DID CLIMATE CHANGES AFFECT SIZE IN LATE PLEISTOCENE BISON?

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Abstract—Some scientists have argued that the body size of late Pleistocene-Holocene bison was controlled by environmental factors, and suggested that the size reduction as late Pleistocene *Bison antiquus* evolved into their modern descendants *Bison bison* was due to climate, not to human predation. Indeed, modern bison show a strong tendency for larger body sizes in colder climates (Bergmann's rule), as demonstrated by the Wood Bison (*Bison b. athabascae*) in northern Canada. The same was true in the late Pleistocene, with the larger *B. priscus* in Alaska, and smaller *B. antiquus* in central North America. This hypothesis can be tested through the excellent sample of fossils from Rancho La Brea, which span the interval from 35,000 years ago (beginning of the last glacial cycle) through the glacial maximum at 20,000 years ago (when the region was covered by closed-cone pines and snow part of the year), and culminating with early Holocene samples as young as 9000 years old. Using measurements of common limb elements (carpal and tarsal metapodials, calcanea, astragali, patellae, and distal humeral widths) from all the well-dated pits with large samples, we found that Rancho La Brea bison show no statistically significant size changes through the entire climate cycle, even at the peak of cooling and vegetation change. This is consistent with trends observed in all the common mammals and birds at Rancho La Brea. It also contradicts the idea that climate was mainly responsible for bison size reduction in the Holocene, and leaves open the possibility that this diminution might be due to human predation or other factors.

INTRODUCTION

Bison (genus *Bison*, family Bovidae) are among the most common mammal fossils in the late Pleistocene of North America. The immigration event from Eurasia of the large Steppe Bison, *Bison priscus*, marks 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*.

Many authors (Skinner and Kaisen, 1947; Guthrie, 1970; Miller and Brotherson, 1979; Kurtén and Anderson, 1980; McDonald, 1981; among others) have commented on the extreme variability of size and morphology in bison samples from many different populations. Van Zyll de Jong (1986) claimed that bison exhibit high morphological plasticity due to environmental changes. There has long been speculation about the causes of this variation, but it is very difficult to determine whether changes are due to abiotic external forcing factors such as climate or changes due to internal factors of their biology or interactions with other species. Bison clearly demonstrate Bergmann's rule, with larger body sizes in colder climates. During the late Pleistocene, the Alaska-northern Canada region was inhabited by *B. priscus*, while various smaller-sized *B. antiquus* or *B. bison* inhabited the intermediate and lower latitudes of North America. Today, there is still the clinal variation in size between the large Wood Bison of northern Canada (*B. b. athabascae*) and the much smaller Plains Bison (*B. b. bison*) (McDonald, 1981; Nowak, 1991).

Recently, Hill et al. (2008) looked at the size of bison from a variety of late Pleistocene and Holocene sites from the Great Plains. They wanted to determine whether the size reduction from Pleistocene *B. antiquus* to the modern *B. bison* was due to human predation or conversely to climatic change. They argued that the size reduction occurred in several short bursts in the early Holocene correlated with increased aridity and changes in the vegetation, and therefore the diminution in size was not due to human hunting. However, their samples were drawn almost exclusively from the Great Plains latest Pleistocene and Holocene. They did measure samples from a few of the pits at Rancho La Brea (RLB), but only examined the length of the calcaneal tuber and the width of the distal humerus. They apparently did not look at other skeletal elements, nor did they focus on the latest Pleistocene interval from 35 ka (35,000 years ago) until the glacial maximum at 20 ka.

