

The fast and the frugal: Divergent locomotory strategies drive limb lengthening in theropod dinosaurs

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Abstract

Limb length, cursoriality and speed have long been areas of significant interest in theropod paleobiology as locomotory capacity, especially running ability, is critical in not just in prey pursuit but also to avoid become prey oneself. One aspect that is traditionally overlooked is the impact of allometry on running ability and the limiting effect of large body size. Since several different non-avian theropod lineages have each independently evolved body sizes greater than any known terrestrial carnivorous mammal, ~1000kg or more, the effect that such larger mass has on movement ability and energetics is an area with significant implications for Mesozoic paleoecology. Here using expansive datasets, incorporating several different metrics to estimate body size, limb length and running speed, to calculate the effects of allometry running We test both on traditional metrics used to evaluate cursoriality in non-avian theropods such as distal limb length, relative hindlimb length as well as comparing the energetic cost savings of relative hindlimb elongation between members of the Tyrannosauridae and more basal megacarnivores

such as Allosauroids or Ceratosauridae. We find that once the limiting effects of body size increase is incorporated, no commonly used metric including the newly suggested distal limb index (Tibia + Metatarsus/ Femur length) shows a significant correlation to top speed. The data also shows a significant split between large and small bodied theropods in terms of maximizing running potential suggesting two distinct strategies for promoting limb elongation based on the organisms' size. For small and medium sized theropods increased leg length seems to correlate with a desire to increase top speed while amongst larger taxa it corresponds more closely to energetic efficiency and reducing foraging costs. We also find, using 3D volumetric mass estimates, that the Tyrannosauridae show significant cost of transport savings compared to more basal clades, indicating reduced energy expenditures during foraging and likely reduced need for hunting forays. This suggests that amongst theropods while no one strategy dictated hindlimb evolution. Amongst smaller bodied taxa the competing pressures of being both a predator and a prey item dominant while larger ones, freed from predation pressure, seek to maximize foraging ability. We also discuss the implications both for interactions amongst specific clades and Mesozoic paleobiology and paleoecological reconstructions as a whole.

Introduction

Non-avian theropod dinosaurs were the dominant terrestrial carnivores during much of the Mesozoic. They occupied much of the available niche space [1-3], and ranged in size from <200g to approximately 9000kg [4, 5]. While no single adaptation is likely to explain such widespread dominance and diversity of form, the bipedal locomotory system employed by theropods is invoked as an important reason for the success of this lineage [6]. For animals, the speed at which they travel is a critical factor in their survival strategy as it impacts all aspects of food collection, dispersal, migration and predator avoidance [7]. Because of this, much work has been done to model locomotion and how it affects different aspects of theropod life history and behavior, such as movement efficiency, turning radius, balance [8-14]. Additionally, studies of the growth across the clade, both ontogenetically and allometrically [15-18], have shown marked difference in traditional markers for cursorial potential [14, 19], such as interlimb ratios, lower

limb length and relative total limb length. This includes comparisons of derived coelurosaurian theropods at all body sizes to more basal clades, and have been suggested to be linked to a refinement of running ability in this group [8, 15, 19].

Recent work by Parson and Currie [14] attempted to further this by quantifying relative cursoriality amongst non-avian theropods the use of the distal hind limb indices (tibia + metatarsal length/ femur). They argued that the application of this metric could identify those taxa with the highest top speed and attempted to establish that it had significant impact on the ecological role and the diversification of theropods. Yet the challenge is that much of an organisms locomotory repertoire, both in terms of percentage of behaviours and duration, is at lower speeds[20], this is especially true in carnivores who often spend hours searching for or pursuing prey and low to moderate speeds between bursts of high speed running[21, 22]. Without considering the fact that much of the energy budget and life history of a predator is spent at lower gears, the relative speed of predators compared to suspected prey items and its role in shaping the evolutionary landscape for theropods as well as the effect of other factors such as body size in their analysis Parson and Currie may have overestimated the importance of top speed.

Here we re-examine locomotion in non-avian theropods, applying indices based on estimates of top speed and energetic expenditures to get a more complete sense of how differences in relative limb lengths, and of components within the limb itself, reflect the paleobiology and paleoecology of these creatures. Our goal is to more accurately understand the selective pressures that shaped limb length and interlimb proportion evolution across theropods, and to compare how the

evolution of extremely body size, greater than 1000 kg, may have altered the drivers for distal limb indices. Through this we seek to more accurately reconstruct patterns of cursoriality and foraging strategies amongst theropods and understand better how they shaped the ecosystems in which they lived.

Materials

Relative leg length and max speed

Measurements of snout to vent length along with hindlimb lengths for 93 specimens for 71 different genera of avian and non-avian theropods were collected from the literature and personal measurements (Sup. Table 1) that had at least one hindlimb element recorded. This included 82 specimens with a complete hindlimb preserved such that leg length and hip height could be estimated and from that speed calculated (Sup. Table 2). Sampling includes members from all major clades and multiple specimens per species, often from different ontogenetic stages, where possible to capture the maximum diversity of Mesozoic theropod hindlimb disparity. These taxa range in SVL size from 70 to over 5000 mm. A subset of this data, 22 non-avian theropods where femoral circumferences were available, were selected to examine how body mass relates to various metrics of leg elongation (Sup. Table 3). We only included non-avian theropods as previous work has suggested significant allometric and functional shifts in the limbs of early avians compared to their non-avian ancestors [15]. This dataset was then expanded to 77 specimens by including multiple taxa without SVL measurements to capture more non-avian theropod diversity (Sup Table 4). We chose several different metrics to evaluate the connection between hindlimb length and speed including total hindlimb length, distal hindlimb index and hindlimb/ SVL, hindlimb length / $m^{1/3}$ and metatarsal length $m^{1/3}$.

To calculate maximal running speed, we used several estimators to be able to compare values across proxies. The first is Froude number, which is a dimensionless number that allows for relative size to be removed from velocity calculations [23]. The second is locomotor velocity, which is calculated as

$$V = \sqrt{Fr / h * g} \quad [10].$$

Where v is the velocity in m/s, Fr =Froude number, h = hip height taken here as hindlimb length and g is gravity. For hip height we chose to estimate it as $0.8 \times$ total limb length, which corresponds to the level of crouch seen in large terrestrial modern birds [24] and mimics the values seen in other similar studies [10]. For taxa with a body mass of less than 1000kg we calculated a range of Froude values from 0.25 to 15 to document behaviors from slow walk to top speed while being within the range possible for both non-avian and avian theropods [11, 25-27]. For larger taxa a maximum Froude number of 5 was used as this is suspected to be the limit that they could achieve [10]. In addition to using Froude number we also calculated maximum speed based on another methodology: the stride length based on either Alexander [28]

$$V = 0.25 g^{0.5} \lambda^{1.67} h^{-1.17}$$

Or the correction by Ruiz and Torices [29]

$$V = 0.226 g^{0.5} \lambda^{1.67} h^{-1.17}$$

Where λ is the relative stride length (RSL). We took for RSL values of 2 and 4.5 corresponding to a slow and a fast burst run and within the range seen in theropod trackways [30]. Finally, we used either published 3-D volumetric estimates of body mass,[9, 31, 32] or generated estimates based on femoral circumference [33] to calculate top speed based on mass limiting factor [7]. This last value is grounded on extant taxa and suggests mass specific limitations on acceleration and top speed, something seen in the modern realm but not factored in by our other metrics.

Energy consumption in large theropods

Estimates of energetic expenditure during foraging amongst the largest bodied theropods were calculated from mass estimates based on several published 3-D body volume reconstructions, one of the most a reliable and comparable method to estimate body mass [9, 10, 31, 32] (Table 1). The advantages of using 3D volumetric mass estimates to compare between taxa is that it is an estimate generated using the an internally consistent, replicated and validated methodology tailored for individual specimens and does not rely on hindlimb dimension, which we are using in other aspects, thus preventing circularity in our arguments. This allows us to compare relative elongation levels with an outside proxy and one that reduces the potential issue that even in the most constrained size reconstruction from femoral length or circumference has the confidence intervals that can span orders of magnitude in mass, thus making it extremely difficult to determine if two taxa, even if they show similar values for said estimator, are actually similar in body mass [33]. Since this is critical for this type of analysis, using more generalized body mass figures obtained through femoral circumference as used in our previous section (Sup. Tables 3-5) would be inadequate for the purposes used here. We attempted, whenever possible, to confine our analysis to looking at taxa only with volumetric mass estimates taken from within the same

study to ensure that differences in volumetric estimations methods do not cause spurious results. When multiple masses were presented we chose to run our analysis using the “best estimate” model as defined in the original papers for all specimens as opposed to the heaviest or lightest. This was done so that we could get direct comparative data using the same variables and not bias the results by artificially inflating or reducing the body mass volumes a priori. This model often produces very similar mass estimates for these two specimens, such as between *Tyrannosaurus* and *Acrocanthosaurus* using which differs only by 1.7% [32].

As a significant proportion of a predator’s daily activity budget is occupied by foraging [21, 22, 34, 35] we choose to reconstruct the energetics values based on cost of foraging [10] using an absolute speed of 2 m/s to simulate a slow walk (Froude number <0.25). This is similar to the estimate used by [35] and well within the walking range estimated from known trackways for large theropods[36-42]. We then combined cost of transport (CoT) with a speed of transport to calculate the costs to forage to both cover a set distance (18 km, the daily expected foraging range of a large theropod [34] and 6570km which is the yearly total) as well as over a series of time intervals (12 hours/ day foraging per [35] and 1 year) to examine the difference in expenditures across comparable sized taxa.

Finally, to compare proportional expenditures we performed two different analyses. First we transformed the difference calculated in kilojoules (kj) into kilograms (kg) of meat by using the energetic conversion values from [43] for large mammalian carnivores. While we understand that the digestive and excretory methods of theropods make it difficult to estimate of the amount of meat required, especially if they excreted uric acid like modern avians which leads to greater

energy loss [43], regardless these parameters are similar to previous studies[35] and defensible based on suspected aerobic capability [10]. In addition, previous work has suggested that the largest theropods would have a metabolic rate equivalent of a 1000 kg carnivorous mammal [44], which is approaching the theoretical maximum size for a terrestrial carnivore [21]. We also compared expenditure values to estimates of Basal metabolic rate based on the equations of McNab [45] and Grady et al.[46]. This allows us to remove the effect of potential digestive absorptive differences between macrocarnivorous mammals and theropods from our data. Regardless of whether these taxa were true truly endotherms or mesotherms, these values should produce reasonable estimates of relative disparities in expenditures to compare between specimens.

