these factors are demonstrated in the Komodo dragon model hypothesized for *D. antirrhopus*, in which hatchlings are highly arboreal, a habitat providing relative safety from nonarboreal, cannibalistic adults and a ready supply of small insects and lizards. Only with the onset of larger sizes do these individuals take on a more terrestrial lifestyle (Auffenberg, 1981; Imansyah et al., 2008).

This hypothetical lifestyle, however, contradicts the relatively common occurrence of juvenile theropods found alongside adults (Currie and Eberth, 2010). Indeed, purported dromaeosaur ontogenetic series are known from individual bonebeds, including a recently-described site containing the remains of at least one 'baby', one juvenile, and one adult *Utahraptor ostrommaysorum* from the Lower Cretaceous of Utah, preserved in a natural mud-trap (Kirkland et al., 2016). Although it is possible that these specimens represent unrelated individuals that were captured by chance, it is more probable that this site represents a social, likely related group. If the latter is true, then this suggests that dromaeosaurs, and possibly other theropods, were gregarious and exhibited some degree of post-nestling care. If so, the occurrence of juvenile or young animals alongside adults imply an absence or reduced presence of the cannibalistic avoidance behavior, making an analogy with the Komodo dragon less palpable. Though *D. antirrhopus* shows ontogenetic diet partitioning, differentiating itself from the highest level of cooperative social mammalian behavior, the lack of spatial separation from adults likely indicates that these dromaeosaurs had hunting strategies on par with many of the avian raptors (Ellis et al., 1993). In avian raptors, post-fledgling behavior can range from completely asocial to relatively gregarious, even within a single species. Further, dromaeosaurs likely showed paternal parental care, similar to modern palaeognaths (Varricchio et al., 2008). This type of rearing is typified by extended protection by the father, where feeding time is reduced and predator vigilance is increased in the parent (Fernández and Rebores, 2003). It is possible that dromaeosaurs showed more ratite-like parental care rather than the completely agonistic relationship seen in Komodo dragons. In this scenario,

parental *D. antirrhopus* may have had reduced feeding efficiency due to their inability to both protect their young and hunt large-sized prey. The young, being precocial, would have maintained some degree of dietary independence based on their own foraging and/or small fare provided by the parent.

7. Conclusions

This study provides evidence indicating the presence of ontogenetic trophic shifts in growing goniopholidid crocodylians and the dromaeosaurid theropod *Deinonychus antirrhopus*, as seen in most living archosaurs. These results are consistent with Roach and Brinkman (2007)'s alternative hypothesis against mammal-like pack-hunting in dromaeosaurids. The low sample size of *D. antirrhopus* teeth available for isotopic analysis hinders immediate further statistical analysis of this hypothesis. Nonetheless, the results obtained in this modest analysis demonstrate the need for further studies of dietary ontogenetic changes in both herbivorous and carnivorous dinosaurs.

Institutional abbreviations

AMNH – American Museum of Natural History, New York, New York; IGM – Mongolian Institute of Geology, Ulaan Bataar, Mongolia; OMNH – Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma; YPM – Yale Peabody Museum, New Haven, Connecticut.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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