The interval between 35 ka and 20 ka is a crucial one, because it corresponds to the increasingly colder and drier conditions of the last glacial cycle and culminated with the peak Wisconsinan Glaciation at 20 ka to 18 ka, followed by the gradual warming through the glacial-interglacial transition between 15 ka and 10 ka. The record at RLB provides an excellent sample of the fossils from one specific region that were trapped in the tar between 35 and 9 ka (Akersten et al., 1983; Stock and Harris, 1992; Friscia et al., 2008). Their chronology is well constrained using radiocarbon dating (Marcus and Berger, 1984; O'Keefe et al., 2009), and come from an area with a well-dated climatic record (Warter, 1976; Coltrain et al., 2004; Ward et al., 2005). Heusser (1998) studied the pollen recovered from well-dated deep-sea cores that were taken just offshore in the Calfornia Continental Borderland shallow shelf region. She found that southern California went through intervals of extreme climatic and environmental changes over the past 59 ka. The landscape of southern California has transformed from oak and chaparral vegetation to pine-juniper-cypress woodlands between 59-24 ka, to snowy forests with juniper and closed-cone pines from 24 to 14 ka, then oak-chaparral and coastal sagebrush with occasional alder from 14 to 10 ka, and finally the modern landscape of oak-chaparral-herbaceous vegetation in the Holocene. Such extreme vegetation and temperature changes are comparable to the clinal contrast seen today between the habitat of the Plains Bison and the northern Wood Bison, so one would expect the body size of RLB *B. antiquus* to go through a similar chronoclinal increase in body size to a maximum at 20 ka, then a reduction to the modern *B. b. bison* by 10 ka.

METHODS

We used an osteometric board and digital calipers to measure complete adult specimens of the most abundant postcranial skeletal elements of *Bison*. We measured only samples from pits with adequate

sample sizes (a statistically significant number of unbroken adult bones). We examined the patellae, carpal and tarsal metapodials (MC3-4 or MT3-4), astragali, and calcanea. Complete specimens of the other longer limb bones (radius, ulna, femur, tibia) were not common in enough pits to be statistically useful for our study. For metapodials, we measured maximum length, proximal width and depth and midshaft width and depth. For astragali and patellae, we measured the proximal-distal length, lateral width and dorsal-plantar depth. To compare our data with those of Hill et al. (2008), we measured the length of the calcaneal tuber. Hill et al. (2008) do not give their anatomical landmarks for this measurement, so we measured from the tip of the tuberosity (the attachment point with the Achilles tendon) to the ridge between the two astragalar facets. We also measured the maximum distal width of the humerus to compare our data with those of Hill et al. (2008).

We entered the data in Microsoft Excel spreadsheets so they could be statistically analyzed and plotted. We used the Shapiro-Wilk test to determine which samples were normally distributed. For those samples that were normally distributed, we used ANOVA to see if there was a significant change in size between samples of different ages.

We studied samples only from pits with adequate radiocarbon control and relatively small statistical error estimates (Marcus and Berger, 1984; O'Keefe et al., 2009), which excluded samples from Pits 4 and 16. Although there is some sexual size dimorphism in bison (McDonald, 1981), we found that the distribution of most samples was not bimodal, but normally distributed, so there we could use parametric tests to analyze significance of differences.

RESULTS

The basic statistics of the samples are given in Table 1. Visual inspection of the plots (Figs. 1-3) show that for any given dimension of the patellae (Fig. 1A), astragalus (Fig. 1B), carpal metapodial (Fig. 1C) and tarsal metapodial (Fig. 1D) there are no significant shifts in the mean, except when the sample size is very small. Not only is there no change in linear dimensions, but there is stasis even in shape metrics. For example, the robustness of the long bones (as measured by the cross-sectional area of the metapodial divided by the length) is constant through time (Fig. 2A-B). Although there is not enough space allotted in this paper to show every plot, this stasis is true for every dimension of the bones we measured (see the mean values in Table 1).

To confirm these visual impressions, we performed the Shapiro-Wilk test for normality on all the samples. All samples were normally distributed, so it was then appropriate to use ANOVA to determine the significance of differences between samples. Results of the ANOVA are shown in Table 2. In every case, the samples from each pit of different ages were statistically indistinguishable from one another ($F < F_{critical}$), so there is no significant difference between individual samples. Thus, contrary to expectation, bison do not get larger during the glacial maximum. This is clearly demonstrated by the samples that span this interval: Pit 3 (18, 593 radiocarbon years), Pit 60 (21,383 radiocarbon years), and Pit 9 (26,427 radiocarbon years) (using the new dates of O'Keefe et al., 2009). Nor is there any evidence of reduced body size in the youngest pits, which are latest Pleistocene, or 11,000 years old (Pit 13), as argued by Hill et al. (2008).