Results

Relative leg length

In comparing the relative hindlimb versus distal hindlimb indices while there is a correlation between them, we also observe a disconnect between the two, notably in small to medium sized theropods less than 1200 mm SVL (Supp. Table 1). This is especially clear when comparing some contemporaneous taxa, such as compsognathids and microraptorines (Figure 1). The former clade has been suggested to be highly cursorial while the latter were not based on evaluation of the hindlimb index alone [14]. Our results dispute this finding, as well as previous work that ignored allometric effects in comparing smaller compsognathids to mid-sized and larger dromaeosaurs such as *Velociraptor* or *Deinonychus*[14]. Focusing on non-avian theropods, as avian theropods have different hindlimb scaling factors compared to non-avian theropods [15], we also note negative allometric scaling in interlimb ratios which alone could influence

comparison between these two clades. Even at similar sizes the divergence between relative hindlimb versus distal limb metrics is clearly illustrated by comparing the Yixian biota contemporaries *Changyuraptor* and *Sinosauroptryx*, both of which are suspected small carnivores that differ in length by 10mm (~ 2% total SVL). *Changyuanraptor* show a relative hindlimb index of 0.96, which is significantly higher than that is seen in *Sinosauroptryx* (0.57) while showing a distal limb index value 8% lower. This pattern of high hindlimb indices while showing relatively mild distal limb values is seen across all small bodied microraptorines and basal troodontids, with the opposite trend seen in small bodied compsognathids and basal birds. Interestingly, amongst anchiornithids (a clade of small bodied paravians who have recently suggested to be more closely related to birds than either dromaeosaurids or troodontids [47, 48]) we see a diverse pattern of values ranging from *Anchiornis* at the high end (92-95%) to *Caihong* (78%) at the lower end, though the latter is still similar to what is seen in the cursorial oviraptorosaur *Caudipteryx* (0.75-0.79). We calculated maximum speed potential with the larger hindlimb indices in many microraptorines allowing them to achieve higher top end speed suggesting a sharp demarcation between burst speed potential between microraptorines, contemporaneous small bodied compsognathids and basal birds (Figure 2, Sup. Table 2). Depending on the speed estimator used *Changyuraptor* shows top speed between 5.13-7.98 m/s which is 1.2-1.9 m/s (4.9-6.9 km/hr) higher than *Sinosauroptryx* using the same metric. We also find that the juvenile tyrannosaur “*Raptorrex*” (a suspected young *Tarbosaurus* specimen [49]), shows significant burst speed potential, even higher than similar sized ornithomimids, oviraptorosaurs or basal tyrannosauroids (Sup. Table 2). This supports the idea that juvenile tyrannosaurids were highly cursorial [9, 13, 14].

To evaluate the general applicability of these various hindlimb ratios across Theropoda as a good proxy for top speed we compared distal limb index, hindlimb index as well as metatarsal and whole leg length compared to body size using top speeds at $FR=5$ and under the mass limiting top speed equation of [7]. Using the primary dataset (Sup. Table 3) we find that all proxies have relatively low correlation value, with distal limb index ($r^2=0.55$) as the only metric showing a significant correlation when using speed based on Froude number. When we take into account the limiting factor of increasing body mass, all metrics show precipitous decrease in correlation value with none of them showing a significant relationship to speed (Figure 3, Sup. Table 3). To confirm this was not due to the taxon sampling we used our larger dataset (Sup. Table 4), which though it did not allow us to evaluate HL/SVL , did allow for testing the other three metrics. Using just Froude number all three metrics showed significant correlations to top speed, with distal limb index showing the highest correlation ($r^2=0.48$) (Figure 4, Sup. Table 5). Once again, when correcting for mass all three metric correlations drop to insignificant levels, with distal limb index showing a correlation coefficient of less than 0.04.

Energy consumption in theropods

To determine whether the greatest selection pressure for hindlimb elongation was a savings in terms of transport costs or maximizing top speed, we compared top speeds calculated using $Fr=5$ or 15 to that accounting for body mass in our expanded limb dataset (Figure 4, Sup. Table 4). Across all speed estimates we find that at lower size classes the estimated top speed is lower than the theoretical maximum generated through [7]. However, this changes in mid to large size theropods. Depending on the speed estimator used the body mass limiting top speed drops below

the others at around 500 kg using a Fr of 15 and 2000kg using a Fr=5. This corresponds to a hip height of ~ 1.5-2.1 m.

Using existing volumetric derived masses, we calculated the cost of transport across a range of theropods and dinosauriforms from 0.25 kg to greater than 9000kg (Table 1). Our results show that, among the large bodied theropods, tyrannosauroids show a significantly lower cost of transport than comparable size more basal taxa, with differences most exacerbated in juvenile and sub-adult size classes (Table 1, 2). If we hold velocity constant at 2 m/s, we see significant differences in energetic values between tyrannosauroids and other large taxa (Table 2), based on the relative elongation of their hindlimbs. In order to assess what level of difference in foraging efficacy in terms of CoT make in terms of overall energy expenditure we reconstructed daily energy expenditure budgets for tyrannosaurids and more basal theropods that differed from each other by less than 3% of total body mass. While the differences in the cost of transport values between tyrannosauroids and other large theropods may appear minimal, ranging from only 0.03-0.62 j/kgm, when they are evaluated for taxa at these large sizes and over longer temporal durations they produce significant differences (Table 3A, B). We chose to look at both basal metabolic rate (BMR) and BMR + foraging costs to gain a baseline to compare relative differences in energy use. This was done to ensure we would not produce an exaggeration of the differences between taxa as, for example, the estimated daily caloric intake according to BMR using [46] for the 660 kg juvenile tyrannosaurid “Jane” is only 2400 calories or about the same as the lead author.

We see significant differences between tyrannosaurids and more basal large theropods, using either BMR or BMR + energetic expenditures for both the hourly and distance based foraging ranges. Using a 12 daily hour foraging regime per [35] we find foraging savings between similar sized tyrannosaurids and more basal forms is between 10% of daily to 300% of daily BMR (Table 2, 3a). We contend this suggests that this metric may be too low a baseline. Using BMR + energetic expenditure values we find differences drop, but the trends remain similar. Differences in total daily expenditure range from 1.3% in the largest *Tyrannosaurus* specimens compared to *Giganotosaurus* up to 35% when comparing the juvenile *Tyrannosaurus* “Jane” to a *Ceratosaurus* (Table 3b). This translates to between 2-16kg of extra meat a day. Interestingly, the highest values are seen when comparing *Acrocanthosaurus* (NCSM 14345) to the “Wankel” *Tyrannosaurus* specimen (MOR 555 [currently USNM 555000 with the transfer of the specimen to the National Museum of Natural History]), but is lower in the largest specimens examined here.

Given the uncertainty on the percentage of the day spent foraging, using distance traveled may provide us with a more robust comparison. Adult tyrannosaurids have been estimated to travel perhaps 18 km per day in foraging [34] which at 2 m/s would correspond to 2.5 hrs of foraging time, comparable to that seen in modern large terrestrial mammalian carnivores[21]. Over the course of a year this would amount to large bodied theropods traversing over 6500 km. If we examine distance traveled we see lower, but still significant, differences in energy expenditure ranging from 0.9 to 19.8% of total expenditure over that distance (Table 3). While these differences, around 1% in the largest theropods, may seem insignificant of the course of a year they are the equivalent of 3-6 days of total energetic expenditures (BMR + daily foraging of

18km). If we translate that to how many meals over the course of a year's foraging, it translates to over 170kg of less meat consumed in the largest specimens. This corresponds to the size of a *Ornithomimus* or subadult *Thescelosaurus* [34] and up to 1250 kg in the “Wankel” specimen compared to *Acrocanthosaurus* which is the equivalent of 5 *Thescelosaurus*.

Discussion

Getting up to speed

We find that using single, simple limb metrics, especially distal limb ratios, directly in judging the “cursoriality” of taxa across Theropoda is not defensible unless supplemented with other means of support. If looking at comparable sized individuals, particularly amongst small theropods less than 500kg, using either HL/SVL or distal limb indices has the potential to allow for accurate assessment of relative level of cursoriality between specimens, but given the low correlation value generated in our analysis, caution is advised on using these as central pillars in paleoecological reconstructions. One major reason for this is that some indices, such as HL/SVL, are highly influenced by allometry. HL/SVL amongst non-avian theropods shows a strongly negative scaling with body size ($\log \text{HL} = 0.85293 \pm 0.022505 * \log \text{SVL} + 0.26446 \pm 0.063007$, $r^2 = 0.96$, $p(\text{uncorr}) > 0.001$, $n = 77$). Thus larger animals, up until they hit the boundary where body size limits speed and acceleration potential [7], will have higher absolute speeds due to their absolutely longer leg length. Thus, at the same Froude number, they will have higher top speed regardless of the proportions of the limb. For example, *Eustreptospondylus* (HL=1209 mm, HL/SVL 0.58, Distal limb index 1.43) has a higher top speed at a Froude of 5 (7.7 m/s) than *Changyuraptor* (4.6 m/s, HL=433 mm, HL/SVL=0.96), Distal limb index 1.83. Distal limb index also shows this pattern of negative allometry, though the correlation is weaker (Distal limb

$\text{index} = -0.41125 \pm 0.064192 \cdot \log \text{SVL} + 3.0372 \pm 0.17972$, $r^2 = 0.39$, $p(\text{uncorr}) > 0.001$, $n = 77$)

which may explain why, without correcting for mass, it shows a significant relationship to top speed.

It is clear when we take into account body mass there is an upper limit on running speed that becomes more influential on the life history and ecology of theropods as one approach's ~1000 kgs. This pattern fits with what is expected theoretical [50] and shown through empirical studies [7, 20, 51]. While this size class only represent a fraction of theropod diversity [52] it represents crucial mid to top level carnivores for much of the Mesozoic since the Early Jurassic [1, 15, 53]. This raises the questions of why certain groups, most notably the tyrannosaurids, elongate their hindlimbs relative to more basal taxa when this costly addition, in terms of growth, was not aiding in increasing speed as they had already maxed out their potential for that. We suggest as one possibility that the likely selective pressure driving this was related to increasing foraging ability or home range size by decreasing the energy spent during low speed locomotion over long distance, as seen in extant taxa [20, 51]. Alternatively (and not mutually exclusive), they may have simply retained this limb proportions from smaller-bodied ancestors or earlier ontogenetic stages in which these proportions were adaptively significance in terms of increased speed [54, 55].

