**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 related to changes in body size [[6](#_ENREF_6)].

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 [[7](#_ENREF_7)]. 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 [[7](#_ENREF_7)].

However, Tyrannosaurs are atypical because of the large number of fossils available for study [[8](#_ENREF_8)]. So 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 instead argue that such marked changes caused an increased tendency towards 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 example, 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, more numerous 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 (*Hyaena brunnea*), displaying a large degree of variation between scavenging behaviour and active predation [[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, 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 argue 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 is a similar pattern to that observed in loggerhead sea turtles (*Caretta caretta*) where the bite force exhibits positive allometry across ontogeny allowing adults access to hard benthic prey, a resource inaccessible to other durophagous competitors [[23](#_ENREF_23)].

This shift would not only see adult *T.rex* avoiding intraspecific competition with younger consepcifics but also with interspecific carnivores of the time. No other large theropods are known from the Late Maastrichtian of western North America [[24](#_ENREF_24)]. Among contemporary competitors [[9](#_ENREF_9)] *Troodon* was unsuited to dealing with bone [[25](#_ENREF_25)]; and although dromaeosaurids had relatively strong bite forces [[22](#_ENREF_22)] and could tackle larger prey items collectively [[26](#_ENREF_26)], 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 onset 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 [[27](#_ENREF_27)]. Some fat rich mammalian bones have an energy density (6.7 kJ / g) comparable with that of muscle tissue [[28](#_ENREF_28)], 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 [[29](#_ENREF_29), [30](#_ENREF_30)]) 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 [[31](#_ENREF_31)] on its tooth apices as well as spalling [[32](#_ENREF_32)]. The animal also had an enormous bite force, with one estimate putting it at 57000 N [[33](#_ENREF_33)]. This is noted as being “large enough to shatter skeletal material during prey dismemberment” [[34](#_ENREF_34)]. A positive allometric scaling relationship in bite performance during ontogeny has also been recorded [[33](#_ENREF_33)]. 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 complete dominance of resource by large adult *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** (this section is wrote in a very preliminary format but feel free to point out what sections need to be expanded or left in the supplementary)

We used binned size categories from a previous study for both the body mass of the prey items and the predators [[13](#_ENREF_13)]. We took an estimate of energy density of carrion from the Serengeti as an analogue for the Late Cretaceous Hell Creek ecosystem (4.38kg/km2/day) [[12](#_ENREF_12)] and assumed each herbivore body size bin attributes an equal amount of "carcass" to this density (I will repeat this for several other more plausible carcass size distributions such as the one found in Hell Creek) [[13](#_ENREF_13)]. Using allometric scaling relationships for bone mass to body mass (Bone (kg) = 0.065 \* Total Body Mass(kg)1.071)[[35](#_ENREF_35)] we could determine the amount of flesh and bone available in kJ/km2/day and the energy content available through both using 6.7kJ/g for bone and 7kJ/g for flesh[28?make sure].

**T.rex searching abilities**

To calculate the daily area searched we used the search rate equation of Ruxton et al [] based on the walking speeds estimated in Pontzer et al [36] and assuming a range of detection distances. As hyenas can detect carcasses up to 2km away [] and *T.rex* is known to possess large olfactory bulbs [] we use the conservative 200meter detection range with additional sensitivity analysis to investigate distance effect range. We also scaled detection distance based on the scaling of olfactory bulb ration scaling (Zelenitsky et al (2009) I haven’t done this yet and maybe this would be better for the discussion to show our figures are conservative as it assumes smaller animals have as high detection range as large. The other possibility is to follow Carbone et al scaling approach but I have’nt got that working yet).

**T.rex energetics**

We estimated the daily energy expenditure of a *T.rex* of mass *Mi* for both inactive resting and for active foraging. For the inactive phase we used resting metabolic rate allometric equations based on both extant reptiles (ectoderm model) and mammals (endotherm model) [White et al 2011]. We estimated the costs of active foraging using the estimated walking speeds and cost of transport equations derived from Pontzer et al [36] for energy consumption based both on limb length calculations and active muscle volume [36]. (for now I fit a log-log linear equation between the values in Pontzer to allow for energies to be scaled for all sizes.). By combining both resting and active searching cost and assuming active foraging for 12 hours/day, (such as seen in hyenas [ref]), we calculate the full daily cost of a T.rex of mass *Mi*. The energy budget is then the sum of the costs as estimated above and the energy intake based on the area searched, the density of carcasses in the environment and their energetic content (I assumed a assimilation efficiency of 0.75 for everything up to this point.).