DISCUSSION

Contrary to the predictions, there was no statistically significant change of the size or shape of the limb elements of the RLB bison over the last 35,000 years. This is true in spite of the fact that the climate became considerably cooler during this time due to the last glacial-interglacial cycle at 20,000 years ago, with closed-cone coniferous forests and significant snow, yet the RLB bison did not change between the samples from Pit 3 (18, 593 radiocarbon years), Pit 60 (21,383 radiocarbon years), and Pit 9 (26,427 radiocarbon years).

Indeed, the data and plots in Hill et al. (2008) confirm our own

TABLE 1. Basic statistics of RLB *Bison antiquus* skeletal elements.

Character	Age (ka)	N	Mean	Variance
MC3-4 length	11	15	218.7	29.6
	14	30	222.6	45.1
	16	8	227.2	35.9
	18	44	222.0	38.3
	23	2	223.5	24.5
	26	4	226.2	26.9
	35	9	221.0	31.0
MC3-4 proximal width	10	2	79.5	4.5
	11	15	77.0	17.3
	14	30	76.4	10.8
	16	8	77.2	12.5
	18	44	78.5	35.4
	23	2	76.0	2.0
	26	4	82.5	22.3
	35	9	78.1	37.1
MC3-4 distal width	10	2	83.5	0.5
	11	15	81.5	20.5
	14	30	80.0	10.9
	16	8	38.7	31.3
	18	46	82.7	35.5
	23	2	79.0	3.0
	26	4	83.2	20.9
	35	9	82.4	27.5
MT3-4 length	11	10	269.1	58.1
	14	20	272.3	67.9
	16	7	273.8	61.1
	18	39	273.0	44.0
	23	6	237.0	65.2
	26	3	277.0	48.0
	35	6	270.6	31.8
MT3-4 proximal width	11	10	61.2	19.5
	14	20	62.1	17.1
	16	7	61.3	16.2
	18	39	62.8	16.8
	23	6	62.1	32.1
	26	3	62.6	12.3
	35	6	56.8	5.3
MT3-4 distal width	11	10	73.9	20.9
	14	20	74.5	15.8
	16	7	73.3	26.5
	18	39	74.8	16.4
	23	6	74.3	29.4
	26	3	71.3	9.3
	35	6	70.0	1.2
Calcaneal tuber length	11	8	126.3	49.6
	18	10	125.9	45.2
	23	37	125.7	24.4
	35	10	123.5	66.0
Astragalus length	11	35	85.5	19.8
	14	62	84.9	32.8
	23	4	85.0	7.5
	26	7	80.8	16.9
	35	33	83.0	37.6
Astragalus width	11	35	53.1	11.2
	14	62	54.3	23.5
	23	4	52.9	52.3
	26	7	50.1	11.2
	35	33	52.3	25.5
Astragalus depth	11	22	46.77	8.6
	14	63	45.9	15.1
	23	4	47.3	11.7
	26	4	39.4	2.4
	35	35	44.9	17.2
Patella length	14	24	73.9	37.3
	16	5	74.7	64.5
	18	25	74.6	37.4
	23	8	68.9	24.6
	35	6	71.8	64.9
Patellar width	14	24	68.1	35.2
	16	5	67.3	48.1
	18	25	71.1	37.4
	23	8	69.1	2.2
	35	6	69.1	7.3
Patellar depth	14	24	42.4	12.5
	16	5	42.5	9.2
	18	25	46.6	36.0
	23	8	44.2	28.8
	35	6	46.7	1.4
Humerus distal width	11	10	93.8	75.9
	18	3	99.3	276.3
	20	20	91.9	27.9
	21	5	92.2	92.2
	35	2	95.0	50.0

