Ontogeny of *Albertosaurus sarcophagus*: speedy adults or fast juveniles, how the development of the species affected the biomechanics and the implications for hunting strategies.

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Abstract:

The focus of this study was to examine the overall speeds that can be reached by *Albertosaurus sarcophagus* and comparing the results of *Struthio camelus* to determine the likelihood of those speeds being reached. The first step of the study was to determine the allometric relations that were present in the hindlimb bones of both *Albertosaurus sarcophagus* and *Struthio camelus*. Allometry was recorded in most of the hindlimb bones present in both *Albertosaurus* and Ostrich. The weights of both *Albertosaurus sarcophagi* and *Struthio camelus* were determined by using methods described by Christiansen and Fariña in 2004, and Anderson et al 1985. The weight method that was determined to provide more reliable methods was the Anderson et al 1985. The weight ranges calculated for *Albertosaurus sarcophagus* were 196kg to 1765kg, and for *Struthio camelus* was 22.6kg to 184.1kg. The over speeds that were determined for *Albertosaurus sarcophagus* for the adults was 33.12Km/h, the sub adult was 23.11Km/h and the juvenile was 13.50Km/h. There were two speeds used for *Struthio camelus*, a running speed and a trotting speed, the running speed was 37.62Km/h and the trotting speed was 24.16Km/h. The speeds obtained for *Struthio camelus* were close to the recorded speed, which suggests that Alexander's 1976 methods produced more reliable methods (Hutchins et al 2002). Because of the speeds that have been calculated for *Albertosaurus sarcophagus* potential pack behaviour can be determined, specifically the hunting strategies. Considering the maximum speed of a ceratopsian, a major source of food for *Albertosaurus sarcophagus*, was approximately 25Km/h; this suggests that the sub adults and the adults would probably have the most active role in the pack for obtaining food. As *Albertosaurus sarcophagus* were close to the speed of the prey, if not faster than the prey; this can allow for active predation to occur. Because of these speed differences, juveniles probably had food brought to them by the parents and sub adults of the pack.

Keywords:

Albertosaurus sarcophagus, Struthio *camelus*, biomechanics, speed differences, hunting strategies, pack behaviour

Introduction:

The biomechanics of dinosaurs has always been a topic of interest to both the scientific community and the community in general. The locomotion of dinosaurs has always fascinated humanity; however, from movies to documentaries there have been multiple interpretations of the locomotion of the dinosaurs. Each movie and documentary has shown a slight difference in how they can move, the biomechanics, and this has encouraged paleontologists to extensively start to study the biomechanics of dinosaurs. Over the years, the perception of locomotion has changed from slow lumbering dinosaurs to fast agile dinosaurs; this has been seen first in movies and documentaries, and then in paleontological studies. However, there are some dinosaurs whose movements within their environments have not yet been studied, such as *Albertosaurus*. Studying *Albertosaurus* can give scientists a better understanding of the environment in which it lived. For instance, if *Albertosaurus* was a pack hunter, this would suggest that the food web would be more complex than originally perceived. Understanding how *Albertosaurus* moved in its environment can give a better indication of how members of the Tyrannosauridae family moved, and the possible evolutionary pressures that were placed on the Tyrannosauridae to develop and refine one method over another.

Albertosaurus sarcophagus was first discovered by Joseph B. Tyrrell in the Drumheller region. It was first given its name by Osborn in 1905, the year when Alberta became a province. It was given the name *Albertosaurus sarcophagus* for the province in which the first specimen was found. *Albertosaurus sarcophagus* is a member of the family Tyrannosauridae, but it is classified as a sub group of the Tyrannosauridae; as member of the Albertosaurinae. Fossilised adults indicate that it was smaller and more agile than the *Tyrannosaurus*. The average length of *Albertosaurus* is approximately 8 meters, while the weight is approximately 2.5 tonnes (Paul, 2010). Though, the largest individuals could probably attain a length of 11 meters. *Tyrannosaurus rex* is approximately up to 12 meters long and its weight has been estimated to be about 6 tonnes (Paul, 2010). By understanding how Tyrannosaurid paleobiology works, including posture, speed, and ontogeny, paleontologists can compare it to that of *Albertosaurus* (Brusatte, 2010, 2012, Carr, 1999). It is also helpful to look at a modern day animal, such as the alligator, to compare to *Albertosaurus* and to consider the environment, as well as how the growth of *Albertosaurus* is effected by the environment (Dodson, 1975). Although the alligator is used for comparisons, it is not considered a good model for the biomechanical properties of *Albertosaurus* as the method of locomotion is too different from *Albertosaurus sarcophagus.* A species that is considered to be more similar to tyrannosaurids family and used extensively to study large extinct theropods is the ostrich. The ostrich is a fast moving, flightless, bird; this species that used for a model of how bipedal locomotion could have occurred in theropods. This is because the ostrich is considered a more basal form of the avian family and therefore the ostrich can potentially share more similar traits with the theropods. Observing ostriches in their environment can provide indications as to how other bipedal dinosaurs could move. Examining the ontogeny of *Struthio camelus*, or also known as the ostrich, biomechanics can give an indication as to how the biomechanics can change in dinosaurs. Because ostriches are one of the fastest animals ever recorded in the wild, examining their biomechanics can also give a better understanding of the evolutionary pressures that were placed on *Albertosaurus sarcophagus*; there was also evolutionary pressure placed on ostriches to become faster than other animals (Rubenson, 2007). The scaling changes that happen in ostriches when they develop (Smith, 2010, 2013) could be similar to that of *Albertosaurus sarcophagus*, or other theropod dinosaurs. With the lighter build of *Albertosaurus sarcophagus*, it is probable that *Albertosaurus sarcophagus* could run faster than *Tyrannosaurus*, achieving similar speeds to that of the ostrich. Through understanding the growth patterns of the ostriches and being able to compare these growth patterns to *Albertosaurus* *sarcophagus* this can assist in understanding how *Albertosaurus sarcophagus* can grow. The growth pattern of *Albertosaurus sarcophagus* was similar to the other Tyrannosauridae in that there was a rapid stage of growth at certain stages of its life. This is indicated by growth rings that are found in their long bones. For example, growth rings in the femur, which indicates the rapid growth during the adolescent stage, approximately 10-15 years of age in *Albertosaurus sarcophagus* (Erickson, 2005). The femur is not the only indication of the rapid stages of growth. There is also evidence found in other bones that can be used as well as the femur. However, the standard bone for estimating sizes and age is the femur for Tyrannosaurids. (Currie, 2003)

Environment of *Albertosaurus sarcophagus*

Albertosaurus sarcophagus has been found to have a large range that spans across most of Alberta and into the northwestern United States, though most of the specimens have been found in Alberta. The environment of Alberta was semi-tropical floodplain and there was a greater biodiversity of both flora and fauna than there is in this region today (Currie 2005). The Bear paw inland sea covered much of North America at this time. The inland sea had a higher oceanic ion concentration than that of fresh water, but it was also more dilute than the oceans due to the fresh water runoff from the land. There is evidence from the large ceratopsian bone beds that the southern portion of Alberta was more prone to flooding, as these bone beds are found extensively throughout the area. (Currie, 2005)

