

HOW DID BISON CALVES GROW UP? POSTNATAL LIMB ALLOMETRY IN *BISON ANTIQUUS* FROM THE LA BREA TAR PITS

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Abstract—The La Brea tar pits preserve a huge sample of juvenile bones of many mammals, one of the few fossil localities known that allows us to study how limb bones changed shape through ontogeny. The extinct Pleistocene species *Bison antiquus* is abundant at La Brea, so we were able to study as many as 70 specimens of the limb bones of juveniles, from the smallest calves to full-grown adults. We measured the diaphysis length and circumference of humeri, radii, femora and tibiae, using a flexible metric tape measure. Previous studies on the growth in the living species *Bison bison* give us a basis for comparison. As a cursorial mammal, we predict that *Bison* should display isometric or robust growth in their proximal limb segments (humerus, femur), but that the distal limb segments (fused radius-ulna, tibia) elongate faster than they get thicker, thus making those elements more gracile. The expected isometric slopes are around 1.0 for length vs. circumference. In the humerus, the growth trend in *B. antiquus* was isometric (slope = 1.03), while *B. bison* was significantly more robust. In the radius-ulna, *B. antiquus* was robust (slope = 0.89), about the same as in *B. bison* (slope = 0.87). The femur showed the same growth trends, with highly robust (slope = 0.85) growth in *B. antiquus*, while *B. bison* had a slope of 0.92. However, the tibia (slope = 1.05) shows isometric growth, compared to the robust slope of 0.75 for the tibia in *B. bison*. This discrepancy is surprising, because previous authors have not commented that limbs of adult *B. antiquus* are remarkably more gracile or robust than those of living *B. bison*—but that is what their allometric growth trends suggest. This lack of gracility in the growth trajectory of bison limbs suggests that (unlike some other artiodactyls that become more gracile as they age), bison were born with gracile limbs at the very start, and maintained these proportions by isometric or slightly robust growth patterns as they matured.

INTRODUCTION

The ontogenetic growth of animals from juvenile stages to adulthood is one of the most important research areas in biology and paleontology. There has been more than a century of research into embryonic and post-natal ontogeny in many kinds of organisms, but it is much more difficult to do in the fossil record. Unlike some fossil invertebrates that preserve growth lines or previous chambers in their shell or skeleton as they grow, vertebrates continually remodel and modify their bones during growth. Thus, the only way to study growth and development in most fossil vertebrates is to assemble a large collection of juvenile and adult bones, and arrange them in a growth series.

Unfortunately, juvenile bones tend to be poorly ossified and thin-walled and fragile, and thus are easily destroyed in the process of fossilization. For the vast majority of fossil vertebrates, there are few or no examples of juvenile individuals to study, and there are even fewer examples of large sample sizes of juveniles and subadults of different ages. However, fossil from the tar pits at Rancho La Brea provide a notable exception to this rule. They preserve over 3 million fossils, including thousands of bones of individual species, and many juvenile bones of common species as well.

The largest samples belong to dire wolves and saber-toothed cats (juvenile growth trends documented by Long et al., 2017, and Gillespy, this volume). One of the most common herbivorous mammals in the Rancho La Brea sample is the extinct bison, *Bison antiquus*. It is a well studied species that was fully monographed by Skinner and Kaisen (1947) and McDonald (1981), found all over North America during the late Pleistocene (Guthrie, 1970; Kurtén and Anderson, 1980; Hill et al., 2008; Scott, 2010; Lewis et al., 2010; Raymond and Prothero, 2011; Heintzman et al., 2016; Froese et al., 2017). The immigration of *Bison* from Eurasia, marked by the appearance of the large Steppe Bison,

Bison priscus, records the beginning of the Rancholabrean land-mammal “age” in North America before 240,000 years ago (Scott, 2010). By the late Pleistocene, *B. priscus* inhabited Alaska and other northern latitude localities, while most of the lower-latitude localities yield specimens referred to *B. antiquus antiquus* (McDonald, 1981) or sometimes referred to as *Bison bison antiquus* (Kurtén and Anderson, 1980). For this paper we follow the current practice of abandoning subspecies in bison fossils (Scott and Cox, 2008) and refer to them as *B. antiquus*.