In many modern hunters, active searching for food does not occupy the entirety of their day [21, 22], though this does increase markedly in scavengers [35]. Of the time spent actively foraging only a fraction of that is accounted for by high speed pursuit. For example, in African wild dogs less than 8% of total hunt distance is traveled at high, yet not top, speed [56] and similar pattern

seen in the amount of running stalking time seen in lions [57]. It is probable therefore that a decrease in the ability to maximize speed would have not been a significant cost to larger theropods, since much of their lives would likely have not been spent in the active pursuit of prey at top speeds. Furthermore, the total energetic cost of hunting prey (pursuit, capture and killing) in modern larger carnivores is notably higher compared to those who favour small prey [21]. We therefore infer that amongst theropods weighing over 1000kg, selection for energetic efficiency was likely significant regardless of the interlimb proportions.

For smaller (<1000 kg) theropods the opposite conditions apply. Not only are they more likely to be small prey specialist, where pursuits are short and prey easy to subdue, limiting the energy losses during hunting. Yet just as importantly these organisms are themselves potential prey items to larger theropods. This means that they have a strong selective pressure to obtain high top speed, especially with a short acceleration time, to facilitate escape. Thus, we find two opposing selective pressures across theropod hindlimb, one at small size to maximize speed which decreases as you get larger to focus more on energetic savings in mid-sized to large members of the theropod community.

Why tyrannosaurids?

In looking for the origins behind the trend of long leggedness in tyrannosaurids, and the potential ecological and behavioural underpinnings for it, one must first determine if it a plesiomorphic feature of a wider Tyrannosauroida or even coelurosaurian condition. That the coelurosaur condition is characterized by elongated hindlimbs is unlikely as other basal coelurosaurs such as compsognathids show reduced hindlimbs, among the lower third of the dataset and though the

tibia is incomplete *Zuolong* shows values closer to *Deinonychus* (59th) than *Tanycolagreus*.

While some basal tyrannosauroids do show elongated hindlimbs compared to femoral circumference (Sup. Table 4,5) such as *Guanlong* (1st), *Tanycolagreus* (12th), and *Moros* (11th), others such as the basal *Coelurus* (65th) or *Dryptosaurus* (42nd), the latter of the two is larger (> 1000kg) and closer to tyrannosaurines, ranks in the lower half. Additionally, if one were to reconstruct the femoral circumference of *Dilong* from its femoral width it would rank in the bottom quartile at around 64th. This combined with significant uncertainty due to the number of partial specimens at the base of the tyrannosauroid tree as well as the potential for the Megaraptora to be basal tyrannosauroids [58], paints an uncertain picture of how to reconstruct the evolution of hindlimb elongation in this clade. What we can say is that all the small long-legged basal members of this clade are well below the inflection point of selective pressures for speed versus efficiency. As such their position as mid-level predators in their ecosystem who were potential prey themselves could lead to species specific selection pressures being confused with clade wide trends. Finally, as we do not have a good understanding of the size of basal members of Tetanurae or Orinoidea, though we suspect they were significantly smaller our cross over point [2, 15, 59]. Without these fossils, we cannot assess if derived tyrannosaurs retained the elongated hindlimbs of their small ancestors as they evolved gigantism or if this was a secondary elongation event confined to the later members of Eutyranosauria.

Despite this the fact that both subadult and mature allosauroids, tyrannosaurines and tetanurans were too large to access upper range of speed due to their hindlimb length, raises the question of why they differ so much in relative limb length. One potential explanation is difference in prey choice. Sauropods were rare in those communities where Tyrannosauridae existed [60], with

only a single taxon, *Alamosaurus*, known from North America restricted to the Southernmost part of *Tyrannosaurus*' range [61], and two (c.f. [62]) small sauropods from the Nemegt which are minor members of the fauna [63]. For tyrannosaurids the most common larger prey taxa are herds of ceratopsians and hadrosaurs which are on the order of 1/5-1/10 the mass of the sauropod prey available to the larger allosauroids and basal tetanurans [52]. Furthermore, sauropods were a ubiquitous component of the ecosystems of these more basal large theropods [64], presenting a common and calorie dense meal source either through direct predation or carcass scavenging. While it is likely that much of the prey captured for theropods were juvenile and subadult specimens regardless of the prey species [65], sauropods would still provide a much larger meal with many species with over 40% of the population consisted of individuals of 3500kg or more [64]. In addition sauropod trackways indicate they tended to walk at slow speeds [66], and their size alone strongly suggests they would have a limited top speed significantly below that of their contemporaneous larger theropod faunas [7]. Thus, sauropods would provide an abundance of larger, slower and more energy dense food resources for more basal large theropod clades. Conversely we are suggesting that the pressure for obtaining more kills due to the fact that each kill provides less resources, thus necessitating minimizing energy expenditure per hunt and maximizing resource extraction per kill, especially if that kill is shared amongst a group, influenced selection for longer limbs in Tyrannosauridae.

Hunting the relatively smaller and faster hadrosaurs and ceratopsians may also have been facilitated by group behavior in tyrannosaurids, something previously documented by track and body fossils in large theropods [38, 67]. Juveniles, less than 10-15 years of age [68, 69] would still be in the zone where their long legs could be used to maximize top speed, potentially

helping run down faster prey items. Beyond this it has been shown that amongst pack hunting animals employing strategy or communication between individuals can allow them to capture prey that is faster than any one individual [70]. Combining these factors we find that pack hunting would only increase the energetic savings differential even more dramatic between tyrannosaurs compared to allosauroids. For example, if we assume a tyrannosaur “pack” consisting of two adults around the size of BHI 3033 or MOR 555 and two subadults with femora approaching 1 m in length and 2500kg in mass and two juveniles the same size as “Jane” the savings versus a similar sized and demographically distributed group of *Acrocanthosaurus* or *Saurophaganax* is between 4000-4300kg worth of prey. This corresponds to about the mass of a 1-2 hadrosaurids [34] or 28-30 days of total energetics for the groups. If similar to modern large terrestrial carnivores the majority of hunts end in failure with only a 20-30% success rate [21], such a savings would reduce the necessity for multiple hunts, where during each on beyond the loss of energy in a failed capture this there is the inherent risk from injury either during the pursuit or capture itself. Such a large amounts of savings, corresponding to several large kills per year, would have significant effect on survivorship of the group.

Finally, there is the fact that meat acquisition does not necessarily have to exclusively come from the capture and killing of live prey items. Most modern primary predators and, likely, extinct ones such as large theropods, probably incorporate a significant fraction of carrion into their diet [35]. We know of several occurrences of likely scavenged tyrannosaurid feeding traces [65, 71, 72] indicating some facultative carrion usage did occur. Recent work [35] has estimated that scavenging would have been most important to mid to large, but not extremely large, sized theropods around the range that we find mass induced upper limits on top speed. While we may

not agree with the assumptions and assertions of the level of scavenging suggested by [35], we do suggest that this is another line of evidence of the increasing role of energy efficiency over long distances locomotion. Given the data we have presented here saving multiple days' worth of feeding requirements due to reduced energetic demands by increased leg length in large tyrannosaurids. Any adaptation that helps reduce the costly and potentially hazardous search, capture, killing and defending a kill would be a significant evolutionary advantage for that lineage and may have been one of the keys to their success in the Late Cretaceous c.f. [73].

Conclusions

Here we find that traditional simple metrics, notably the distal limb index, fail to reflect true measures of cursorial and especially top speed potential across Mesozoic theropods. When direct comparisons of similar sized individuals are performed several clades, most notably the compsognathids and basal birds which show high levels of distal limb elongation, do not show comparable total limb relative lengths or top speed to microraptorines or basal troodontids. Without accounting for the allometric influence on any of these limb metrics we remain highly skeptical of their broad application. Additionally we also show that when we include the fact that there is a parabolic distribution of top speeds, with a local maxima between 500-2000kg depending on the Froude number used to estimate speed, there is no significant relationship between distal limb index (or indeed any other commonly used hindlimb index) and top speed across theropods. We argue that selection for intralimb lengths is likely multifaceted, clade specific and unlikely to be captured in a simply, overarching metric.

Factors such as clade history, diet and prey capture methods, for example the role of the hindlimb in subduing prey in eudromaeosaurs [74] likely has implication for why they tend to have short metatarsals, all combine with speed and cost of transport influences to shape the final product. Despite saying this we do propose that, at a first order of magnitude, we can argue that there body size likely has a major role. Body sizes is here postulated to be strongly influential in the shifting the speed versus endurance/ energy savings balance in the paleobiology of theropods. Smaller taxa are more likely to take smaller prey, which reduces foraging and capture costs but conversely are they themselves much more likely to be predated upon. For them a fleet foot may be the difference not just in a full or empty belly but in life or death. In larger taxa this balance shifts to be more “waste not, want not” as they are much less likely to be hunted while they are searching for prey.

We also find that amongst the large bodied theropods tyrannosaurids show markedly reduced values of cost of transport due to their elongated limbs. While their body size makes this unlikely to be of much value in increasing running speed, it does significantly save on the cost of daily foraging expenditures. These savings, up to several tones of meat per year per individual, would dramatically reduce the need to engage in the costly, dangerous and time-consuming act of hunting. When coupled with the evidence that tyrannosaurids were, at least on occasion, living in groups as well as the fact their primary prey was on average smaller and more elusive than the sauropods that were a major component of the diet of more basal large theropods, this paints a picture where efficiency would be a major evolutionary advantage. While we cannot clearly ascertain if the “legginess” of tyrannosaurs was an adaptation itself or the retention of the ancestral condition of elongated hindlimbs as gigantism evolved in this clade both options

present interesting evolutionary scenarios with broader implications for the paleobiology and paleoecology of the Late Jurassic to Late Cretaceous ecosystems of Laurasia.

Interestingly, additional analyses support the hypothesis that tyrannosaurids were more agile (that is, capable of turning more rapidly and with a smaller turning radius) than other comparable-sized large-bodied theropods [9]. This similarly reflects a specialization with Tyrannosauridae for hunting large-bodied ornithischians such as hadrosaurids and ceratopsids themselves likely more mobile and agile than sauropods. When combined these two lines of evidence for an energy efficient, yet still nimble, design of the Tyrannosauridae hindlimb reflect a likely long-distance stalker with a final burst to the kill likely in a pack or family unit, similar to modern wolves. This further reinforces the notion, that beyond being the apex predator of the latest Cretaceous Laurasian ecosystems, the tyrannosaurids were amongst the most accomplished hunters amongst large bodied theropods. We find that their anatomy, at once efficient and elegant, yet also capable of burst of incredible violence and brute force, lives up to their monikers as the tyrant kings and queens, of the dinosaurs.

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Table 1: Specimens used for costs of transport analysis based on published 3D volumetric data.

HL stands for hindlimb length which here is taken as femur + Tibia + central metatarsal lengths.

HH is hip height, calculated as $0.8 \cdot HL$. CoT is cost of transport, see text for details.