Biomechanics and Hunting Strategies

Evidence suggests that *Albertosaurus sarcophagus* lived in familial groups; Dr. Phil Currie found many *Albertosaurus sarcophagus* fossils, in different developmental stages, in the same geological formation, extremely close to one another. This is strong evidence that these *Albertosaurus sarcophagus* could have been from the same pack. However, there is also debate on this: another theory is that the fossils could have accumulated in the same formation when many individuals of *Albertosaurus sarcophagus* were scavenging a dead animal. However, due to the number of specimens that were found, it is more likely that *Albertosaurus sarcophagus* formed familial groups, or at the very least was a social theropod. (Currie, 2010) Forming familial or social groups could have provided an evolutionary advantage to *Albertosaurus* if the biomechanics changed between youth and adulthood. If there was a change in the ability to move at greater speeds from one developmental stage to another, *Albertosaurus* might have been able to take advantage of this and achieve a greater capture rate for prey. For example, if the adults could chase down their prey, they could bring it back to the offspring to ensure the offspring had a higher chance of surviving until they could hunt for themselves, or, if the offspring could move more quickly than the adults, they could drive the prey into an ambush by the adults. Also by forming a pack structure this can help *Albertosaurus* by increasing the ability to successfully rear their young, as seen in the *Corvus corone*, or carrion crow. The theory of young adults assisting the parents care for the offspring has been proven that the increase in the family size in the crow is beneficial and allows for a greater chance for the young to survive. (Canestrari et al 2008)

Because *Albertosaurus* is extinct it is important to know how biomechanics in extant animals works because known fundamentals can then be applied to *Albertosaurus sarcophagus* and therefore more accurate conclusions can be made. (Alexander 2003, Cooke 1991) The biomechanics of *Albertosaurus sarcophagus* will be similar in parts to those of *Tyrannosaurus rex* as they share a typical body structure that is associated with this family, especially with regard to the pelvic and leg structure. However, there are notable differences in the bones, as *Albertosaurus sarcophagus* would have a lighter body build than *Tyrannosaurus*. This may give a better understanding of how *Albertosaurus sarcophagus* might have been able to move, as extensive research has been done on the biomechanics of *Tyrannosaurus* rex. The similarities between *Albertosaurus* and *Tyrannosaurus* in physical bone structure enable comparison between the two species. Many papers have suggested that *Tyrannosaurus* was not biomechanically able to achieve high speeds, (Hutchinson, 2002, 2005). However, *Tyrannosaurus* might have been able to achieve small bursts of higher speeds, to allow it to more effectively catch prey. There is a *Tyrannosaurus* footprint that shows the hallux digit, or the first toe of the hind limb. This could only have been left in the impression if the *Tyrannosaurus* was running, as the foot would have to have been almost horizontal to the ground for the hallux digit to make an impression due to how far up the foot the toe is located. (Carpenter 2013) This suggests that the *Tyrannosaurus* was running, as this is the most probable explanation for why there is a hallux impression in the footprint impression. Why this *Tyrannosaurus* was running is still unknown, but it may have been running after prey. Much like the African hyena, if there is the ability to scavenge for the food then there would no need to chase after prey. However, when there is a shortage of carrion available, the hyenas would hunt. Many believe that *Tyrannosaurus* could hunt, and most likely did; it has been suggested that the *Tyrannosaurus* may have tipped over the prey and then killed it. (Krauss, 2013) This behaviour might also have been present in *Albertosaurus sarcophagus*, due to its anatomical similarities to the *Tyrannosaurus*, including short arms. It is important to determine which hunting strategies were exhibited by *Albertosaurus sarcophagus* as this can give insight into past hunting strategies which may not be displayed by modern animals. This can already be seen in some extinct mammals from the Pliocene era which was in an intermediate stage between ambush and capture hunting methods (Andersson, 2003). Determining the hunting strategies can also give indications about the evolution of the behaviours of both the predators and prey. Predator-prey interactions can also give a better indication as to the health of the environment. The co-adaptation of behaviours allow for balanced populations of both predators and prey. Both solitary and pack hunting have advantages and disadvantages. For example, if *Albertosaurus* was a pack hunter there would be a higher likelihood of successful hunts, but the kill would have to be shared amongst the pack. The solitary hunter need not share its prey, but there would be a higher risk for each hunt, and there is a lowered chance of being successful with each hunt

Track ways

Track ways are one way of examining the speed capabilities of the theropod family, as by examining what types of speeds they could achieve that are found in the impressions left in the substrate. As these track ways can show many relations that might not be determined solely through computation biomechanical analysis; such as the ability to go from a trot to a run, or even a walk to a trot in three steps. (Dalman 2012) As well as determining if the theropod, or dinosaur in general was walking, trotting, or running; this is determined by calculating the stride length against the hip height in the formula Stride Length/Hip height, or relative stride length, RSL, as proposed by Thulborn in 1983. If the calculated number is higher than 2.9 then animal is running, if the number is between 2.1-2.9 the animal is trotting and anything under 2.1 the animal is considered to be walking. This method is used by many paleontologists to help determine what the animal was doing when it left the impressions in the ground. Examining the relative stride length that the animals could achieve is important to understanding interactions that could have occurred in the environment, such as why animals might have been trotting or walking and the fossil. (Weems et al 2006) There have been many studies conducted on track ways and trying to determine what animal might have left the tracks behind. For the smaller tridactyl impressions there is debate about if the track ways were left behind by a small theropod or by an ornithopod instead, as the impressions are hard to distinguish between them. (Thulborn 1990) The speeds of the dinosaurs can be calculated readily by using two formulas, Alexander's 1976 method and Thulborn's 1990 method. These are the methods that most paleontologists use when determining the speed of the dinosaur that left the track way impressions. Track ways while being extremely useful, there are short comings of these impressions, as at this time it is hard to determine which animal left the impressions down to the species level, right now it is just the family level that can be determined. (Thulborn 1982, Gillette 1989) Knowing the speed of the prey animals is important as well, as it can help to determine if the predator was able to chase after them, or be primarily a scavenger. One of the dinosaurs that were part of *Albertosaurus* diet was ceratopsians that lived in the same range that *Albertosaurus* was found. The typical maximum speed that a ceratopsian could reach was a trot at around 25Km/h (Thulborn 1982). Due to the front limbs being a different length than the rear limbs, this allowed for the animal only to reach a trotting like speed, and not be able to reach a running speed. (Thulborn 1982)

There can be a significant difference in speeds between the juveniles and the adults of any species; in *Albertosaurus* this is based on the change in morphology that occurs during the rapid stage of growth in. During the period rapid growth, the juveniles put on a lot of weight and therefore need better, more stable support in their hind limbs. But while they are juveniles, they have longer legs in comparison to their bodies and should have been able to maintain higher speeds for longer than the adults. Furthermore the juveniles have different proportions in the hind limbs (longer tibia in comparison to their femur, which results in a longer movement arm), giving the young the capability of running at greater speeds than the adults. Because of these factors, *Albertosaurus sarcophagus* would be able to use hunting strategies that would be similar to what a wolf pack would use, ambush hunting that if the ambush did not go as planned *Albertosaurus* could then run after their prey until they are able to exhaust the prey.

<u>Methods and Procedure</u>

Measurements taken of both *Albertosaurus sarcophagus* and *Struthio camelus* have been obtained from the personal data of Dr. Philip J. Currie. The measurements were then transformed into logarithms, and then graphed to determine the allometric. When the allometric relations were determined by using the least squares method and from there the line of best fit was calculated and the resulting equation was used to determine the K, B and R^2 values. Then the weights were calculated by using the formula put forward by Anderson et al in 1985. This formula is $W=0.16FC^{2.73}$ where W is weight and FC is femur shaft circumference this was used for both *Albertosaurus sarcophagus* and *Struthio camelus.*(Anderson et al 1985) The other formula that was used to determine weights is Christiansen and Fariña's 2004 formula. This formula involves logarithmically transforming the femur length of the individual specimen and then using the following formula log weight= (0.0006*log femur) +2.3992, then transforming the weight back by using $10^{\text{log weight}}$. (Christiansen and Fariña, 2004) To determine the hip height which affects the stride length and therefore the speed, two methods again where tested to determine which would produce the more reliable methods. Henderson's method that was used had the formula of 4*FL, where FL is footprint length. (Henderson, 2003) The other method was Thulborn's adjustments, and the adjustments that were used were for a large theropod was 4.9*FL, for a small theropod 4.5*FL, and for *Struthio camelus* 4.6*FL were FL is footprint length. (Thulborn, 1990)The speed was determined by using two methods as well, these were using Alexander's formula and Thulborn's formula. (Alexander, 1976, Thulborn, 1990) Alexander's formula is $v = 0.25*g^{0.5}*SL^{1.67}*h^{-1.17}$ where g= acceleration from gravity=9.8m/s^2, h=hip height (m), SL=Stride Length (m), v=locomotion. (Alexander 1976) Thulborn's formula is $v= [g*h\ (SL/1.8h)^{2.56}]^{0.5}$ where g= acceleration from gravity=9.8m/s^2, h=hip height (m), SL=Stride Length (m), v=locomotion. (Thulborn, 1990)