**Including competition into scavenging model**

To include competition into our model we use the approach of Carbone et al [] to estimate the average number of predators present on a carcass on arrival (For now I have took the figures form the paper directy and used the ratios of animals found (the problem with that is it includes scaling of detection range and so underestimates the amount of smaller animals, however this is conservative as this would increase the importance of intra-specific competition in these models)). As the carcass are assumed to last seven days the number present on arrival is depended on 1; density of other scavenging therapods which are calculated based on Damuths scaling such as used in Carcone et al [], and 2; their search rates. We assume that when a theropod larger then a *T.rex* of mass *Mi* is present on a carcass then the *T.rex* is completely excluded from those resources. The proportion of the seven-day lifespan of a carcass in which no larger competitor is present is then used as the proportion of carcass that is available to a *T.rex* of mass *Mi*.

We considered circumstances when only meat was available, when only bone was available and when both were available with estimated loss due to competition. (I haven’t done all of these yet)

**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 [[37](#_ENREF_37)]. 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), [36](#_ENREF_36)]. 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 an empty gut which has a capacity of 240 kg (derived from the allometric equation: Gut capacity (G, kg) = 0.075 M 0.94)[[38](#_ENREF_38)]. A 20kg dromaeosaur has a capacity of 1.25kg. We set *T. rex* carcass detection range as 2km and the *Dromaeosaurus* range at 1km. We assumed a 12 hour foraging day in the model.

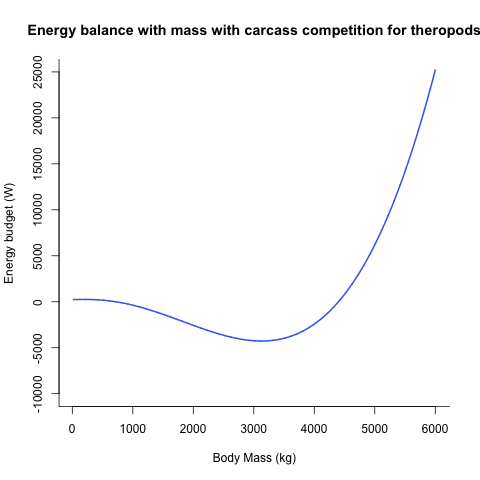
The initial state of the model has all dinosaurs and carcasses located randomly in the environment. The dinosaurs then set off in a random direction at their assigned speed searching for carrion. They keep the same walking speed for the duration of the model and have a constant turning rate. *T.rex* loses energy according to the cost calculated above. Upon finding a carcass it walks towards it and starts to feed, until it fills its gut. Similarly, *Dromaeosaurs* feed until they reach their gut capacity. If nothing remains for the animals to eat and they are not entirely sated they begin to forage again. Flesh and bone are processed with 90 and 50% efficiency respectively. 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** (These are only preliminary results)

In the complete absence of competition a 6 ton *T.rex* can survive on a diet of just bone if it has a minim detection distance of just 15 meters using the ectotherm model. In comparison such a animal would need a detection distance of 700 meters in our endotherm model if we base cost of transport on active muscle volume and 256 meters if we base cost of transport limb one length (and if we assume bone energy is at the min value we found in the literature then it would be 856 for low endotherm and 2350 for the high endotherm model). In the absence of competition the most efficient size for a scavenger with a detection range of 200 meters peaks at 365kg and rapidly declines. Figure 1. Macintosh HD:Users:kevinhealy:Desktop:dino chart.pdf

Figure 1. Relationship between body mass and energy budget for theropods scavenging on skeleton remains.

When compititoin is included scavenging on bone itself becomes unviable for any individual with a negative budget for all sizes tested between 0 and 6 tons (I reckon this is because I assumed even small animals have access to bones while in reality it would only be the largest indviduals). However when the full carcass is included within the energy budget a clear pattern is seen with an increased compititve advantage in larger animals (Figure 2).

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**Discussion**

Brown hyenas can detect carcasses 2km downwind [[39](#_ENREF_39)] and the olfactory bulbs of *T. rex* indicate an impressive ability in this respect [[40](#_ENREF_40)]. Scavengers are often attracted to carrion by the presence of other scavengers too [[41](#_ENREF_41)] and this would increase the likelihood of visual detection.

Gut capacity scales almost isometrically with body mass [[38](#_ENREF_38)] 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 [[42](#_ENREF_42)]].

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**------------------------------------------------#

# #----------------------------------------------------------------------------------------------------------------##

Table 1. Carcass numbers in the environment; mass categories for carcasses and allometric scaling of bone with body mass across carcass categories

|  |  |  |  |
| --- | --- | --- | --- |
|  | **Carcass Numbers/2500km2/day** | **Carcass Mass (M, kg)** | **Bone Mass (kg) = 0.065\*M1.071** |
|  | 147 | 75 | 6.62 |
|  | 50 | 216 | 20.56 |
|  | 16 | 700 | 72.45 |
|  | 4 | 2500 | 283.21 |
|  | 2 | 5000 | 594.99 |
|  | 1 | 8500 | 1050.32 |
|  | 0.5 | 25000 | 3335.09 |