Source	Taxon	Specimen	Mass (kg)	HL (mm)	HH (cm)	CoT
Bates et al. 2009	<i>Struthiomimus</i>	BHI 1266	423	1800	144.0	1.97
Bates et al. 2009	<i>Allosaurus</i>	MOR 693.	1500	1699	135.9	2.06
Bates et al. 2009	<i>Tyrannosaurus</i>	MOR 555/USNM 555000	6072	3036	242.9	1.31
Bates et al. 2009	<i>Acrocanthosaurus</i>	NCSM 14345	6177	2675	214.0	1.45
Bates et al. 2012	<i>Tyrannosaurus</i>	BHI 3303	7655	3196	255.7	1.26
Pontzer et al. 2009	<i>Archaeopteryx</i>	MB.Av.101	0.25	158	12.6	12.80
Pontzer et al. 2009	<i>Marasuchus</i>	Composite	1.00	170	13.6	12.10
Pontzer et al. 2009	<i>Microraptor</i>	IVPP V13352	1.20	291	23.3	8.00
Pontzer et al. 2009	<i>Compsognathus</i>	BSP AS I563	3.00	209	16.7	10.32
Snively et al. 2018	" <i>Raptorex</i> "	LH PV18	47	998	79.8	3.10
Snively et al. 2018	<i>Eustreptospondylus</i>	OUM J13558	206	1245	99.6	2.61
Snively et al. 2018	<i>Dilophosaurus</i>	UCMP 37302	372	1412	113.0	2.37
Snively et al. 2018	<i>Gorgosaurus</i>	TMP 91.36.500	496	1825	146.0	1.95
Snively et al. 2018	<i>Tyrannosaurus</i>	BMRP 2002.4.1	660	2120	169.6	1.73
Snively et al. 2018	<i>Ceratosaurus</i>	USNM 4735	678	1429	114.3	2.35
Snively et al. 2018	<i>Gorgosaurus</i>	AMNH 5664	688	1928	154.2	1.87
Snively et al. 2018	<i>Tarbosaurus</i>	ZPAL MgD-I/3	727	1845	147.6	1.93
Snively et al. 2018	<i>Allosaurus</i>	USNM 4734, UUVF 6000	1512	1985	158.8	1.82
Snively et al. 2018	<i>Allosaurus</i>	MOR 693	1683	1795	143.6	1.97
Snively et al. 2018	<i>Yangchuanosaurus</i>	CV 00215	2176	1988	159.0	1.82
Snively et al. 2018	<i>Sinraptor</i>	ZDM 0024	2374	2340	187.2	1.61
Snively et al. 2018	<i>Gorgosaurus</i>	AMNH 5458	2427	2640	211.2	1.46
Snively et al. 2018	<i>Gorgosaurus</i>	NMC 2120	2427	2634	210.7	1.47
Snively et al. 2018	<i>Tarbosaurus</i>	PIN 552-1	2816	2415	193.2	1.57
Snively et al. 2018	<i>Acrocanthosaurus</i>	NCSM 14345	5474	2676	214.1	1.45
Snively et al. 2018	<i>Giganotosaurus</i>	MUCPv-CH-1	6908	3020	241.6	1.32
Snively et al. 2018	<i>Tyrannosaurus</i>	CM 9380	6987	3124	249.9	1.29
Snively et al. 2018	<i>Tyrannosaurus</i>	FMNH PR 2081	9131	3261	260.9	1.24
Person and Currie 2014	<i>Khaan</i>	MPC-D 100/1127	5	391	31.3	6.37
Person and Currie 2014	<i>Velociraptor</i>	MPC1--/986	15	592	47.4	4.63
Person and Currie 2014	<i>Ajancingenia</i>	MPC-D 100/30	17	634	50.7	4.39
Person and Currie 2014	<i>Ornithomimus</i>	TMP 95.11.001	150	1220	97.6	2.65
Person and Currie 2014	<i>Gorgosaurus</i>	TMP 91.36.500	400	1815	145.2	1.95

Person and Currie 2014	<i>Tyrannosaurus</i>	BHI 3303	5622	3196	255.7	1.26
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Table 2: Foraging costs amongst large bodied theropods based on volumetric reconstructions.

A) costs in KJ on an hourly, daily and yearly basis. B) Costs of foraging in KJ per unit distance assuming a 18km daily foraging distance as per Carbonne et al (2011) for 1Km, 1 day (18 Km) and 1 year (6570Km).

A)

Taxon	specimen	Mass (kg)	HL (mm)	HH (cm)	CoT	Foraging 12 hrs/ day		
						hr	day	year
<i>Tyrannosaurus</i>	MOR 555	6072	3036	242.9	1.31	57481	689771	251766250
<i>Acrocanthosaurus</i>	NCSM 14345	6177	2675	214.0	1.45	64462	773541	282342590
<i>Tyrannosaurus</i>	BHI 3303	7655	3196	255.7	1.26	69657	835879	305095703
<i>Tyrannosaurus</i>	BMRP 2002.4.1	660.23	2120	169.6	1.73	8241	98892	36095640
<i>Sinraptor</i>	ZDM 0024	2373.5	2340	187.2	1.61	27457	329487	120262751
<i>Gorgosaurus</i>	AMNH 5458	2427.3	2640	211.2	1.46	25589	307067	112079592
<i>Gorgosaurus</i>	NMC 2120	2427.3	2634	210.7	1.47	25634	307606	112276127
<i>Tarbosaurus</i>	PIN 552-1	2816.3	2415	193.2	1.57	31798	381573	139274251
<i>Acrocanthosaurus</i>	NCSM 14345	5474.1	2676	214.1	1.45	57110	685320	250141950
<i>Giganotosaurus</i>	MUCPv-CH-1	6907.6	3020	241.6	1.32	65658	787893	287580837
<i>Tyrannosaurus</i>	CM 9380	6986.6	3124	249.9	1.29	64700	776397	283384765
<i>Tyrannosaurus</i>	FMNH PR 2081	9130.87	3261	260.9	1.24	81808	981697	358319261
<i>Tyrannosaurus</i>	BHI 3303	5622	3196	255.7	1.26	51157	613888	224068980

B)

Source	Taxon	specimen	mass (kg)	per km	18 km	6570 km
Bates et al. 2009	<i>Tyrannosaurus</i>	MOR 555	6072	7983	143702	52451302
Bates et al. 2009	<i>Acrocanthosaurus</i>	NCSM 14345	6177	8953	161154	58821373
Bates et al. 2012	<i>Tyrannosaurus</i>	BHI 3303	7655	9675	174141	63561605
Snively et al. 2018	<i>Tyrannosaurus</i>	BMRP 2002.4.1	660.23	1145	20603	7519925
Snively et al. 2018	<i>Sinraptor</i>	ZDM 0024	2373.5	3814	68643	25054740
Snively et al. 2018	<i>Gorgosaurus</i>	AMNH 5458	2427.3	3554	63972	23349915
Snively et al. 2018	<i>Gorgosaurus</i>	NMC 2120	2427.3	3560	64085	23390860
Snively et al. 2018	<i>Tarbosaurus</i>	PIN 552-1	2816.3	4416	79494	29015469
Snively et al. 2018	<i>Acrocanthosaurus</i>	NCSM 14345	5474.1	7932	142775	52112906
Snively et al. 2018	<i>Giganotosaurus</i>	MUCPv-CH-1	6907.6	9119	164144	59912674
Snively et al. 2018	<i>Tyrannosaurus</i>	CM 9380	6986.6	8986	161749	59038493
Snively et al. 2028	<i>Tyrannosaurus</i>	FMNH PR 2081	9130.87	11362	204520	74649846
Person and Currie 2016	<i>Tyrannosaurus</i>	BHI 3303	5622	7105	127893	46681037

Table 3: A) Cost of transport during daily foraging during and energy expenditure calculated using basal metabolic rate (BMR) estimates per [45, 46] in Kj. B) Comparison of daily energy expenditure (foraging + BMR) between Tyrannosauridae and similar sized basal large bodied theropods.

A)

Source	Taxon	specimen	mass (kg)	HL	CoT	Foraging	BMR [45]	BMR[46]
Snively et al. 2018	<i>Tyrannosaurus</i>	BMRP 2002.4.1	660	2120	1.73	98892	20270	10226
Snively et al. 2018	<i>Ceratosaurus</i>	USNM 4735	678	1429	2.35	137647	20676	10454
Snively et al. 2018	<i>Gorgosaurus</i>	AMNH 5664	688	1928	1.87	110818	20887	10573
Snively et al. 2018	<i>Sinraptor</i>	ZDM 0024	2374	2340	1.61	329487	51915	29199
Snively et al. 2018	<i>Gorgosaurus</i>	AMNH 5458	2427	2640	1.46	307067	52778	29740
Snively et al. 2018	<i>Gorgosaurus</i>	NMC 2120	2427	2634	1.47	307067	52778	29740
Snively et al. 2018	<i>Acrocanthosaurus</i>	NCSM 14345	5474	2676	1.45	685320	95950	57938
Person and Currie 2016	<i>Tyrannosaurus</i>	BHI 3303	5622	3196	1.26	613888	97848	59218
Bates et al. 2009	<i>Tyrannosaurus</i>	MOR 555	6072	3036	1.31	689771	103546	63078
Bates et al. 2009	<i>Acrocanthosaurus</i>	NCSM 14345	6177	2675	1.45	773541	104859	63971
Snively et al. 2018	<i>Giganotosaurus</i>	MUCPv-CH-1	6908	3020	1.32	787893	113839	70112
Snively et al. 2018	<i>Tyrannosaurus</i>	CM 9380	6987	3124	1.29	776397	114794	70769

B)

Taxon	specimen	total daily (basal + 12 hours walking)				18 km + daily BMR			
		BMR [45]	% difference	BMR[46]	% difference.	BMR [45]	% difference	BMR[46]	% difference
Tyrainnosaurus	BMRP 2002.4.1	119162	32.5	109118	35.5	40873	19.8	30828	26.2
<i>Ceratosaurus</i>	USNM 4735	158323	x	148101	x	49352	x	39131	x
<i>Gorgosaurus</i>	AMNH 5664	131705	20.4	121392	22.1	43974	12.7	33660	16.6
<i>Sinraptor</i>	ZDM 0024	381402	x	358686	x	1205583	x	97842	x
<i>Gorgosaurus</i>	AMNH 5458	359845	6.2	336808	6.7	116750	4.0	93712	5.0
<i>Acrocanthosaurus</i>	NCSM 14345	781270	x	743258	x	238725	x	200713	x
<i>Tyrannosaurus</i>	BHI 3033	711736	10.0	673106	10.6	225741	6.6	187111	8.0
<i>Tyrannosaurus</i>	MOR 555	793316	x	752848	x	247248	x	206780	x
<i>Acrocanthosaurus</i>	NCSM 14345	878400	9.5	837512	10.0	266013	6.6	225125	7.8
<i>Giganotosaurus</i>	MUCPv-CH-1	901731	x	858005	x	277983	x	234256	x
<i>Tyrannosaurus</i>	CM 9380	891191	1.3	847165	1.4	276543	0.9	232518	1.0