To determine the speeds that both *Albertosaurus sarcophagus* and *Struthio camelus* can achieve track ways will be used. The track ways that will be used are those of a large, medium and small theropod to determine the speeds of both the adults and juveniles respectively. *Struthio camelus* were examined as well to determine how accurate the speed results can be, and to ensure that the calculations were done correctly. The track ways measurements that were for a large theropod were obtained from Dr. James O. Farlow. (Personal Communication March 13, 2014) For the small and medium sized theropods the data was obtained from Petti et al. (Petti et al 2011). *Struthio camelus* track way data was obtained from Farlow. (Farlow, 1989)

Results

Albertosaurus sarcophagus Allometric Data Table 1: The allometric relations exhibited by *Albertosaurus sarcophagus*. Y and X are the values that are being compared. N is the sample size of *A. sarcophagus.* K, B, and R^2 are the values that have been determined by using the least squares method, k and b are constants determined while R^2 is the correlation value. There is positive allometry when the value of k is greater than 1.00, is isometric when the value of k = 1.00, and shows signs of negative allometry when k is than 1.00. The dw = distal width, F=Fibula, L=length, T= Tibia, T.M = Tibiometatarsus, T.t=Tibiotarsus, Mt, I, II, and III, IV= refers to digits of the foot, pw=proximal width, sc = shaft circumference, Sw=Shaft width sw/Ant/post=shaft width measured at the anterior/posterior plane, sw/transverse is the shaft width measured at the transeverse plane

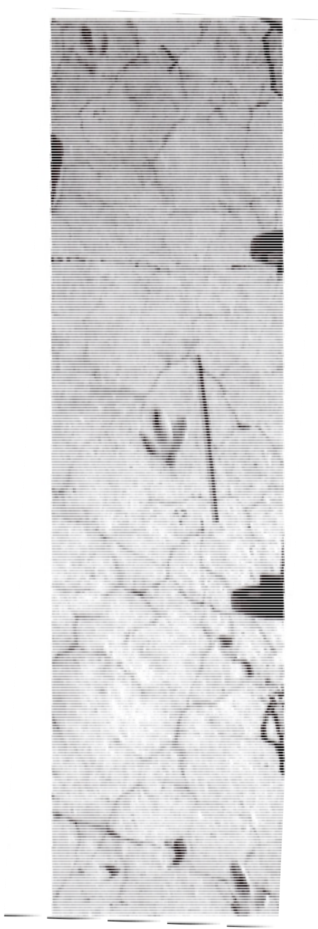
Y	X	n	R^2	k	B
F.pw	Femur L	9	0.425	0.849	-0.154
F.sw/ant-post	Femur L	10	0.412	0.817	-0.472
F.sw transeverse	Femur L	13	0.438	0.793	-0.325
F shaft circum	Femur L	13	0.612	0.916	-0.204
F.dw	Femur L	9	0.786	1.573	-2.344
Tibula L	Femur L	10	0.979	0.781	0.630
T-ast L	Femur L	5	0.989	0.878	0.367
T dw	Femur L	12	0.731	1.216	1.259
T pw	Femur L	10	0.158	0.334	1.357
T sw Transverse	Femur L	11	0.917	1.369	-2.051
Tibula L	Femur L	10	0.979	0.781	0.630
Fibula L	Femur L	12	0.989	0.675	0.898
Fibula dw	Femur L	10	0.925	1.451	-2.571
Fibula pw	Femur L	15	0.493	0.856	-0.381
Fib sw	Femur L	14	0.926	1.259	-2.187
Mt I	Femur L	2	1.000	0.956	0.163
Mt II	Femur L	15	0.551	0.552	1.052
Mt III	Femur L	12	0.992	0.619	0.904
Mt IV L	Femur L	19	0.960	0.599	0.940
Mt V L	Femur L	6	0.965	0.711	0.215
Toe III L	Femur L	3	0.986	1.438	-1.535
I-1	Femur L	14	0.866	0.970	-0.931
I-2 Straight	Femur L	11	1.000	1.005	-0.067
II-2	Femur L	14	0.932	0.885	-0.619
II-3	Femur L	5	0.239	0.716	-0.098
II-3 Outside Curve	Femur L	4	0.831	1.124	-1.186
III-1	Femur L	13	0.943	0.925	-0.541
III-2	Femur L	14	0.797	0.992	-0.920
III-3	Femur L	25	0.981	1.152	-1.477
III-4	Femur L	4	0.919	2.255	-4.546

Y	X	n	R^2	k	B
III-4 Outside Curve	Femur L	3	0.597	1.296	-1.749
IV-1	Femur L	14	0.974	1.042	-1.047
IV-2	Femur L	7	0.874	1.097	-1.341
IV-4	Femur L	8	0.956	1.161	-1.832
IV-5 Outside Curve	Femur L	6	0.076	0.312	0.983

Struthio camelus: Allometric relations exhibited by *Struthio camelus*. Y and X are the values that are being compared. N is the sample size of *Struthio camelus.* K, B, and R^2 are the values that have been determined by using the least squares method, k and b are constants determined while R^2 is the correlation value. There is positive allometry when the value of k is greater than 1.00, is isometric when the value of k = 1.00, and shows signs of negative allometry when k is than 1.00. The dw= distal width, F=Fibula, L=length, T= Tibia, T.M = Tibiometatarsus, T.t=Tibiotarsus, Mt, I, II, and III, IV= refers to digits of the foot, pw=proximal width, sc = shaft circumference, Sw=Shaft width sw/Ant/post=shaft width measured at the anterior/posterior plane, sw/transverse is the shaft width measured at the transeverse plane

Y	R^2	K	b
F.pw	0.3223	1.0223	-0.5957
F. sw/ant-post	0.4159	1.4874	-2.0219
F. sw/transverse	0.4497	1.4261	-1.8997
F shaft circ	0.7394	1.3472	-1.2013
F.dw	0.7519	1.0946	-0.7116
T.ast L	0.9019	0.9096	0.4731
T.dw	0.0285	0.437	0.7421
T.pw	0.0298	0.6978	0.2592
T.sw/transverse	0.5514	1.3828	-1.8912
T circ	0.918	1.1424	-0.7723
T.m L	0.256	0.4145	1.6361
T.m dw	0.0014	0.067	1.5479
T.m pw.	0.2008	1.6359	-2.2434
T.m circum	0.922	0.5083	0.766

Large Theropod track way:



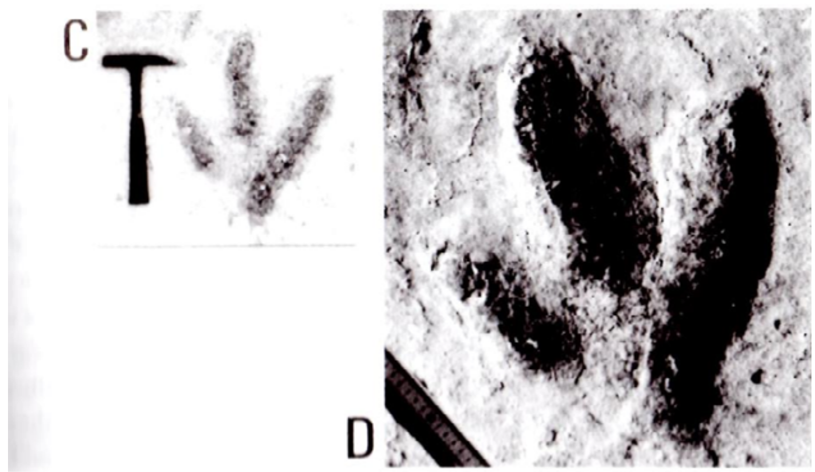


Figure 1: Images of track way data obtained by personal communication with Dr. James O. Farlow, images from Farlow 2012. First image shows the large running theropod track way, the second image is the middle impression of the running track way seen in the first image, this middle impression is indicated by the measuring stick next to it.

