**Ontogenetic dietary partitioning in *Tyrannosaurus rex***

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**Abstract**

**Introduction**

By foraging at different times or locations or by targeting different resources animals can avoid direct competition with conspecifics. This partitioning of resources can occur across ontogeny when the life stages are distinct; so, for example, an agile juvenile may focus on smaller, faster prey than an adult. Such ontogenetic dietary partitioning is known across a diversity of species including crocodiles, fish etc [[1-5](#_ENREF_1)] and is often in particular related to changes in body size [Woodward & Hildrew 2002, some other ref might be good too].

Here we suggest that such partitioning may have taken place in the theropod dinosaur *Tyrannosaurus rex*. *T. rex* fits into theropod ‘morphotype one’ as defined by Weishampel [[6](#_ENREF_6)]. The animals in this category are extremely large, exceeding 10m, have huge skulls, short forelimbs and as such have no living analogues which makes it difficult to draw any conclusions about their mode of life [[6](#_ENREF_6)]. However, Tyrannosaurs are atypical as through the large number of fossils available for study [[8](#_ENREF_8)] it is known that *T. rex* exhibited remarkable growth through its development [[8](#_ENREF_8)] and underwent dramatic ontogenetic changes in its morphology which has led some researchers to argue for a concomitant change in its ecological habits [[8](#_ENREF_8)]. For instance, adults had a powerful, deep, robust skull with thick teeth in contrast with the more gracile features of juveniles. One suggested result of this change was a dietary shift from small, agile prey to larger more cumbersome herbivores [[8](#_ENREF_8)]. However, we argue that such marked changes developed with an increased opportunity to avail of resources through scavenging[[9](#_ENREF_9)].

There have been a number of studies looking at the theoretical possibility of obligate scavenging across species including *T. rex* [[10-15](#_ENREF_10)]. For instance, Horner pointed to its slow speed, reduced forearms, large olfactory bulb and incredible bite force to support this view [[16](#_ENREF_16), [17](#_ENREF_17)]. Fossil material has also been discovered which suggests scavenging behaviour as bite marks were located in a flesh poor region [[18](#_ENREF_18)]. Energetic approaches have concluded for [[12](#_ENREF_12)] and against [[13](#_ENREF_13)], the latter study arguing that interspecific competition would undermine the possibility of a scavenging *T.rex*; smaller competing species would find and consume any carcass before the larger *T.rex* could benefit. Yet, obligate scavengers are rare among terrestrial vertebrates with even the most common example of a terrestrial scavenger, the brown hyena (Latin name), displaying a large degree of variation between scavenging behaviour and active predation [ref from hyena book, [19](#_ENREF_19), [20](#_ENREF_20)]. Instead, most carnivores are opportunistic and will take carrion as well as actively hunting prey [[19](#_ENREF_19)] and mounting evidence suggests that *T.rex*  behaved similarly to extant opportunistic predators such as hyenas. Along with earlier indications of active predation [that earlier ref on hadrosuars], more recently, a herbivorous hadrosaur was found with a *T. rex* tooth crown embedded in its tail. The wound had healed around the tooth indicating that the prey item escaped and that this was an active predation attempt [[21](#_ENREF_21)].

In this study we move away from the polarised predator-scavenger debate and argue that *T. rex* underwent an ontogenetic dietary shift, increasing the proportion of carrion in its diet as it aged due to both the increased availability of carrion through direct intraspecific competition and also by exploiting resources unavailable to it smaller competitors. We argure this was accomplished by both being able to dominate carcasses occupied by smaller individuals and also by exploiting a resource unavailable to its competitors, namely bone. Indeed it has been noted before that the laterally compressed dentition of juveniles would mean they were unable to consume bone [[22](#_ENREF_22)] in contrast to the banana-shaped teeth of the adults.

This shift would not only see adult *T.rex* avoiding intraspecific competition with younger consepcifics but also with interspecific carnivores of the time. Among contemporary competitors [[9](#_ENREF_9)] *Troodon* was unsuited to dealing with bone [[23](#_ENREF_23" \o "Fiorillo, 2008 #193)]; and although dromaeosaurids had relatively strong bite forces [[22](#_ENREF_22)] and could tackle larger prey items collectively [[24](#_ENREF_24)], individually their small size meant they would leave much of the skeletal material behind and would be easily displaced by the larger adult *T.rex*. Most direct competition between these taxa would have occurred during juvenile stages of *T.rex* ontogeny before the unset of a large growth phase in *T.rex* [[22](#_ENREF_22)].

Osteophagy is known in extant taxa such as the Bearded Vulture (*Gypaetus barbatus*) and hyena species [[25](#_ENREF_25)]. Some fat rich mammalian bones have an energy density (6.7 kJ / g) comparable with that of muscle tissue [[26](#_ENREF_26)], making skeletal remains an enticing resource. But considering the immense size of the skeletons of some coeval prey items (e.g. *Alamosaurus sanjuanensis* at 20m long and at least 32 tonnes [[27](#_ENREF_27), [28](#_ENREF_28)]) it seems likely that only the most specialized of morphologies could process them.

However, as alluded to earlier, the morphology of an adult *T. rex* skull does suggest an ability to process bone. More direct evidence comes in the form of distinctive wear marks [[29](#_ENREF_29)] on its tooth apices as well as spalling [[30](#_ENREF_30)]. The animal also had an enormous bite force, with one estimate putting it at 57000 N [[31](#_ENREF_31)]. This is noted as being “large enough to shatter skeletal material during prey dismemberment” [[32](#_ENREF_32)]. A positive allometric scaling relationship in bite performance during ontogeny has also been recorded [[31](#_ENREF_31)]. Further, *T. rex* coprolites were discovered with bone fragments, *prima facie* evidence that it did consume bone.