Figure Captions

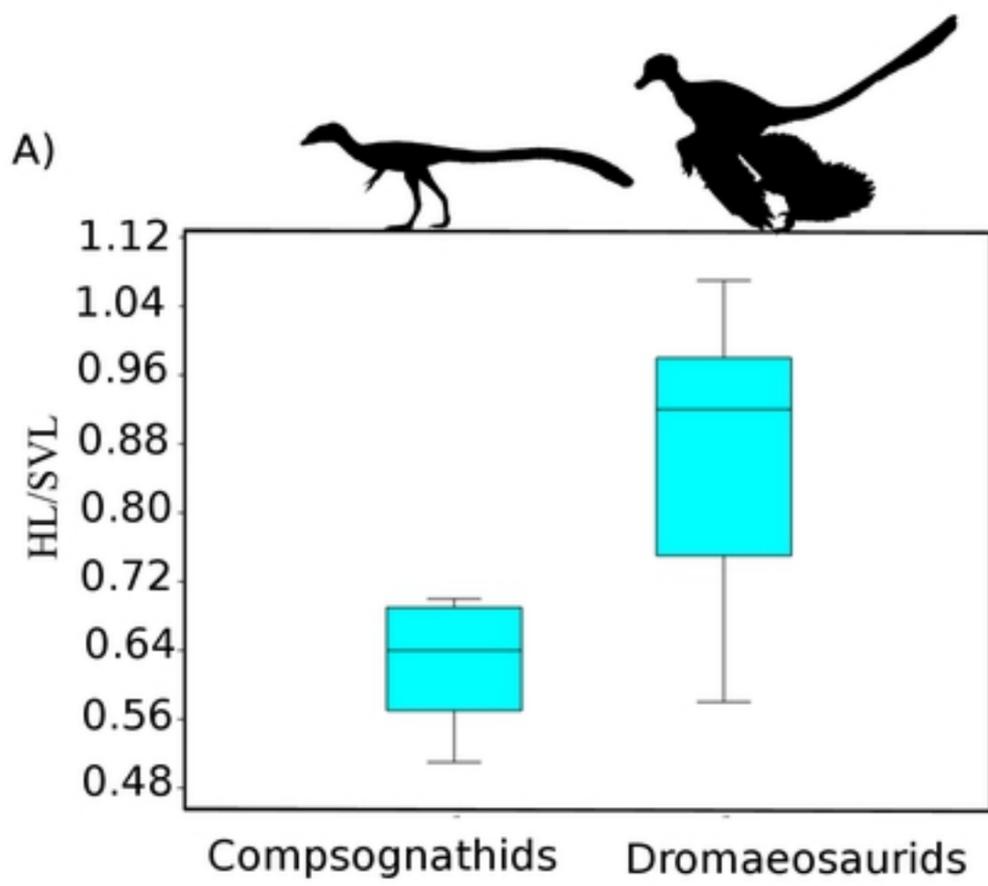
Figure 1: Comparison of two small bodied theropod clades, the compsognathids and dromaeosaurids, using different hindlimb indices purported to be associated with cursorial ability. Note the significant difference in how the running ability and top speed would be reconstructed depending on the metric selected. Using relative hindlimb length (A) we find a significant difference between the two groups (unequal variance t-test 5.1471, $p=0.001$) and would reconstruct dromaeosaurids as significantly faster than compsognathids. Using distal limb index (B) we see no difference between clades (unequal variance t-test 0.7713, $p=0.45$). Silhouette modified from those in Phylopic image repository (Phylopic.org) created by Joh Conway and Brad McFeeters.

Figure 2: Top speed comparison between clades using speed calculated from equations in [28], though all reconstruction methods show similar patterns, either including (A) or excluding (B) *Halszkaraptor* based on its proposed unique semi aquatic lifestyle. Note that at lower speeds the dromaeosaurs, more specifically microraptorines, show distinctly higher top speed than comparably size compsognathids, *Archaeopteryx* specimens or basal birds and similar values to troodontids. Silhouette modified from those in Phylopic image repository (Phylopic.org) created by Joh Conway, Matt Martyniuk, Gareth Monger and Brad McFeeters.

Figure 3: Evaluation of the fit of hindlimb index proxies to estimated top speed at Froude=5 (A) and using the mass induced limitation as proposed in [7] using the primary dataset of taxa with SVL data. Skeletal image of *Microraptor* modified from the illustrations of S. Hartman.

Figure 4: Evaluation of the fit of the distal limb index proxy to estimated top speed at Froude=5 (A) and using the mass induced limitation as proposed in [7] in the larger hindlimb dataset (Sup. Table 4). Skeletal image of *Microraptor* modified from the illustrations of S. Hartman.

Figure 5: Observing the effect of increasing body mass on top speed in non-avian theropods by evaluating the difference between various reconstructive methods. Note that at smaller body size, less than 100 kg, there is a large and increasing gap between the top speed limit imposed by [7] and top end estimates from other methods. This gap becomes largest in specimens between 10-100 kg indicating that perhaps these specimens had the highest ceiling to increase running speed by exaggerating hindlimb muscle size, altering insertion location, moment arm length, total leg length or stride frequency. Silhouette modified from those in Phylopic image repository (Phylopic.org) created by Joh Conway, Scott Hartman, Emily Willoughby and Matt Martyniuk.



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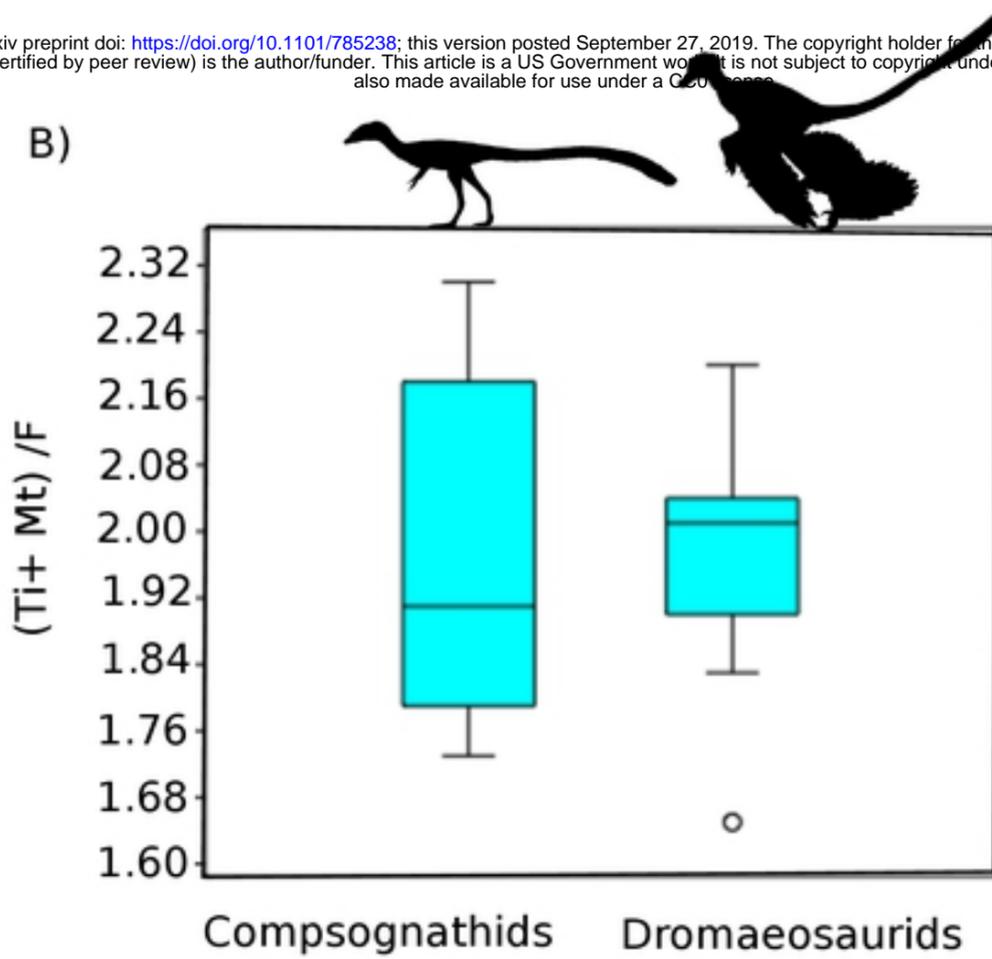