Table 3: The measurements of the track way were obtained in a personal communication from Dr. J.O Farlow. Footprint length is the length of the footprint impression measured from the tip of middle toe (III) to the heel of the impression. Step 1 is the distance from the first footprint, the one that is measured, to the opposite footprint impression or the middle footprint. Step 2 is the distance from the middle footprint to the end print. Stride length is from the first print to the last print. Hip Height is measured as 4*Footprint length (Henderson, 2003) and a conversion for the large theropod with the 4.9 conversion for hip height. All the measurements are taken in mm.

Large Theropod Track way Henderson's Method	
What is measured	(mm)
Footprint L	370
Step 1*	2718
Step 2*	2616
Stride Length	5309
Hip Height	1480

Large Theropod Track way Thulborn's Method	
What is measured	(mm)
Footprint L	370
Step 1*	2718
Step 2*	2616
Stride Length	5309
Hip Height	1813

Table 4: These measurements were obtained from Patti et al 2011. This study had averaged the footprints that were recorded. Step length was not included in that study by Patti et al. Where this footprint is still under the 250mm measurement it is considered a small theropod, however, with this footprint being larger than the 144.7mm foot print it is for the purpose of this study considered to be a medium sized theropod.

Medium Theropod Track ways		**Medium Theropod Track way**	
What is measured using Henderson's method		**What is measured using Thulborn's method**	
	(mm)		(mm)
Footprint L	180	Footprint L	180
Step 1*	n/a	Step 1*	n\a
Step 2*	n/a	Step 2*	n\a
Stride Length	2.5839	Stride Length	2.5839
Hip Height	720	Hip Height	810

Table 5: The measurements obtained from Petti et al. 2011. This study averaged the footprint length and did not include step measurements. There was a pace and stride length recorded by Patti et al and for continuity the stride length was chosen. A small theropod is defined as having a footprint length that is smaller than 250mm in length (Thulborn 1990). All the measurements were taken in mm

Small Theropod Track ways		**Small Theropod Track way**	
What is measured using Henderson's method		What is measured using Thulborn's method	
	(mm)		(mm)
Footprint L	144.7	Footprint L	144.7
Step 1*	n/a	Step 1*	n\a
Step 2*	n/a	Step 2*	n\a
Stride Length	1486.5	Stride Length	1486.5
Hip Height	578.8	Hip Height	651.2

Table 6: This data was obtained from J.O Farlow 1989. For the running speed there was no step length measured, however for the trotting speeds there was a step length that was determined. The measurements were taken in mm

Struthio camelus	**Trotting**		**Running**
What is measured	(mm)	**What is measured**	(mm)
Footprint L	220	**Footprint L**	220
Step 1*	1448	**Step 1***	n\a
Step 2*	1600	**Step 2***	n\a
Stride Length	3023	**Stride Length**	4270
Hip Height Henderson Method	880	**Hip Height(H.M)**	880
Hip Height Thulborn Method	1012	**Hip Height(T.M)**	1012

Conclusions:

Figure 1: Allometric relations experienced in *Albertosaurus sarcophagus* the values were obtained by logarithmic conversion of both the measurement and the Femur and then graphing those values and generating a line of best fit and determining the equation from the graph. X is the constant that Y is being compared to. K is the allometric growth, b is a constant, and R^2 is the correlation of the data. For the allometry charts dw= distal width, F=Fibula, L=length, Mt I,II,III, IV, -1, -2, -3,-4,-5= all refer to the digits, T= Tibia, pw=proximal width, sc = shaft circumference, Sw=Shaft width sw/Ant/post=shaft width measured at the anterior/posterior plane, sw/transverse is the shaft width measured at the transeverse plane.

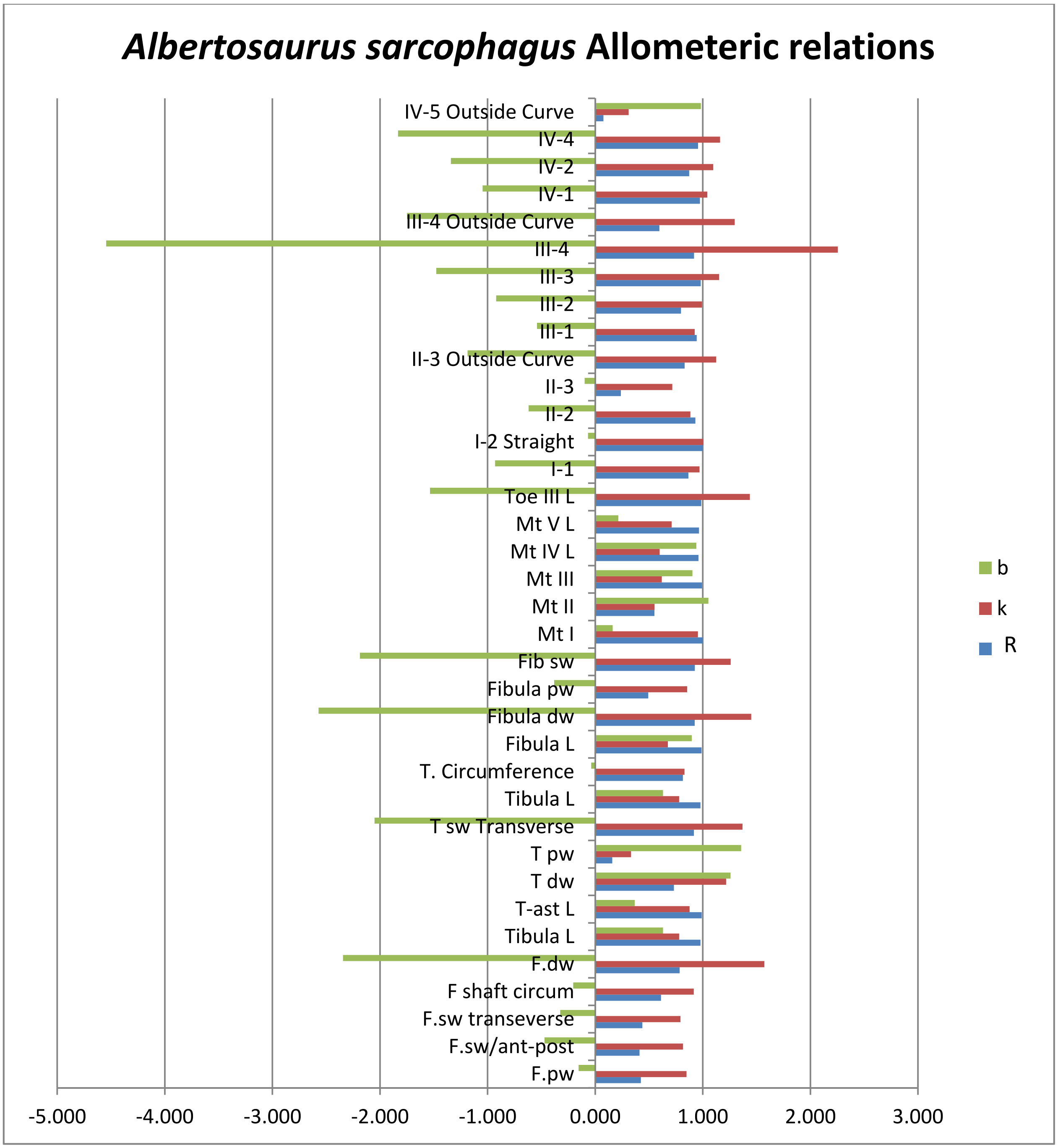


Figure 2: Allometric relations experienced in *Struthio camelus*. The values were obtained by logarithmic conversion of both the measurement and the Femur and then graphing those values and generating a line of best fit and determining the equation from the graph. X is the constant that Y is being compared to. K is the allometric growth, b is a constant, and R^2 is the correlation of the data. For the allometry charts dw= distal width, F=Fibula, L=length, T= Tibia, T.M = Tibiometatarsus, T.t=Tibiotarsus, pw=proximal width, sc = shaft circumference, Sw=Shaft width sw/Ant/post=shaft width measured at the anterior/posterior plane, sw/transverse is the shaft width measured at the transeverse plane. The digits were not included in the figure as there was on most of the specimens the keratin sheath, or the claw, still present on the digits and therefore added length to the measurements of the digits.