While previous energetic studies of T.rex foraging rule out scavenging as major foraging strategy we include two unusual aspects of such terrestrial systems 1; the almost complet dominance of resource by large adulat T.rex and 2. The abundance of large carcasses that would provide bones material extensive half lives. We follow an energetics approach in our study to explore the effect of this previously unrealised resource on the ecology of *T.rex* and look at the impact of the proposed ontogenetic dietary shift.

**Methods**

**Kev’s model**

An animal’s daily foraging area is a function of the daily distance walked, multiplied by the prey/carcass detection distance, by two. We varied both the detection radius and average walking speed of *T. rex* to determine the sustainability of carrion feeding. We considered circumstances when only meat was available, when only bone was available and when both were available.

**NetLogo model**

We created a spatially explicit agent-based model to allow us better understand the effect of competition on *T.rex* if it was restricted to scavenging with a view to incorporating the effect of bone as a resource uniquely available to it. Our model was designed in the program NetLogo [[33](#_ENREF_33)]. The simulation space is a 50x50km square corresponding to a 2500km2 landscape. We used an estimate of energy density of carrion from the Serengeti as an analogue for the Late Cretaceous Hell Creek ecosystem [[12](#_ENREF_12)]. We used carcass categories of 75kg, 216kg, 500kg, 700kg, 2500kg, 5000kg, 8500kg and 25000kg which had been defined in a previous study of *T.rex* [[13](#_ENREF_13)]. The model had two mobile agent types which corresponded to *T.rex* and its competitors. The numbers of carcasses, the number of theropods, carrion decay rates, detection distances and walking speeds were taken from literature estimates [[12](#_ENREF_12), [13](#_ENREF_13), [34](#_ENREF_34)]. We used equations describing the allometry of skeletal mass to body mass (Bone (kg) = 0.065 \* Mass(kg)1.071)[[35](#_ENREF_35)] to assess the amount of skeletal material found in the dinosaurs *T. rex* was likely to feed on. The competitors could only feed on flesh not bone of the carcasses. *T.rex* starts off with a full gut of 267kg of flesh (derived from the allometric equation: Gut capacity (G, kg) = 0.075 M 0.94)[[36](#_ENREF_36)]. A 20kg dromaeosaur has a capacity of 1.25kg. *T.rex* has a daily cost of 942998kJ as derived by the scaling relationships described here [[34](#_ENREF_34)]. We assumed a 12 hour foraging day in the model.

The initial state of the model has all dinosaurs and carcasses located randomly in the environment. The dinosaurs then set off in a random direction at their assigned speed searching for carrion. They keep the same walking speed for the duration of the model and have a constant turning rate. *T.rex* loses energy according to the cost calculated above. Should the energy of the *T.rex* reach zero it will die. Upon finding a carcass it walks towards it and starts to feed, extracting energy from it at a rate of 75kg per hour. *T.rex* continues to feed until the carcass decays entirely. Dromaeosaurs feed at a rate of 1.25kg per hour (gut capacity) until the carcass is reduced to bone. When nothing remains for the animals to eat they begin to forage again. Without any predators the carcasses decay over a seven day period at a constant rate, eventually all the flesh decays leaving only bone which then decays until nothing remains. At the start of a new day, the amount of energy the *T.rex* has is reported and new carcasses are deposited according to the calculations of carrion density for the area. We make the reasonable assumption that *Dromaeosaurs* were competitively subordinate to *T. rex* and so in the model the former actively avoid the latter if they come within visual range.

**Results**

**Discussion**

Brown hyenas can detect carcasses 2km downwind [[37](#_ENREF_37)] and the olfactory bulbs of *T. rex* indicate an impressive ability in this respect [[38](#_ENREF_38)]. Scavengers are often attracted to carrion by the presence of other scavengers too [[39](#_ENREF_39)] and this would increase the likelihood of visual detection.

Gut capacity scales almost isometrically with body mass [[36](#_ENREF_36)] so a larger animal is better able to cope with the ephemerality of carrion by relying on its reserves during times of scarcity and also by being able to consume a larger portion of a carcass in one sitting [[11](#_ENREF_11)]. Thus, adult *T.rex* were more suited to scavenging than juveniles. [Survival time or fasting endurance (ts) may be estimated by dividing usable energy stores by minimal survival requirements: ts = 9.30 Mb0.44 where Mb is total body mass in kg [[40](#_ENREF_40)]].

Ecologically, *T.rex* was unusual. Census records show it to have had a population higher than would be expected for a typical apex predator suggesting that its mode of life was unusual with Horner and colleagues positing a hyena-like niche for the animal [[9](#_ENREF_9)].

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#-------------------------------------------**Figures and Tables**------------------------------------------------#

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Table 1. Allometric Scaling of bone with body mass across carcass categories

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| --- | --- |
| **Carcass Mass (M, kg)** | **Bone Mass (kg) = 0.065\*M1.071** |
| 75 | 6.62 |
| 216 | 20.56 |
| 700 | 72.45 |
| 2500 | 283.21 |
| 5000 | 594.99 |
| 8500 | 1050.32 |
| 25000 | 3335.09 |