Figure 1

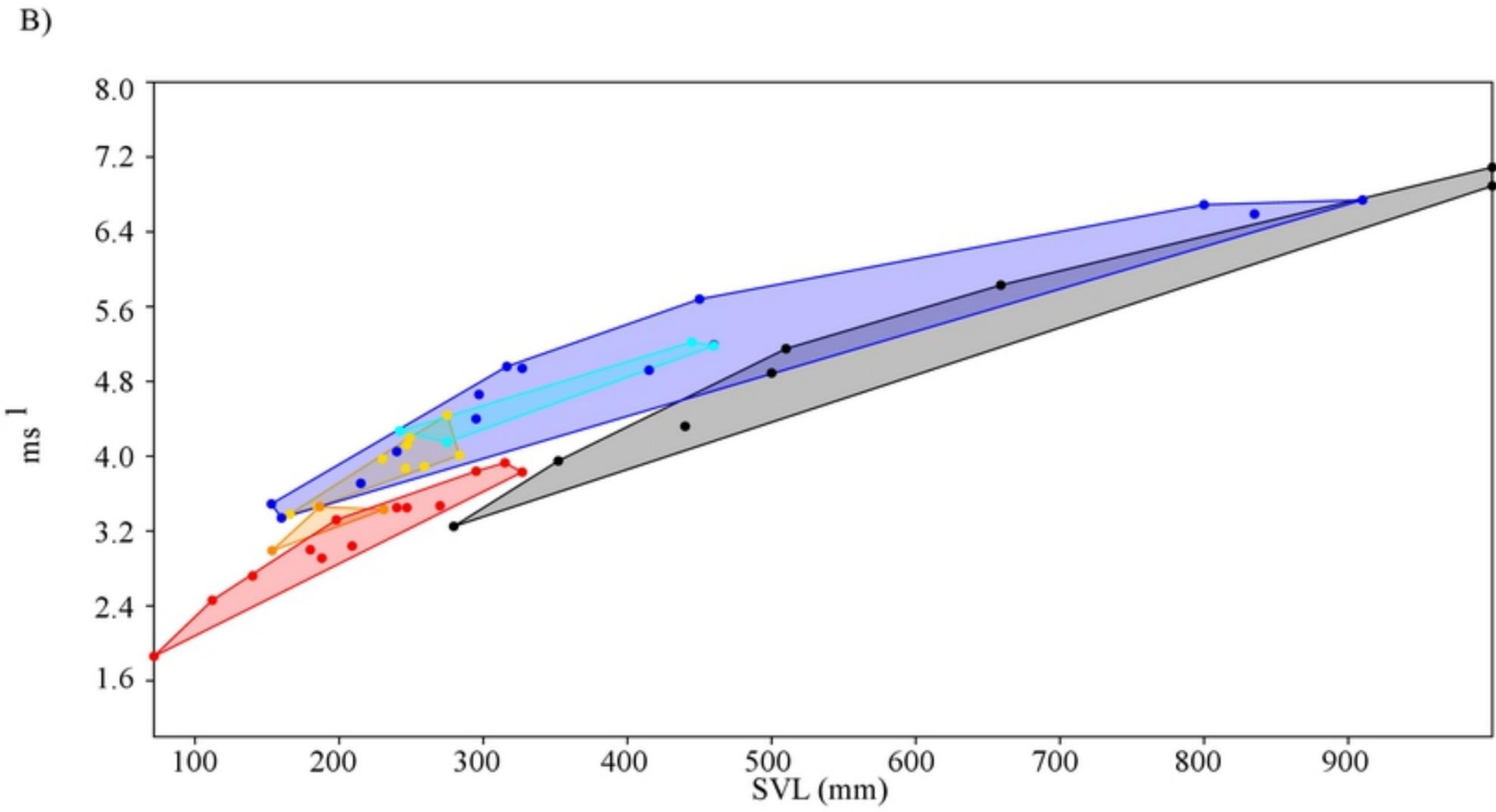
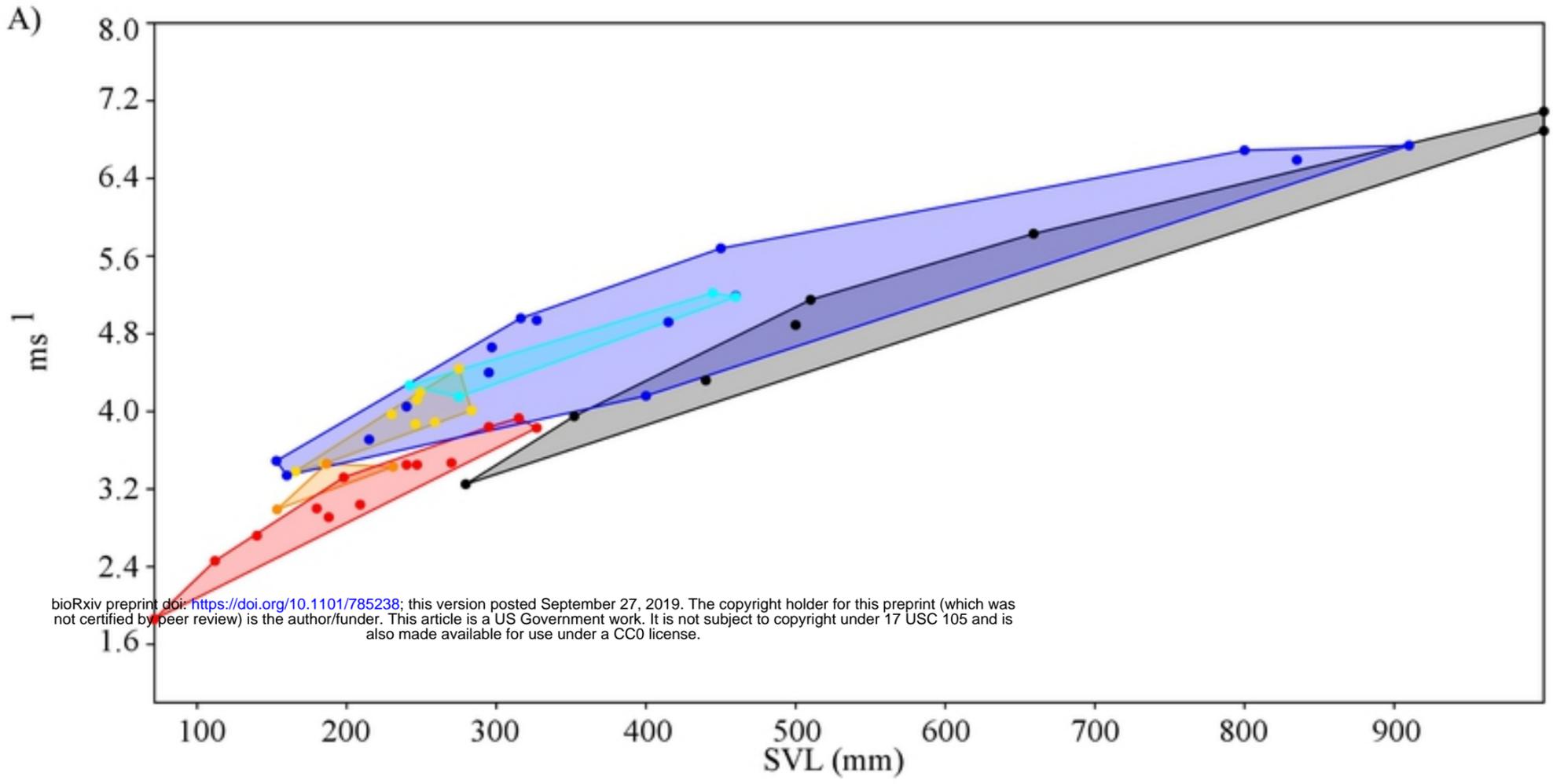
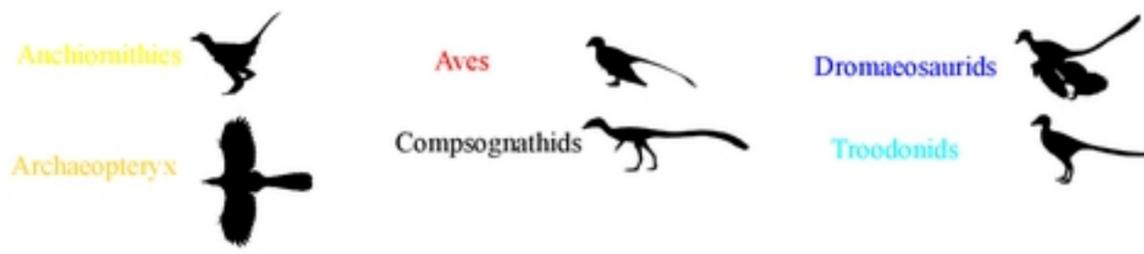
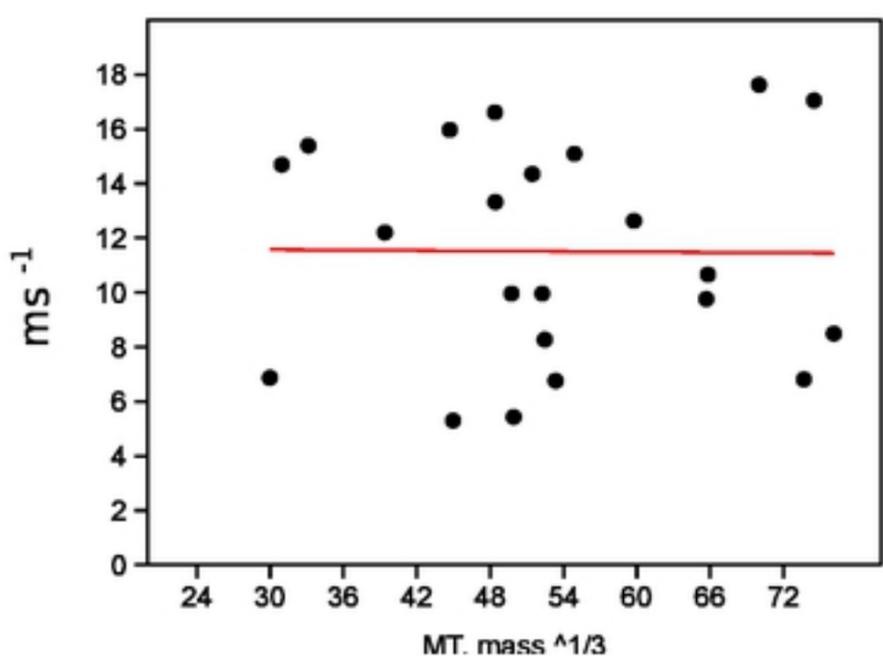
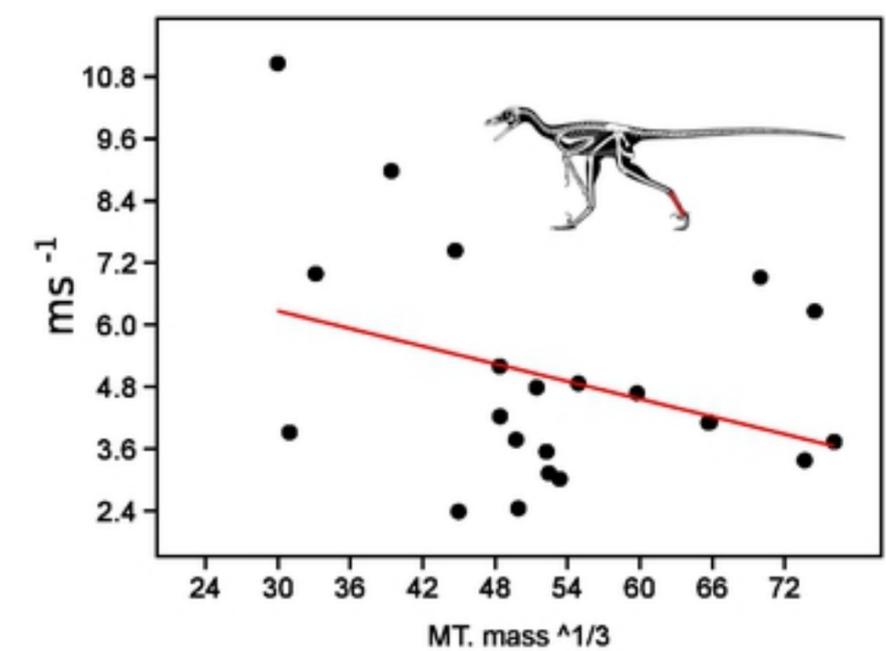