The large number of juvenile bones (particularly juvenile limb bones) at Rancho La Brea provides an unparalleled opportunity to examine growth trends in an extinct mammalian species. We restricted this study to just specimens from La Brea tar pits, because most other bison samples found in Pleistocene localities in North America do not include a significant number of juvenile bones. In addition, there was no need to look at subsamples separated by age of the pits, because Raymond and Prothero (2011) showed that there is no significant difference in size or shape of the limb bones through the entire age span of the pits at Rancho La Brea (from 37,000 years ago to about 9000 years ago).

Of particular interest is how this growth occurred. Do the limb dimensions change by the same linear amount with time, resulting in what is known as isometric growth? Or do they follow a more common tendency for the limbs to change shape as they grow, so that one dimension changes faster or slower than another? For limb elements, a common trend is for the limb to grow more robust as the animal gets larger, because volume (and therefore mass) increases as a power of three, while cross-sectional area of a limb only increases as a power of two, so an elephant limb must necessarily be more robust than a mouse limb. On a log-log plot, which produces lines of the exponents of the growth formula, a slope of 1.0 indicates isometric growth.



FIGURE 1. Growth series of juvenile to adult tibiae of *Bison antiquus* in the collections of the La Brea Tar Pits Museum. (Photo by D.R. Prothero).

Slopes of greater than 1.0 or less than 1.0 indicate that one dimension is changing allometrically, growing faster or slower than the other.

In the case of bison, it would be expected that the limbs would grow longer and more slender and gracile as they get older. In particular, the distal limb elements in cursorial mammals like most ruminant artiodactyls and horses might be expected to grow longer and more slender with age, because cursorial mammals shorten the proximal limb elements (femur, humerus) with respect to distal limb elements (radius-ulna, tibia, metapodials). Long, slender distal limbs not only increase stride length in running, but minimize the rotational inertia of the bones as they go through each stride (Hildebrand, 1985; Hildebrand and Hurley, 1985; Kilbourne and Hoffman, 2015).

Recent advances in understanding growth and allometry in living mammals has made it possible to make meaningful comparisons to the limbs in extinct mammals, because previously there were no established data for how living mammals grow and change their limb proportions through ontogeny. Kilbourne and Makovicky (2012) published a pioneering study that sampled a wide diversity of juveniles and adults of living mammal species for the first time, and determined their growth patterns. This included not only living *Bison bison*, but also other bovids such as the wildebeest, plus deer, pronghorns, and okapis. It should be instructive to compare the growth patterns of extinct *Bison antiquus*, not only with its living counterpart *Bison bison*, but with other long-limbed large-bodied artiodactyls that are somewhat or completely cursorial.

METHODS

We measured every unbroken juvenile humerus, fused radius-ulna, femur, and tibia of *Bison antiquus* in the collections of the La Brea Tar Pits and Museum (formerly the George C. Page Museum of La Brea Discoveries) to obtain the largest sample size possible for this analysis (ranging from 46 to as many as 70). Juveniles were recognized by their size and the lack of fused epiphyses. The identification of specimens as *B. antiquus* was done by the early workers on the La Brea collections, but because there are no other large bovids in the La Brea collections, identification of *B. antiquus* was unambiguous. Measurements were made following the protocols of Kilbourne and Makovicky (2012), focusing on measuring the length of the diaphysis of the shaft of each bone, and the circumference of the midshaft. In the case of adult or subadult bones that had the epiphysis attached, measurements of shaft length were made from the diaphyseal-epiphyseal sutures. Measurements were taken to the nearest millimeter. Those dimensions shorter than 460 mm were measured with metric digital calipers; those over 460 mm, and circumference measurements, were made with a flexible metric measuring tape. In addition to measuring

diaphysis length, we measured midshaft circumference.

Basic statistics and regressions were calculated and plotted using Microsoft Excel. Following the conventions of most allometric studies, raw data were converted to natural logs and plotted in log-log space, so that the exponential slope of allometry would give a simple linear slope. We also used Excel to calculate the simple least-squares regression of the data. Because there is no dependent or independent variable in this study (an assumption of the least-squares regression method), we adopted the more commonly used Reduced Major Axis (RMA) method of correlation to determine the slope between the two variables (calculated using the R program “smatr”) (Warton et al., 2006, 2008).

We followed the conventions of Kilbourne and Makovicky (2012) in plotting length on the Y axis vs. circumference on the X axis, which should give an isometric slope in log-log space of approximately 1.0 (linear dimension vs. linear dimension), and allometric slopes greater than 1.0 if the limb is gracile (positive allometry), and less than 1.0 (negative allometry) if it is robust. This allowed us to compare our results to the data of living mammals examined by Kilbourne and Makovicky (2012).