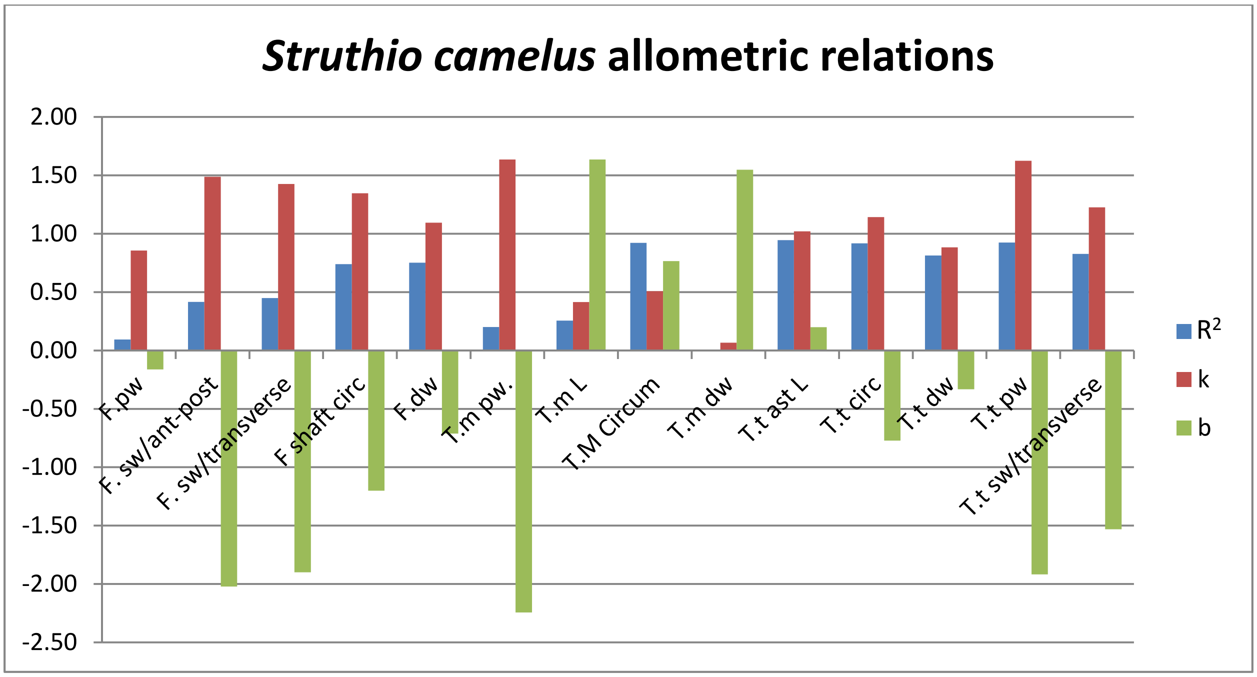


Figure 3: Weight estimated based off of Christiansen and Fariña's 2004 methods for *Albertosaurus sarcophagus.* The length of the femur was logarithmically transformed and then the formula of log weight= (0.0006*log femur) +2.3992, then transforming the weight back by using $10^{\text{log weight}}$. (Christiansen and Fariña, 2004)

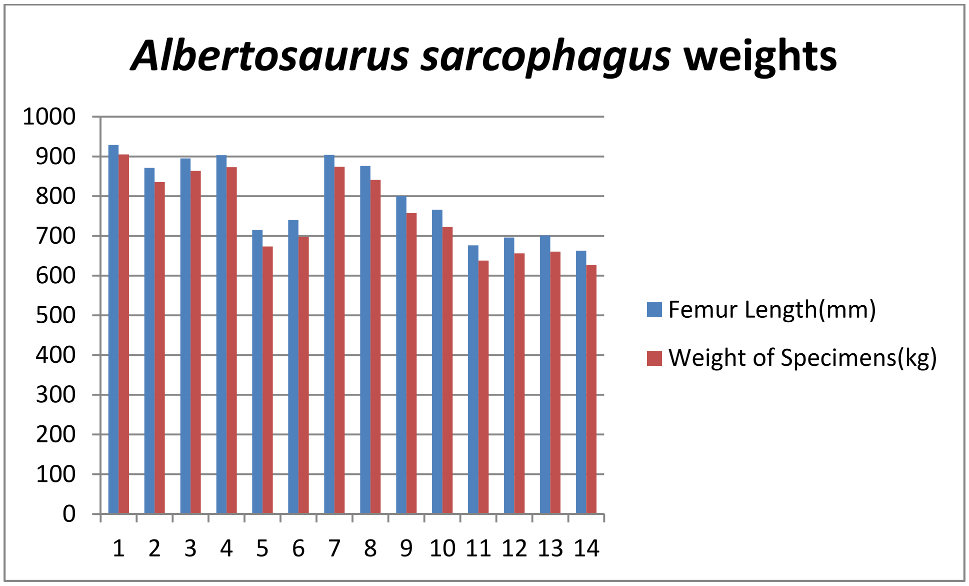


Figure 4: Weight estimated based off of Christiansen and Fariña's 2004 methods for *Struthio camelus*. The length of the femur was logarithmically transformed and then the formula of log weight= (0.0006*log femur) +2.3992, then transforming the weight back by using $10^{\text{log weight}}$. (Christiansen and Fariña, 2004)

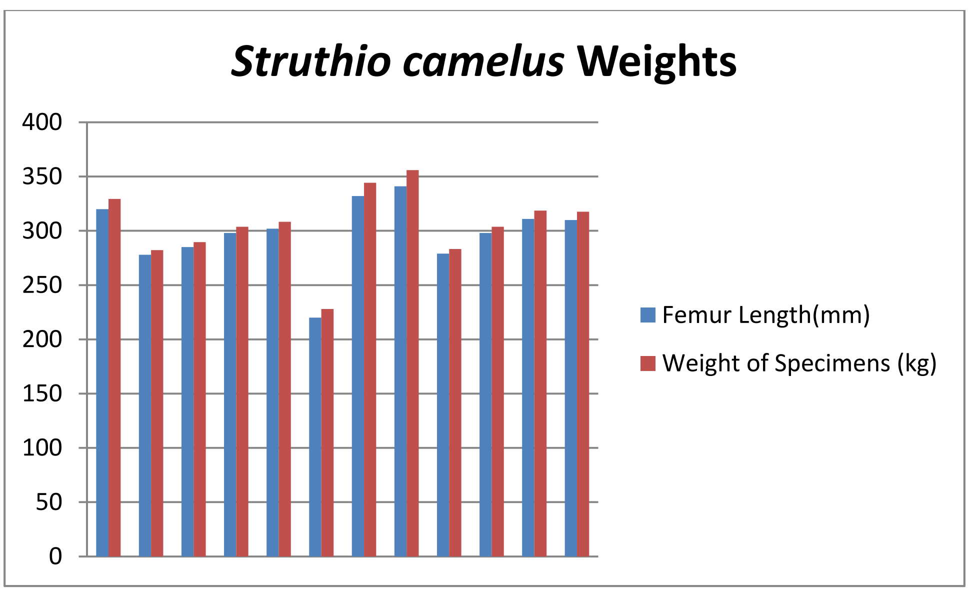


Figure 5: Weight estimates based off of the calculations proposed by Anderson et al 1985. This is calculated by the formula $W=0.16FC^{2.73}$ where W is weight and FC is femur shaft circumference. The range of weights varies from 196kg as the lightest to 1765kg as the heaviest. (Anderson 1985)