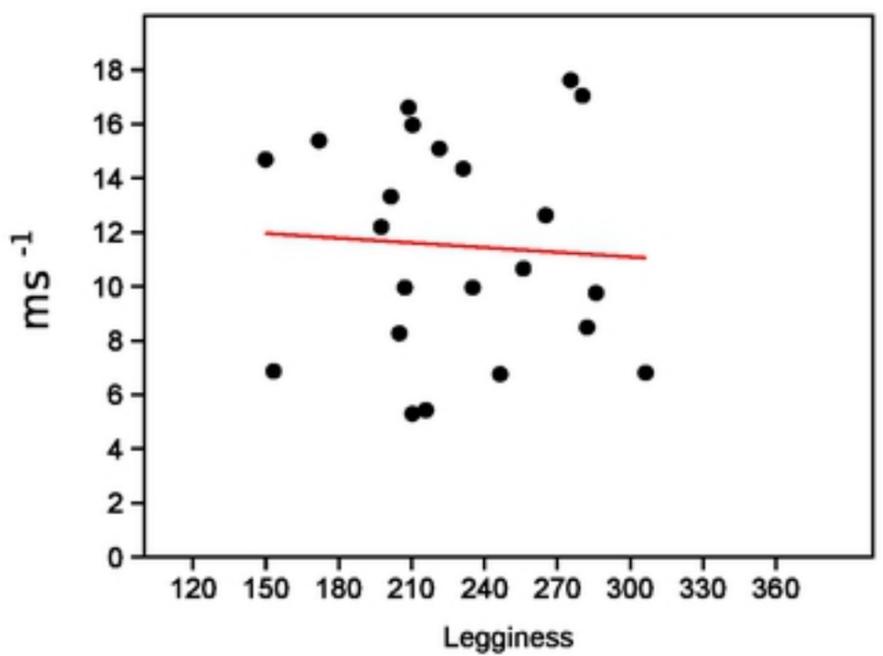
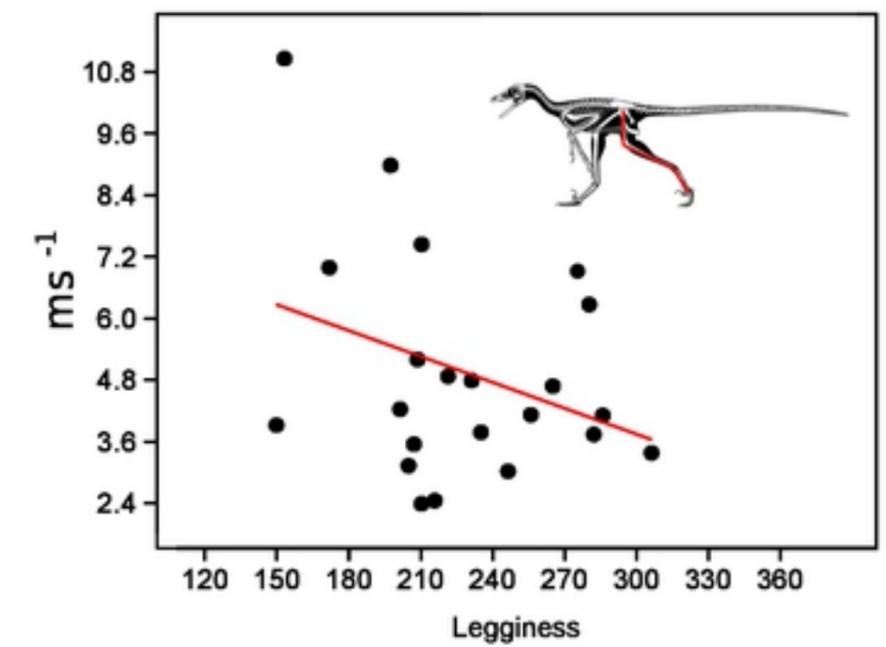
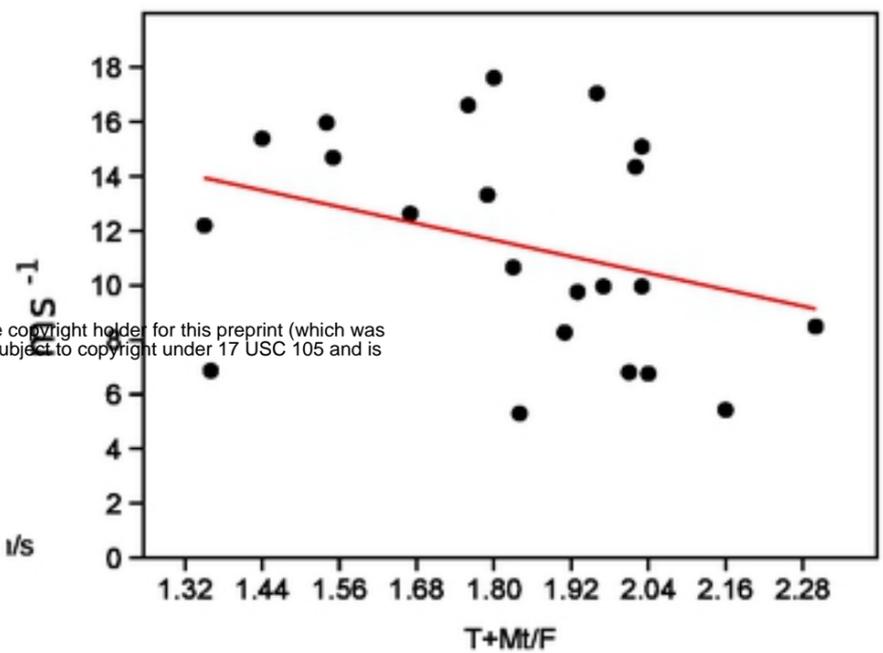
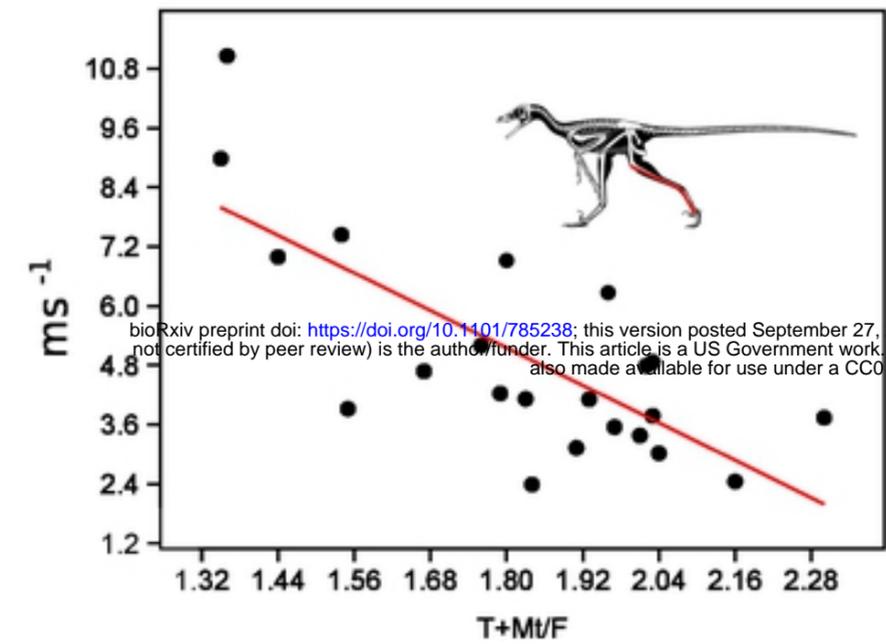
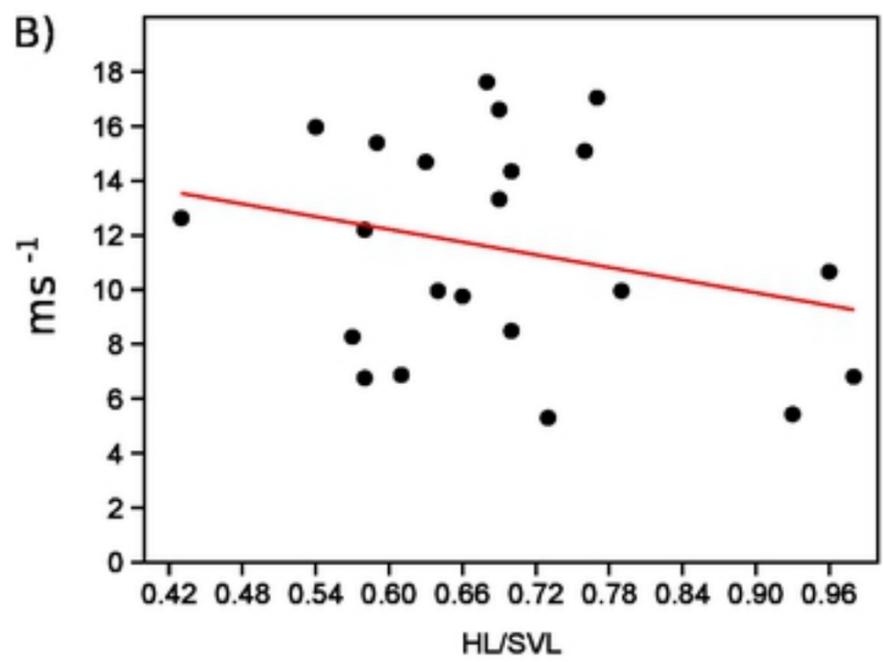
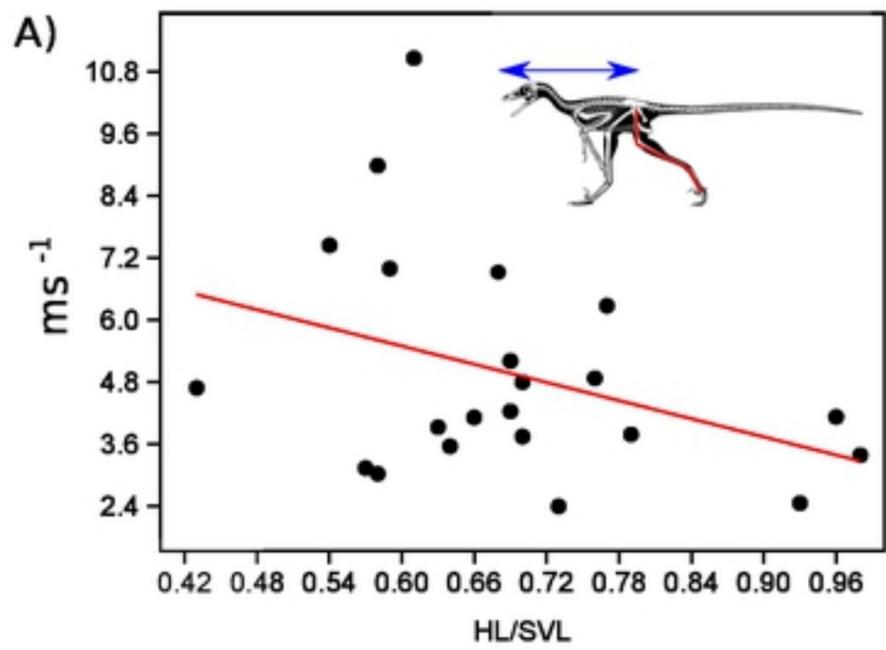