RESULTS

Results of our analyses are shown in Figure 2, and in Tables 1–4. The prediction for most cursorial mammals would be that the proximal limb elements show isometric growth, or at least not show highly gracile growth trends (Hildebrand, 1985; Hildebrand and Hurley, 1985; Kilbourne and Hoffman, 2015). For the humerus (Table 1), the slope of 1.03 (with confidence intervals that encompass an isometric slope of 1.0) in *B. antiquus* is less robust than the slope of *B. bison* of 0.79, and both are isometric or robust, as expected for a proximal limb element. The humeri of pronghorns (slope = 0.75) and wildebeest (slope = 0.86) are similarly robust, while the slopes of the white tailed deer (slope = 1.03) and the extinct La Brea camel *Camelops hesternus* (slope = 1.08) are isometric within confidence limits. However, the okapi (slope = 1.26) is significantly more gracile than expected. Thus, not even slightly or extremely cursorial artiodactyls show a consistent trend in the humerus.

The other proximal limb element, the femur (Fig. 2C, Table 3), yields a few artiodactyls that show the predicted isometry, including modern bison, the extinct La Brea camel, the pronghorn, and the wildebeest. However, both the white-tailed deer and the okapi are significantly more gracile than the isometric expectation (based on the isometric slope falling outside the confidence intervals). *Bison antiquus*, in contrast to all the others, has a highly robust slope of 0.85, significantly different from living *Bison bison*. Thus, the prediction that proximal limb elements should be either isometric or relatively more robust as the limbs grow is not supported by either our data or the data of Kilbourne and Makovicky (2012).

What about the prediction that the distal limbs should show more gracile growth patterns with the limbs getting longer more rapidly than they get thicker? For the fused radius-ulna (Fig. 2B, Table 2), *Bison antiquus* has a robust slope of 0.89, similar to the modern bison with a robust slope of 0.87. Only one artiodactyl in the Kilbourne and Makovicky (2012) data set, the okapi, shows a significantly gracile growth trend, while the pronghorn and white-tailed deer are isometric (within confidence intervals), and the wildebeest and La Brea camel are actually more robust than expected.

The other distal limb bone, the tibia, is even more at odds with the prediction that distal limb bones in cursorial artiodactyls should grow more gracile. This is actually true only of the okapi among the mammals sampled here (slope = 1.29), while all the rest of the mammals in this data set are robust. In fact, *B. antiquus* has an isometric slope of 1.05, while the 0.75 slope of *B. bison* is one of the most robust bones in this study, and not too