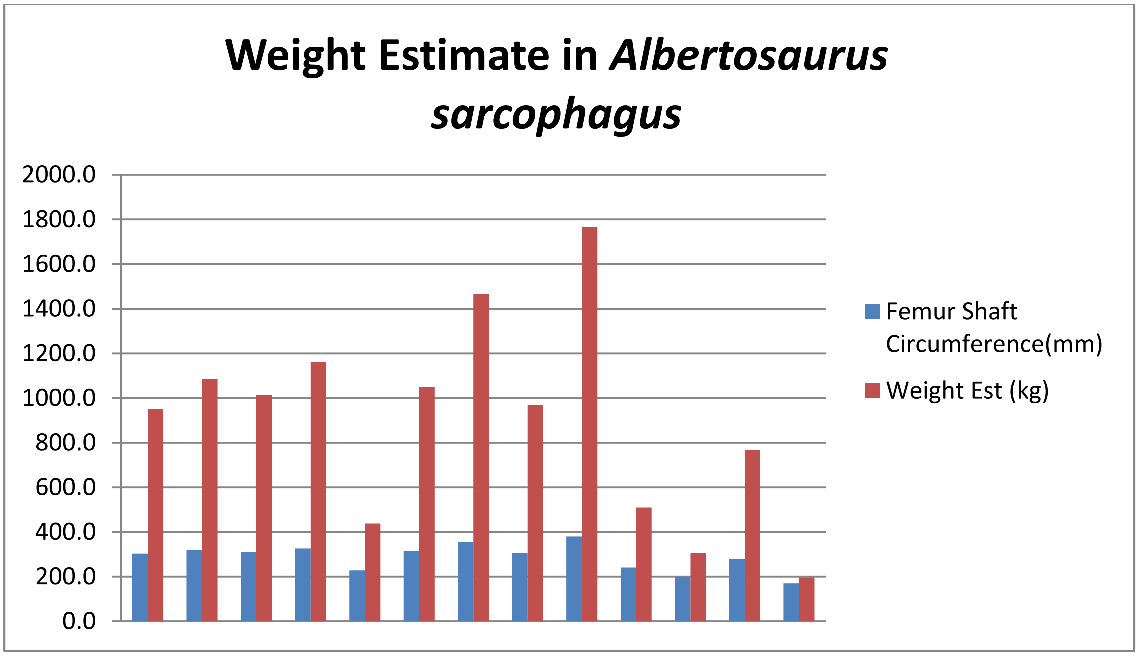
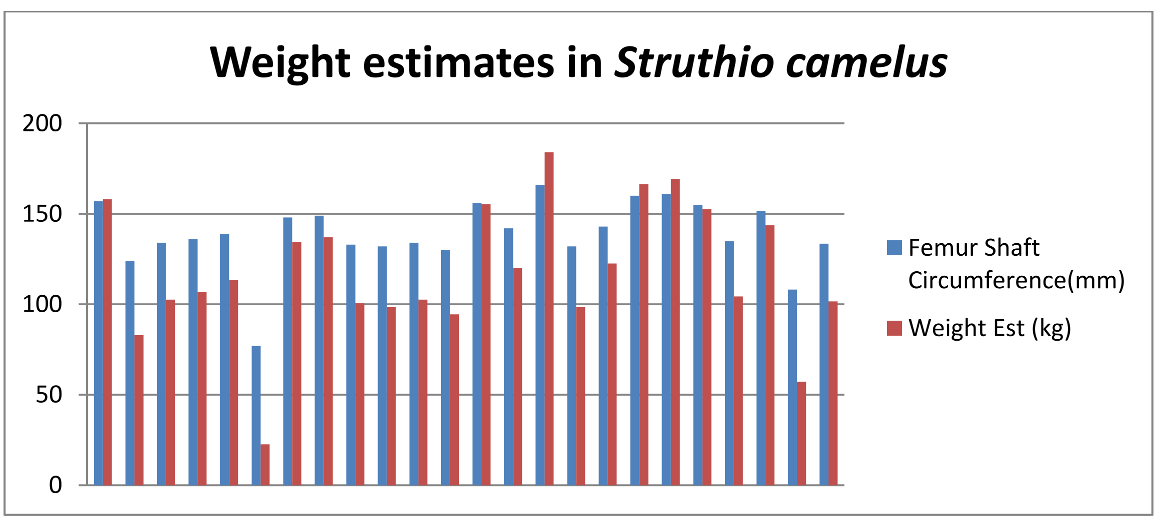


Figure 6: Weight estimates based off of the calculations proposed by Anderson et al 1985. This is calculated by the formula $W=0.16FC^{2.73}$ where W is weight and FC is femur shaft circumference. (Anderson 1985) The lightest weight is 22kg and the heaviest weight is 184kg. This is in the expected range for *Struthio camelus* as the recorded range is 63-157kg. (Hutchins et al 2002)



Large Theropod track way speed determination:

Table 7: Speed is determined by using Alexander's formula as well as Thulborn's formula to determine which method would provide more accurate results. Different methods of determining hip height was used as well, Henderson's method (Henderson 2003) and Thulborn's adjustment for dinosaurs (Thulborn 1990). The method that was determined to be the best is Henderson's calculation for Hip Height and the average for Thulborn and Alexander's method for calculating speeds. Thulborn's 1990 formula for determining speed is $v= [g*h\ (SL/1.8h)^{2.56}]^{0.5}$ Alexander's 1976 formula is $v = 0.25*g^{0.5}*SL^{1.67}*h^{-1.17}$ where g= acceleration from gravity=9.8m/s^2, h=hip height (m), SL=Stride Length (m), v=locomotion. . Speed m/s is meters per second, and speed Km/h is kilometres per hour. The relative stride length, or RSL, is calculated to determine if the theropod is running, trotting, or walking. Running is defined as a RSL<2.9, trotting is RSL <2.1>2.9 and walking is RSL>2.0. This Theropod is running as the RSL is greater than 2.9, as using Henderson's 2003 hip height calculation it is determined that the RSL is 3.58.

Large Theropod Speed.			
g= acceleration due gravity=9.8m/s			
h=hip height(m)			
SL=Stride Length(m)			
v=locomotion			
Just considering the 4* foot length proposed by Henderson			Relative Stride Length
Method	Speed m/s	Speed Km/h	SL/h=5.309*(.37*4)=3.58
Thulborn's Method	9.20	33.12	
Alexander's Method	8.04	28.94	
Mean Speed	8.62	31.03	
Considering Thulborn's adjustment for Large Theropods			Relative Stride Length
Method	Speed m/s	Speed Km/h	SL/h=5.309*(.37*4.9)=2.92
Thulborn's Method	7.85	28.26	
Alexander's Method	6.33	22.79	
Mean Speed	7.09	25.52	

Medium Theropod speed determination from track ways

Table 8: Speed m/s is meters per second, and speed Km/h is kilometres per hour. The relative stride length, or RSL, is calculated to determine if the theropod is running, trotting, or walking. Running is defined as a RSL<2.9, trotting is RSL <2.1>2.9 and walking is RSL>2.0. This Theropod is running as the relative stride length is 3.59.Thulborn's 1990 formula for determining speed is $v= [g*h (SL/1.8h)^{2.56}]^{0.5}$ Alexander's 1976 formula is $v = 0.25*g^{0.5}*SL^{1.67}*h^{-1.17}$, where g= acceleration from gravity=9.8m/s^2, h=hip height (m), SL=Stride Length (m), v=locomotion.