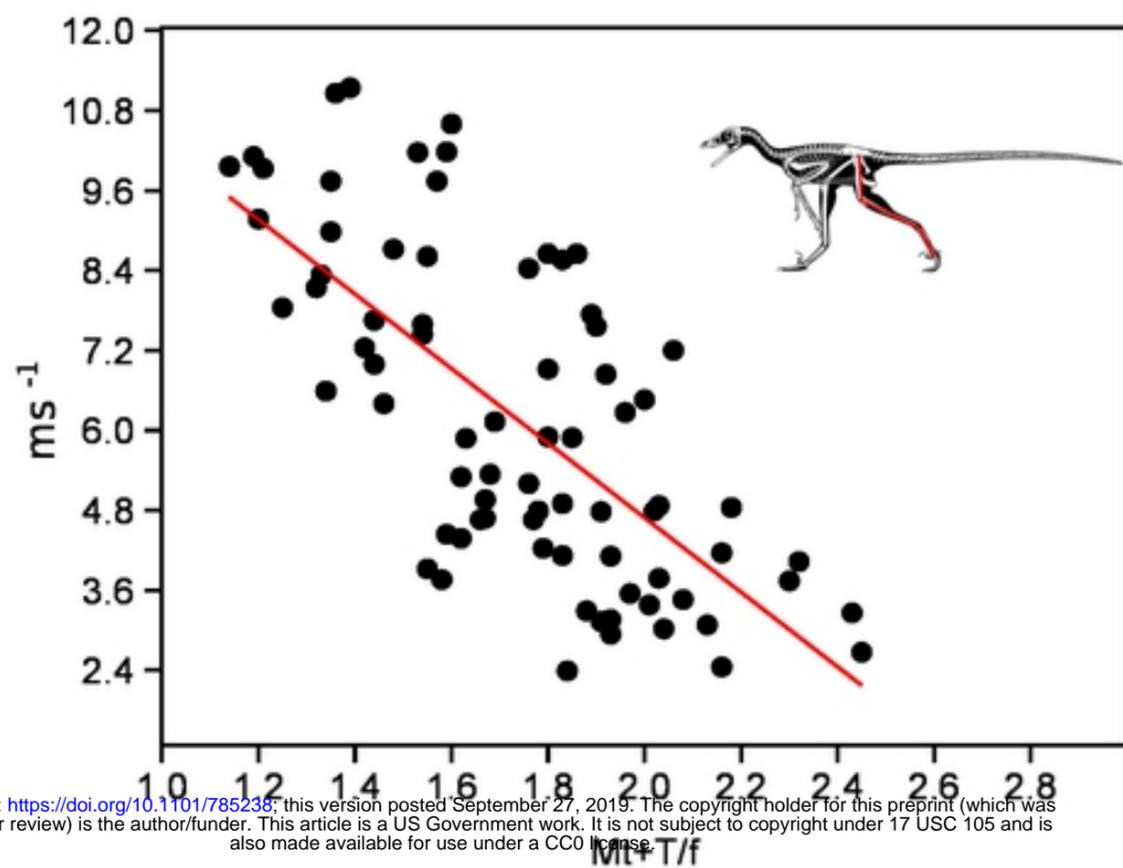
Figure 2



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Figure 3

A)



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B)

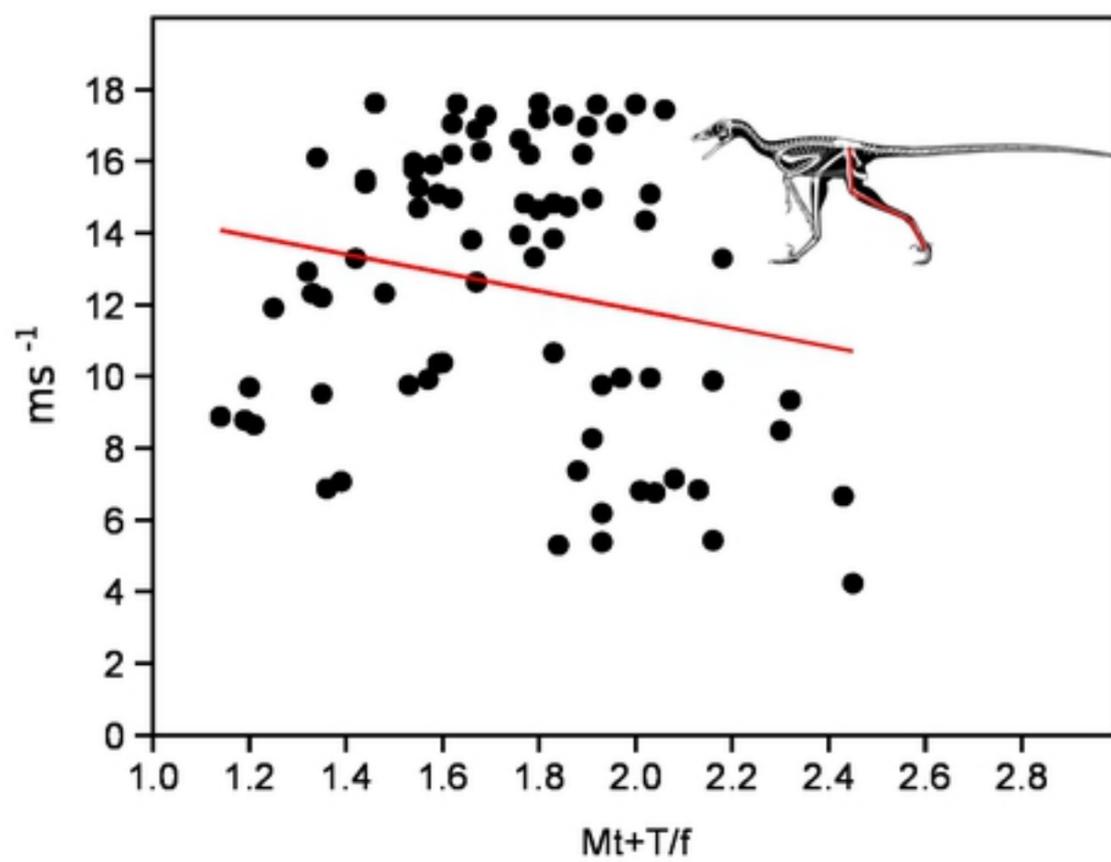


Figure 4

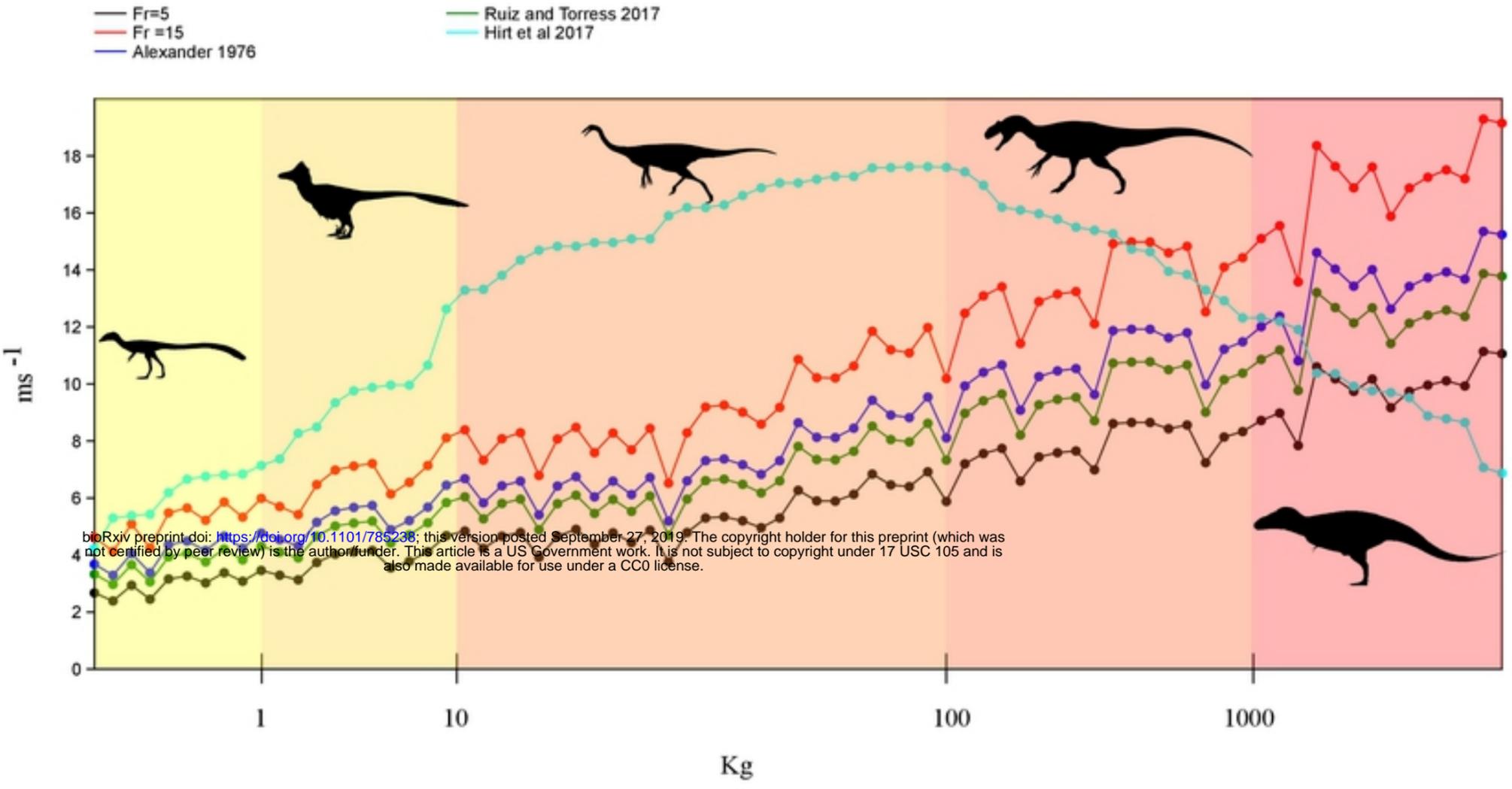


Figure 5