measurements. They measured a smaller sample from fewer pits (they did not have data from Pit 13 and Pit 60 in their Table 1), but we tried to reproduce and expand their original data set to see if we obtained the same result. Our plot of calcaneal tuber length (Fig. 3A) confirms the stasis shown in their figure 6. Likewise, our data for distal humerus
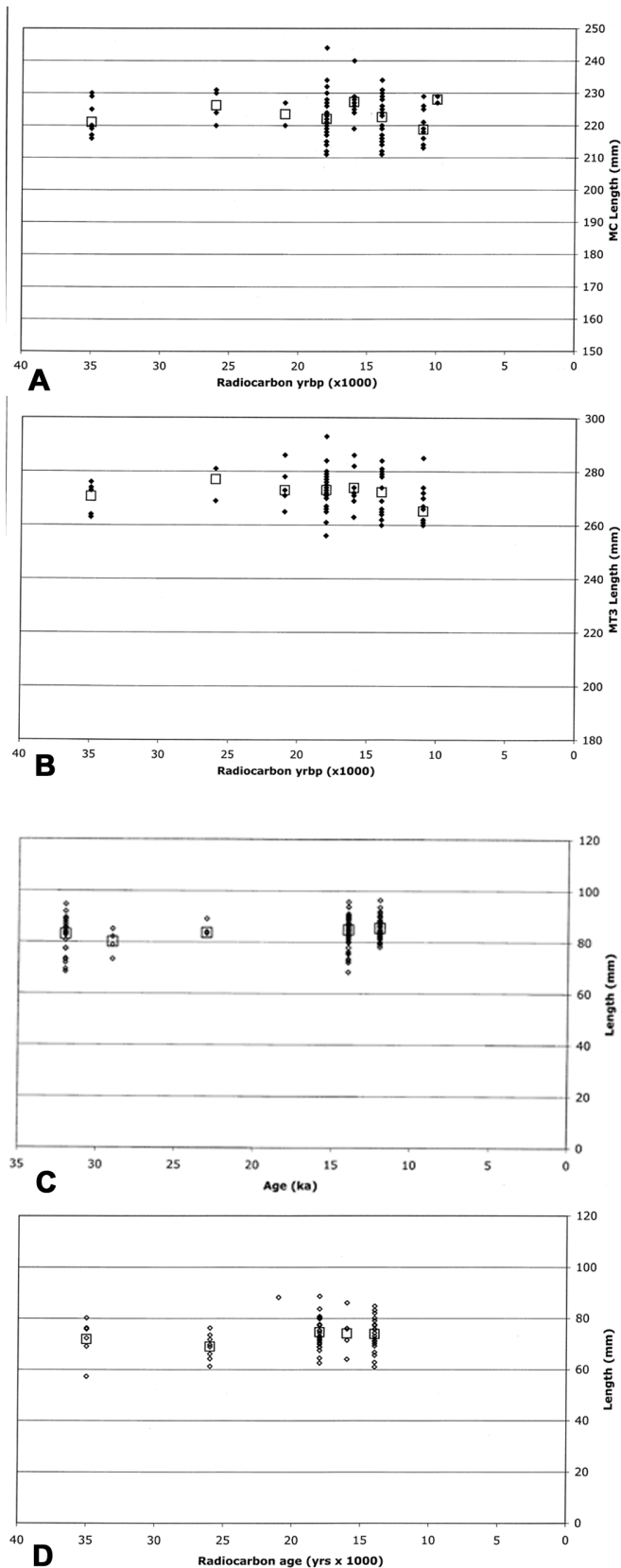
FIGURES 1. **A-D**, Plots of dimensions of *Bison* bones against the age of the pit sample. Open squares indicate the means for each time interval; solid diamonds are individual specimens. **A**, Metacarpal length. **B**, Metatarsal length. **C**, Astragalus length. **D**, Patellar length.
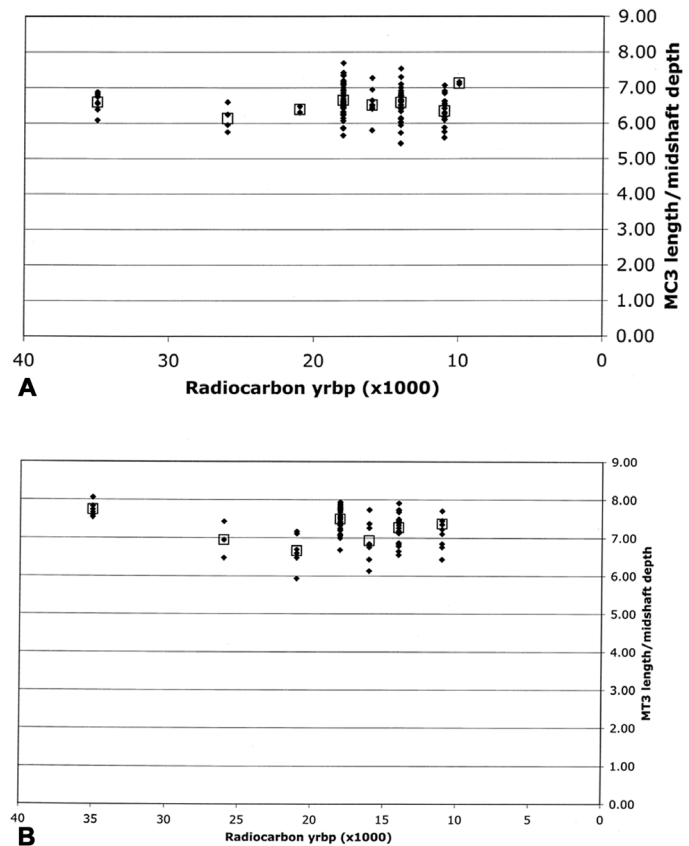