Just considering the 4* foot length proposed by Henderson			**Relative Stride Length**
Method	Speed m/s	Speed Km/h	SL/h=2.5839/(.180*4)= 3.59
Thulborn	6.42	23.11	
Alexander	5.61	20.20	
Mean	6.02	21.65	
Medium Theropods			
Considering Thulborn's adjustment for Small Theropods			Relative Stride Length
Method	Speed m/s	Speed Km/h	SL/h=2.5839/(.180*4.6)= 3.12
Thulborn's Method	5.76	20.74	
Alexander's Method	4.76	17.14	
Mean Speed	5.26	18.94	

Small Theropod speed determination from track ways

Tablet 9: Speed m/s is meters per second, and speed Km/h is kilometres per hour. The relative stride length, or RSL, is calculated to determine if the theropod is running, trotting, or walking. Running is defined as a RSL<2.9, trotting is RSL <2.1>2.9 and walking is RSL>2.0. This Theropod is trotting which is defined as a slower speed than running as the relative stride length, or RSL is smaller than 2.9 that would indicate a running speed, the relative stride length calculated is 2.57. Thulborn's 1990 formula for determining speed is $v= [g*h (SL/1.8h)^{2.56}]^{0.5}$ Alexander's 1976 formula is $v = 0.25*g^{0.5}*SL^{1.67}*h^{-1.17}$ where g= acceleration from gravity=9.8m/s^2, h=hip height (m), SL=Stride Length (m), v=locomotion. The methods that have been selected for this study are Thulborn's 1990 method for determining speeds, and Henderson's 2003 methods for determining the hip height of the theropod

Just considering the 4* foot length proposed by Henderson			
Method	Speed m/s	Speed Km/h	Relative Stride Length
Thulborn	3.75	13.50	SL/h=1.4865/(.1447*4)=2.57
Alexander	2.87	10.33	
Mean	3.31	11.92	

Considering Thulborn's adjustment for Small Theropods			Relative Stride Length
Method	Speed m/s	Speed Km/h	SL/h=1.4865/(.1447*4.6)=2.23
Thulborn's Method	3.36	12.10	
Alexander's Method	2.42	8.71	
Mean Speed	2.89	10.40	

Struthio camelus track way speed determination

Table 10: Speed m/s is meters per second, and speed Km/h is kilometres per hour. The relative stride length, or RSL, is calculated to determine if the theropod is running, trotting, or walking. Running is defined as a RSL<2.9, trotting is RSL <2.1>2.9 and walking is RSL>2.0. There are two sets of data for *Struthio camelus* as there was a trotting theropod and two running theropods, and to ensure continuity the trotting and running speeds were included. As the relative stride lengths are .Thulborn's 1990 formula for determining speed is $v= [g*h (SL/1.8h)^{2.56}]^{0.5}$ Alexander's 1976 formula is $v = 0.25*g^{0.5}*SL^{1.67}*h^{-1.17}$ where g= acceleration from gravity=9.8m/s^2, h=hip height (m), SL=Stride Length (m), v=locomotion. The running that occurred here was not the top speed for the ostrich, as the pen that it was held in was not large enough for the top speed to be reached.

Considering the 4* foot length proposed by Henderson	**Trotting**		**Running**	
Method	Speed m/s	Speed Km/h	Speed m/s	Speed Km/h
Thulborn's Method	6.71	24.16	10.45	37.62
Alexander's Method	8.02	28.87	10.26	36.94
Mean Speed	7.37	26.51	10.35	37.28
Relative Stride Length SL/h	3.44		4.85	
Considering Thulborn's adjustment for Small Dinosaurs (4.6* foot length)	**Trotting**		**Running**	
Method	Speed m/s	Speed Km/h	Speed m/s	Speed Km/h
Thulborn's Method	6.02	21.67	9.20	33.12
Alexander's Method	4.94	17.78	8.79	31.64
Mean Speed	5.48	19.73	9.00	32.38
Relative Stride Length SL/h	2.99		4.22	

The methods that have been selected to use in this study are Henderson's 2003 method for hip height determination, as well as Thulborn's 1985 calculations to determine speed. This is considering *Struthio* *camelus* being used as a control to determine which calculation would result in speeds that are either consistent with or closer to what has been recorded for *Struthio camelus.*

Discussion:

Allometry present in *Struthio camelus*; Femur distal width, the Femur proximal width, Femur shaft width measured at anterior posterior plane, Femur shaft width measured at the transverse, Femur shaft circumference, Tibiometatarsus length, Tibiometatarsus proximal width, Tibiometatarsus Circumference, Tibiometatarsus distal width, Tibiotarsus astragal, Tibiotarsus circumference, Tibiotarsus distal width, Tibiotarsus proximal width, and Tibiotarsus shaft width measured at the transverse plane. In *Albertosaurus sarcophagus* the Fibula distal width, Fibula length, Fibula proximal width, Femur distal width, Fibula proximal width, Fibula shaft width, Tibia astragal length, Tibia distal width, Tibia circumference, Tibia Length, Tibia proximal width, and Tibia shaft width measured at the transeverse plane, exhibit signs of allometry. For this study the hind digits are not being included due to the fusion of bone, as well as some of *Struthio camelus* digits still being covered in the keratin sheath, and in the few bones that did not have this covering the digit was smaller than what was recorded in the keratin covered bone, because these errors that would affect the allometric equations, this data was excluded from this study. A potential reason for the difference in the allometric relations that does not have a resemblance of consistency could be due to the variations in development that causes this range. There were some *Struthio camelus* bones that were not fully fused, and this could affect the allometric relations as parts of the bones that were not fused, or were mounted as a display specimen and the mounting process caused bones to become more prominent than what would be expected. There were many bones that almost exhibited allometric relations, as the calculated values are mostly in a range from .70 to .90 for *Albertosaurus sarcophagus* though there were some lower points as well. *Struthio camelus* also had bones that almost exhibited a positive allometric relation with the femur, though the range was wider, and there were a few bones that exhibited almost a neutral allometric relationship to the femur, the range was 0.07 to 0.88. However, in comparison to *Albertosaurus sarcophagus* where there was a more consistent range of allometric ranges, *Struthio camelus* did not have this range. This could be due to the smaller sample size of *Struthio camelus* and any outlier would more greatly affect the allometric relations than in *Albertosaurus* as there are more sample sizes to draw from.

For the weight of *Albertosaurus sarcophagus* and *Struthio camelus* the method that was used is the method proposed by Anderson. This method produced the most feasible results when examining both *Albertosaurus sarcophagus* and *Struthio camelus*, as the weights that were calculated for *Struthio camelus* were closer to those that were recorded by Hutchins et al 2002; though the weights did not indicate if the recorded values were those obtained in wild birds, or in captive bred birds, and if there was an age range that was measured, or the weight was averaged for all the specimens weighted. This is important to note as the sample of *Struthio camelus* bones that are being examining both confirmed juveniles and adults. As the youngest confirmed age is 18 months and the oldest confirmed age is 20 years, these were captive bred birds, which could be heavier than those in the wild as the calculations are indicating that there is a heavier bird than the recorded range. A reason that the captive bred birds might have a heavier body mass than the wild birds is the readily available nutrient sources that the wild birds would not have access to. Other methods for calculating weight were investigated, such as Anderson and Fariña's 2004 method which for *Albertosaurus sarcophagus* seemed to produce reliable results; however, when determining the weight of *Struthio camelus* it was not as reliable as it over estimated the weight of the bird, and therefore was not chosen for the purpose of this study.