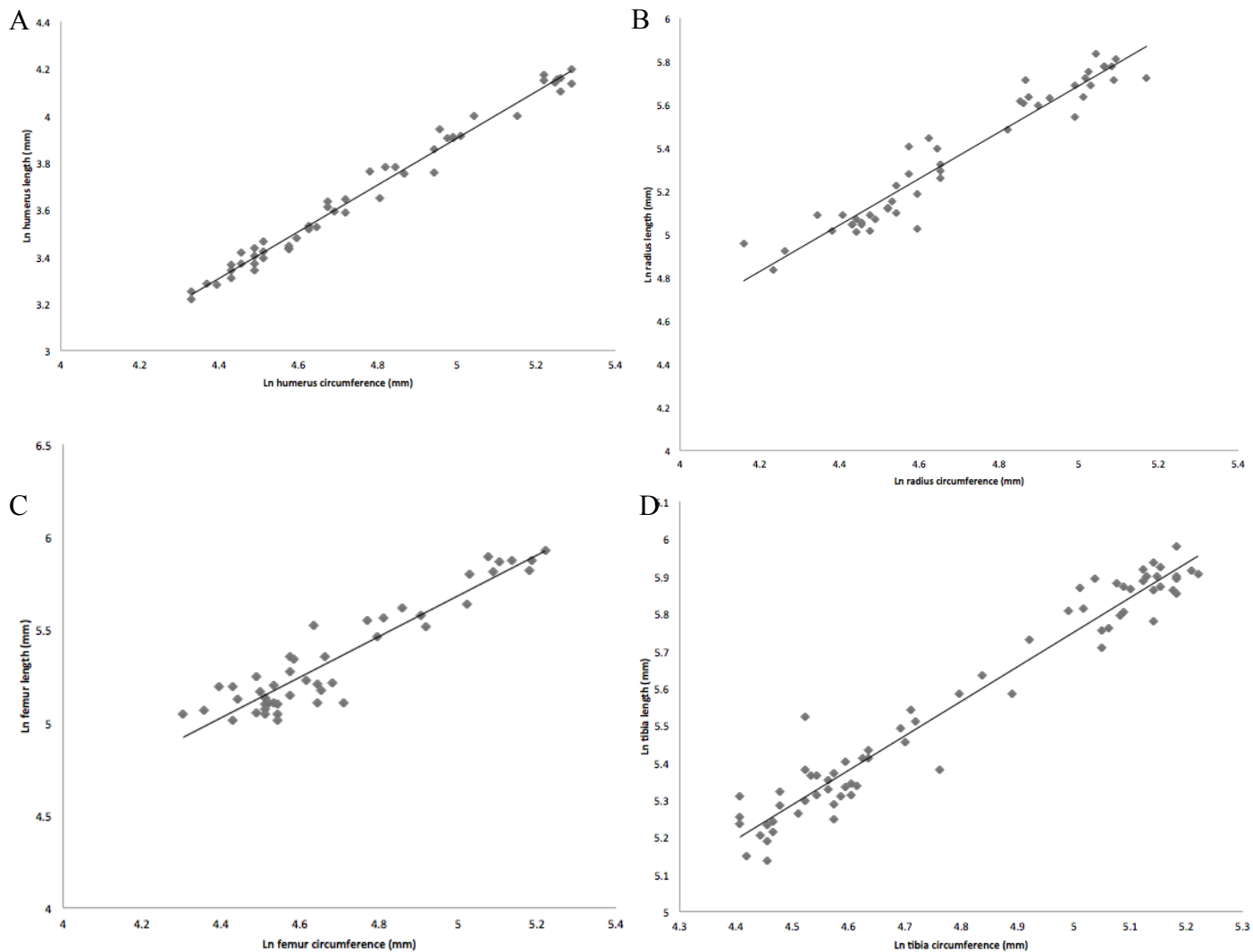


FIGURE 2. Plots of natural log (ln) of circumference (X-axis) vs. natural log (ln) of length (Y-axis) for limb bone elements of *Bison antiquus*, with the RMA slope shown. **A.** Humerus. **B.** Radius-ulna. **C.** Femur. **D.** Tibia.

different from the slope of 0.89 for the pronghorn, 0.90 for the white-tailed deer, and 0.88 for the wildebeest.

In short, the simplistic predictions about growth in cursorial artiodactyls is not borne out, either in the living mammals sampled by Kilbourne and Makovicky (2012), or the extinct mammals from La Brea that have been studied so far. All of the data so far show mixed results, with an unpredictable pattern of species that grow very robust, very gracile, or isometric. Extinct *B. antiquus* shows similar growth patterns to living *B. bison* in

the humerus and tibia (both more robust than expected), but completely different slopes in the radius-ulna and femur. Clearly, there are more complex factors at work in the locomotion of cursorial artiodactyls than the predictions based on models of cursoriality that focus on the distal-proximal axis of growth. The simplest explanation for this pattern is that these highly cursorial artiodactyls were born with very gracile limbs. For example, wildebeest calves must be able to run with their mothers within minutes of being born, as must some of the others. Because

TABLE 1. Humerus data of various artiodactyls. **CI** = slope confidence interval limits; **L.S. SLOPE** = least squares slope; **RMA** = reduced major axis slope. **(G)** = gracile; **(I)** = isometric; **(R)** = robust. *B. antiquus* results from this study; *Camelops hesternus* from Htun et al. (this volume); all other data from Kilbourne and Makovicky (2012). The taxa are *Antilocapra americana*, the pronghorn; *Odocoileus virginianus*, the white-tailed deer; *Okapia johnstoni*, the okapi; *Connochaetes taurinus*, the wildebeest; and *Bison bison*, the American Plains bison. No least squares slopes were given by Kilbourne and Makovicky (2012).