FIGURE 2. Plot of ratios of *Bison* metapodial robustness (midshaft cross-sectional area divided by the length) against the age of the pit sample. Large open squares indicate mean of temporal sample; solid diamonds are individual data points. **A**, Mc3-4. **B**, Mt3-4.

width (Fig. 3B) are concordant with the stasis shown in their Figure 7. We are not sure why Hill et al. (2008) neglected to discuss this obvious example of stasis not only in the RLB sample that spanned the glacial maximum, but in the rest of their High Plains samples as well. Nevertheless, such stasis weakens their case that climatic change drives bison size change.

Some authors have claimed Northern Plains bison gradually declined in size from 10 ka to 4 ka (Hughes, 1978), while others claim that bison size decreased abruptly between 8 ka and 6 ka in the Southern Plains (Lewis et al., 2010). Neither of these studies, however, address the issue of stasis in the late Pleistocene bison. Lewis et al. (2010) attributed this size reduction to the increase of lower-nutrition C_4 grasses and decreased tree coverage. This is consistent with the observations of Coltrain et al. (2004), which documented only C_3 grasses at RLB.

Such stasis in size and shape of the limb bones goes against the predictions of Bergmann's rule, which states that within a species the body mass tends to increases with latitude and colder climate. As we have already pointed out, bison show clinal variation in size (Bergmann's rule) from northern cold climates (*B. priscus* in the late Pleistocene; *B. b. athabascae* today) to lower latitudes and warmer drier climates (*B. antiquus* in the late Pleistocene; *B. b. bison* today). Yet our data show no similar chronocline in size when the climates of the peak glacial, with conifers and snow like that of high latitudes, prevailed in the RLB region. Based upon our study of RLB specimens, bison are apparently not as sensitive to climate and environmental change as widely thought.