When choosing the track ways for the small and medium sized theropods that are being examined for this study have been chosen by using the relative stride length to determine if the theropod is running or not. The 144.7 footprint while the RSL suggests that this theropod was trotting and not running, this was still included over the over small footprint as it had a higher RSL, and as the top speed is the focus of this study, the other footprints were excluded. This is also why the 180.0 mm track way was chosen for the medium as this was the only track way of a medium size that had an RSL greater than 2.9. Thulborn's method of classifying theropod size is any footprint that is less than 250mm in length is small, and any footprint that is over 250mm as large. (Thulborn 1990) There is no medium classification in Thulborn's system. For the purpose of this study the following classifications are used, less than 150mm is classified as small and 160-250mm is classified as medium, and 250mm and upwards is large. The only two footprints that where in the ranges that were trotting or running were the 144.7mm and 180mm footprint impressions.

The speeds that the adults would be able to reach are approximately 33.12km/h or 9.20 m/s. With these speeds the adult *Albertosaurus sarcophagus* would have been slower than what was proposed for the *Tyrannosaurus rex*, which the top speed for the *Tyrannosaurus rex* was estimated to be at around 11 m/s or 39.6 km/h (Hutchinson 2002). *Albertosaurus sarcophagus* was able to achieve speeds slightly below the *Tyrannosaurus rex*. However the actual speed of *Albertosaurus sarcophagus* could be higher that what has been shown, this is due to using track ways to determine the top speed that was achieved. Another factor could be that these impressions are left in a substrate that might demonstrate a slower speed than what the adults could reach, as the substrate that is prone to allowing track ways to form is that of a thick sticky mud which can reduce the speed abilities of the animals. However, though the study of track ways is still necessary to further understand the potential biomechanical abilities as this field of study allows for paleontologists to determine speeds that the animals were able to achieve in the environment. While track ways are important, these impressions cannot, at this time, be traced back to the species that made them and generalizations will occur about which animal left the impressions. Though it is still important to know how fast the families of dinosaurs can travel and what speeds they can achieve. With the adults being able to achieve speeds of approximately 33 km/h this can prove a significant advantage to the potential pack structure as this can perhaps allow for a similar pattern of hunting that the wolf packs will use where the adults will “tag” each other off and rest while the prey is being chased. This tagging off can provide the predators an advantage as this will allow for rest periods, while causing fatigue and exhaustion in the prey, which when the animal is caught it most likely could be too exhausted to put up much of a defense against the attack.

The medium sized theropods were determined to have speeds of 23.11Km/h. This is slower than the adult’s maximum of 33.12Km/h. At these speeds *Albertosaurus sarcophagus* sub adult can assist with the hunting and also they can also help with rearing of the juveniles, as seen in *Corvus corone*, or carrion crow. (Canestrari et al 2008) With the sub adults assisting with raising the offspring, this can increase the chances of the offspring to live and reach a reproductive stage and therefore increase the reproductive success of *Albertosaurus sarcophagus.* As with carrion crows it was found that the more food the offspring were able to receive in that critical window of 10 days, the offspring had a higher probability of survival and being able to reproduce themselves. (Canestrari et al 2008) For a predator this would have an advantage as there would be more predators in the familial pack that would be able to have a higher prey capture rate, as the sub adults would be able to mostly keep up with the adults during a hunt. In doing so the sub adults would be able to bring more food to the offspring and can potentially defend the offspring from predation by other predators.

The small sized theropods or the juveniles can only achieve a speed of 13.50 Km/h. While in comparison to the sub adults and the adults this speed is slower, although it would be fast enough for the juveniles to be able to catch smaller slower prey items such as perhaps hatchling of a prey item such as a ceratopsian, or even resorting to being an insectivore if required. This would be advantageous as the juveniles could still ensure the nutritional requirements were met if there was a lack of ceratopsians or other larger prey items available for the pack to hunt, which could then allow for them to continue grow and develop.

With the larger size of *Albertosaurus sarcophagus* it is more probable that *Albertosaurus sarcophagus* would show pack hunting behaviours, as this would provide many advantages to the success of *Albertosaurus sarcophagus*. These advantages are; more consistent successful hunting rates, higher prey capture rates, higher survivorship in the juveniles because of the increased availability of food, having the sub adults assist with the rearing of the juveniles, and the lowered risk of injury when actively hunting prey such as ceratopsians. The pack structure that is more probable is that of the adults lying in wait to ambush the prey as they are being driven towards the trap by primarily the adolescent's or sub adults. Though the juveniles might assist with the hunting, as the values given here are just at a trotting speed and not a running speed, they could not actively be involved in the hunting without the help of either the adults or the sub adults due to the juveniles overall size and potentially being slower and therefore more at risk while hunting with the pack. The main source of prey items for *Albertosaurus sarcophagus* is ceratopsians that also lived in the same environment with *Albertosaurus sarcophagus*. Ceratopsians maximum speed that they would be able to sustain for short periods of time is 25Km/h. (Thulborn 1982) This speed is slower than the adult *Albertosaurus sarcophagus*, but faster than the sub adults and the juveniles, though it would be fast enough to allow for the ambush trap to be set. And if the ambush failed the adults could join in and drive the prey to exhaustion. Another method of hunting is having the sub adults drive the prey towards the adult *Albertosaurus sarcophagus* and the adults tipping over ceratopsians in an ambush strategy, this strategy would be beneficial as it would be difficult for a ceratopsian to roll over and get back on its feet to escape. This hunting strategy works best in a large pack structure considering if the adults and sub adults are able to work together to trap and tip over a ceratopsian a large pack could successfully hunt multiple ceratopsians simultaneously;

Albertosaurus sarcophagus would be able to feed the pack with the ceratopsians that were killed. Because with the use of this hunting strategy it is effective to hunt in packs rather than as a solitary animal as there are reduced risk of injury and while the kill does need to be shared amongst the pack, if enough prey is killed, there should be enough to feed the pack; and with the work load spread out between the different age groups, this method would be an even more effective hunting strategy using the ambush method to acquire the food needed to feed the pack.

An interesting find that came out with this study and something that warrants future research is the relationship with the size of the dinosaur footprint and the speed that was calculated. With the smaller theropod, while it was trotting, it produced a speed of 13.50Km/h, and then the medium sized theropod produced a speed that was almost 10Km/h and the larger theropod was 10Km/h faster than the medium theropod. Though this could be a coincident that occurred while the speeds were be calculated and considering the smaller theropod RSL indicated that this animal was trotting and not running. Considering in the other methods there also seems to be a correlation of the speeds increasing as the footprint length also increases, considering Alexander's method of calculating speed did not produce correlations of similar magnitude as using Thulborn's method to determine speed and Henderson's method to determine hip height in the theropods there is still a correlation present.(Alexander, 1976 Thulborn, 1990, Henderson, 2003) Another factor could be that the track ways are not in the same geographical area, as the small and medium theropod track ways were found in early Jurassic formations in Southern America, while the adults track ways were found in the early Jurassic formations in North America, there could be an effect of this geographical distance on the biomechanics due to different potential evolutionary stresses placed on these theropods. Future studies examining the biomechanical potentials of the juveniles and adults of theropod family is needed to determine if this data calculated is a coincidence or if this suggests that there is a scaling difference in the speeds generated by the different age groups.

Acknowledgments:

I would like to thank my supervisors Drs. Sheri Dalton and Philip Currie for their assistance with this project, with helping me obtain the data that I needed and the guidance if I needed it. And to Dr. James Farlow for his assistance with helping me obtain track way data. I would also like to thank the Calgary Zoo for allowing me access to observe the ostriches. As well I would like to thank, the Royal Alberta Museum's Dr. Jocelyn Hudon, the Royal Tyrrell's Brandon Strilisky, the University of Calgary's Warren Fitch for allowing me access to the collections of each institution. Thanks to my employer, Mountain Equipment Co-op, for giving me assistance with a portion of my tuition. I would also like to thank my editors Brittany, Jason and Cindy who took their time to thoroughly go through each draft of my paper from beginning to end.

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