TAXON	N	L.S.SLOPE	Y-INTERCEPT	R ²	CI	RMA
Length vs. circumference						
<i>B. antiquus</i>	50	0.993	-0.364	0.919	0.95,1.12	1.03 (I)
<i>B. bison</i>	16		1.785	0.958	0.71,0.91	0.79 (R)
<i>C. hesternus</i>	29	1.048	-0.838	0.935	0.98,1.19	1.08 (I)
<i>A. americana</i>	19		2.069	0.946	0.63,0.82	0.75 (R)
<i>O. virginianus</i>	23		0.969	0.960	0.94,1.11	1.03 (I)
<i>O. johnstoni</i>	20		-0.304	0.982	1.16,1.37	1.26 (G)
<i>C. taurinus</i>	14		1.714	0.976	0.74,0.87	0.80 (R)

TABLE 2. Radius-ulna data of various artiodactyls. Conventions as in Table 1.

TAXON	N	L.S. SLOPE	Y-INTERCEPT	R ²	CI	RMA
Length vs. circumference						
<i>B. antiquus</i>	50	0.993	-0.364	0.928	0.83,0.97	0.89 (R)
<i>B. bison</i>	12		1.560	0.971	0.81,0.99	0.87 (R)
<i>C. hesternus</i>	29	1.048	-0.838	0.881	1.12,1.64	1.36 (G)
<i>A. americana</i>	18		1.889	0.858	0.65,1.09	0.87 (I)
<i>O. virginianus</i>	12		1.742	0.965	0.77,1.02	0.89 (I)
<i>O. johnstoni</i>	12		0.251	0.955	0.95,1.43	1.21 (G)
<i>C. taurinus</i>	13		1.844	0.988	0.80,0.92	0.86 (R)

TABLE 3. Femoral data of various artiodactyls. Conventions as in Table 1.

TAXON	N	L.S. SLOPE	Y-INTERCEPT	R ²	CI	RMA
Length vs. circumference						
<i>B. antiquus</i>	46	0.796	0.437	0.873	0.76,0.95	0.85 (R)
<i>B. bison</i>	16		1.427	0.975	0.86,0.99	0.92 (I)
<i>C. hesternus</i>	36	0.906	-0.445	0.851	0.86,1.12	0.98 (I)
<i>A. americana</i>	18		1.916	0.955	0.73,0.92	0.85 (I)
<i>O. virginianus</i>	23		0.805	0.961	1.02,1.21	1.13 (G)
<i>O. johnstoni</i>	20		-0.419	0.970	1.17,1.43	1.31 (G)
<i>C. taurinus</i>	15		1.261	0.989	0.92, 1.01	0.96 (I)

TABLE 4. Tibia data of various artiodactyls. Conventions as in Table 1.

TAXON	N	L.S. SLOPE	Y-INTERCEPT	R ²	CI	RMA
Length vs. circumference						
<i>B. antiquus</i>	70	1.025	0.905	0.949	0.99, 1.11	1.05 (I)
<i>B. bison</i>	17		2.232	0.923	0.64,0.89	0.75 (R)
<i>C. hesternus</i>	29	1.219	-2.201	0.902	1.13,1.45	1.28 (G)
<i>A. americana</i>	17		1.986	0.932	0.69,0.97	0.89 (R)
<i>O. virginianus</i>	20		1.892	0.962	0.80,0.98	0.90 (R)
<i>O. johnstoni</i>	21		-0.179	0.977	1.16,1.41	1.29 (G)
<i>C. taurinus</i>	14		1.851	0.989	0.82,0.93	0.88 (R)

they already start out with highly gracile limbs, their further growth is isometric or even slightly robust to maintain these gracile proportions through adulthood. This is similar to the pattern seen in saber-toothed cats, which were born with highly robust limbs, and then followed the normal felid growth pattern through ontogeny (Long et al., 2017).

CONCLUSIONS

Cursorial animals are predicted to lengthen their distal segments by allometric growth of length compared to thickness of limb bones, and distal elements are expected to grow longer and more gracile than proximal elements. However, *Bison antiquus* juvenile limb bones do not show such a simple pattern, nor do any of the other artiodactyls studied by Kilbourne and Makovicky (2012). Both the humeri and tibiae of *B. antiquus* and *B. bison* actually show more robust or isometric growth patterns than the simple prediction. In the radius-ulna and femur, *B. antiquus* does not show the predicted gracile slope of growth, but a highly robust growth pattern, as does *B. bison* and most other cursorial artiodactyls; they are either isometric or robust (except for the okapi). Thus, simplistic predictions of what limbs should do during growth are not borne out by the data obtained by Kilbourne and Makovicky (2012), nor by our data on La Brea bison. Instead, it appears that many of these cursorial artiodactyls were born with highly gracile limbs, and those proportions are maintained through growth to adulthood.

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