Such stasis in body size and shape is prevalent among most Pleistocene mammals (Barnosky, 1994, 2005). In addition to this project, we
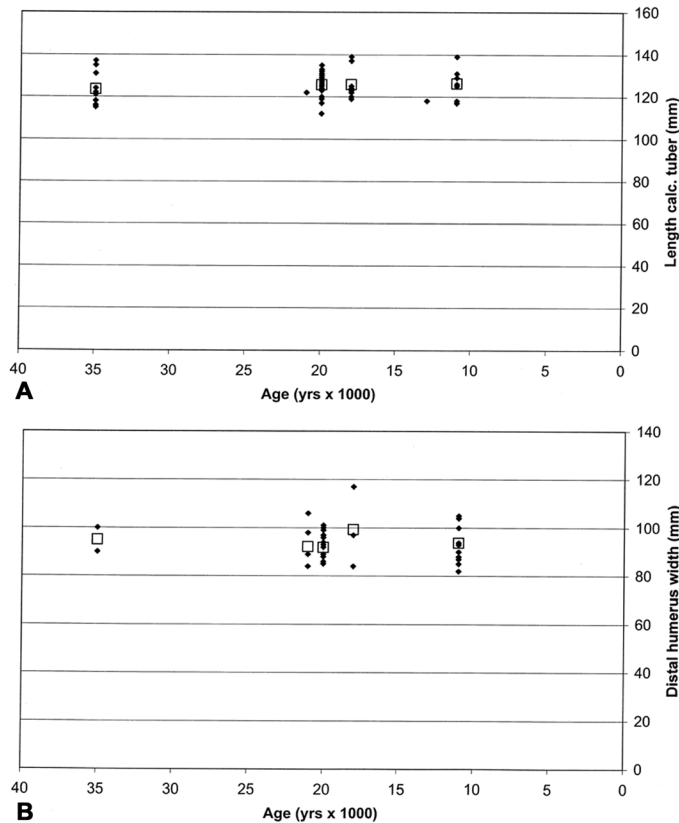
FIGURE 3. Plots of *Bison* bone dimensions through time, following the conventions of Hill et al. (2008). Symbols as in Figs. 1 and 2. **A**, Length of calcaneal tuber. **B**, Distal width of humerus.

TABLE 2. ANOVA of different pit samples of the different dimensions of RLB *Bison antiquus* bones, showing that none of the dated pit samples are significantly different ($F > F_{critical}$) from one another, and that stasis prevails.

Element	F	F_{crit}	p	df	Significant?
MC3-4: length	2.076	2.186	0.06	6	No
MC3-4: proximal width	1.129	2.097	0.35	7	No
MC3-4 distal width	1.149	2.095	0.33	7	No
MT3-4 length	0.702	2.208	0.64	6	No
MT3-4 proximal width	1.921	2.208	0.08	6	No
MT3-4 distal width	1.506	2.208	0.18	6	No
Calcaneum: tuber length	0.457	2.755	0.712	3	No
Astragalus: proximal-distal length	1.866	2.438	0.119	4	No
Astragalus: lateral width	1.517	2.438	0.200	4	No
Astragalus: dorsal-plantar depth	1.769	2.445	0.006	4	No
Patella: proximo-distal length	1.386	2.517	0.248	4	No
Patella: lateral width	1.024	2.517	0.401	4	No
Patella dorsal-plantar depth	1.962	2.520	0.026	4	No
Humerus: distal width	0.646	2.641	0.633	4	No

CONCLUSION

Although there is well-documented clinal variation in size between larger high-latitude bison and smaller mid- to lower-latitude bison due to Bergmann's rule, the sequence of samples of bison from RLB from 35 ka to 11 ka shows no evidence of a chronocline of larger body size or robustness at the peak of the last glacial maximum 20,000 years ago, even though the climate and vegetation in the RLB were much colder and snowier than at any time before or since. This contradicts the argument of Hughes (1978), Hill et al. (2008) and Lewis et al. (2010) that several short climatic events in the late Pleistocene-early Holocene, along with increased aridity, caused the reduction in size of bison from large *B. antiquus* to Holocene *B. bison*. It also negates their efforts to rule out human predation as a cause for this size reduction, so that we can no longer conclude that the size change was a simple function of climate. Instead, it could have been due to other extrinsic environmental factors, human predation, or possibly also to intrinsic biological factors (Prothero, 1999).

have analyzed most of the other common mammals and birds from Rancho La Brea. Our results indicate that the common mammal species such as horses, camels, ground sloths, dire wolves, saber-toothed cats, and American lions demonstrate complete stasis from the late Pleistocene through the end of the Pleistocene (Prothero et al., 2009; Prothero and Raymond, 2008; DeSantis et al., this volume). A similar degree of stasis has been documented for all the most common birds at Rancho la Brea, including turkeys, condors, caracaras, and golden and bald eagles (Syverson and Prothero, 2010; Fragomeni and Prothero, this volume; Molina and Prothero, this volume).

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