The Evolution of *Bison bison*:
A View from the Southern Plains

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**ABSTRACT**

Morphological changes in late Quaternary bison generally have been defined by a rapid decline in body size and a reorientation of the horns. This morphological shift is used to mark the emergence of modern *Bison bison*, a transition conventionally thought to have originated on the Northern Plains after 5,000 B.P. Hypotheses regarding the impact of human hunting on this morphological transition vary from negligible to the driving force behind a speciation event. New data from the Southern Plains, however, define better the transition and the role that hunting may have played in driving this event. This research on Southern Plains bison indicates that fully modern bison appear on the Southern Plains much earlier (between 8,000 to 6,500 B.P.) than on the Northern Plains and that this morphological transition also involved a decrease in relative bone strength (robusticity). The morphological transition in bison does not correlate with changes in tool technology, hunting intensity, or hunting techniques. Therefore, the impacts of human hunting do not adequately account for the observed morphological changes in bison morphology. The change in bison morphology on the Southern Plains is correlated better with the spread of the *C₄* short grass ecosystem between 8,000 to 7,500 B.P. The properties of *C₄* grasses explain both the size reduction and the gracilization of late Quaternary bison.

**INTRODUCTION**

The North American bison was a critical species for people inhabiting the Plains during the late Quaternary, serving as an important source of food and raw materials for many cultures. More broadly, however, bison impacted the lives of all Plains-dwelling peoples as the keystone species of the Plains ecosystem (Frison 1991; McHugh 1972). Any change in bison would have had a significant impact on the peoples of the Plains, and the evolutionary forces acting to change bison would have impacted all other species that were part of the Plains ecosystem, including humans. For these reasons, defining and understanding the changes in late Quaternary bison and the underlying causes for those changes are essential to the interpretation of prehistoric Plains cultures.

Hypotheses proposed to explain the morphological changes in bison following the Wisconsin glaciation constitute some of the most compelling and contentious questions surrounding the evolution of Quaternary macrofaunas (McDonald 1981; Reeves 1973). Most hypotheses implicate either climatic changes (e.g., Wilson 1975) or the effects of human hunting (e.g., Lott 2002; McDonald 1981) to explain changes in the bison lineage, and are based primarily on data from the Northern Plains. While Southern Plains bison have been studied from an archeological point of view (e.g., Bement 1999; Johnson 1987), hypotheses concerning the emergence of modern bison have yet to be explored fully in this region. New data, however, from a continuous and well-dated sequence of bison metapodials from the Lubbock Lake Landmark site, supplemented with specimens from two other Southern Plains localities, allow an improved understanding of the pattern of morphological change in the late Quaternary bison lineage. These new data have led to the formulation of a new hypothesis regarding the selective force guiding these changes in bison.

Changes in the bison lineage during the terminal Pleistocene and early Holocene generally are described as a decrease in overall body size (ca. 20% reduction in linear measurements) and a reorientation of the horn cores (Dalquest and Schultz 1992; McDonald 1981; Wilson 1974a, 1975). These changes are suggested to have occurred gradually beginning in the late Pleistocene and continuing through the Holocene. Modern bison
are reportedly present on the Northern Plains after ca. 5,000 B.P. (uncalibrated radiocarbon age) (McDonald 1981; Wilson 1975). Changes in horn core morphology are vague, however, due to their highly variable nature (McDonald 1981; Wilson 1975) and plasticity (Guthrie 1966), such that attempts to use horn cores in taxonomic and phylogenetic analyses find them to be of limited utility. As such, horn cores, accepted as being fully modern in morphology on the Southern Plains by 10,000 B.P. (Dalquest and Schultz 1992), are not addressed further.

Both human hunting and climatic change have been posited as the principle force behind the decrease in bison body size. Human hunting hypotheses generally suggest that hunting selected either for smaller body sizes or against larger body sizes (Lott 2002; McDonald 1981). Climatic hypotheses associate the warming temperatures of the Holocene with decreases in body size, following Bergmann’s rule (Bergmann 1847) and the modern size cline (a decrease in body size from north to south) seen in today’s bison (Wilson 1975). Most of the evidence given in support of these hypotheses is derived from Northern Plains populations from multiple localities, and is based principally on cranial characteristics known to be highly variable. To define better the rate and pattern of change in bison populations, a morphologically conservative element should be used and the sample broadened to include populations beyond the Northern Plains. Correlations between changing bison morphology and parameters associated with human hunting and climatic change hypotheses then can be examined. This study, therefore, focuses on Southern Plains bison metapodials to determine if the timing and pattern of change is similar to that defined on the Northern Plains and which of the competing hypotheses is best supported.

METHODS

While much of the historic research regarding bison phylogeny has relied heavily on cranial characteristics (Guthrie 1990; McDonald 1981; Skinner and Kaisan 1947; Wilson 1975; Wyckoff and Dalquest 1997), this study focuses on the metapodials. Metapodials are functionally important weight-bearing elements for bison (Bedord 1974) and, more broadly, for the family Bovidae (Scott 1985). Metapodials are conservative morphologically, showing little variation in shape across the bovids (Scott 1985). Any significant changes in metapodial morphology, therefore, likely represent a functional, behavioral, or genotypic shift in bison relevant to hypotheses about the forces that were acting to shape the bison skeleton. Metapodials also are common elements in late Quaternary faunal assemblages (Kreutzer 1992), allowing for robust statistical analyses.

Metapodial size, shape, and robusticity (relative cortical bone thickness) data were collected from osteometric and radiographic examination of a temporal series of 463 late Quaternary bison metapodials from three sites on the Southern Plains (Figure 1). Of those metapodials, 254 specimens were from Lubbock Lake (Johnson 1987) in western Texas. Dates were assigned to the Lubbock Lake specimens using multiple radiocarbon ages associated with archeological features and geologic strata (Holliday et al. 1983, 1985). In addition, 75 metapodials from Cooper (Bement 1999) and 134 from Certain (Buehler 1997), both sites located in western Oklahoma, were examined. These metapodials were dated according to radiocarbon assays and known ages of diagnostic stone tools (Bement 1999; Buehler 1997).
Proximal and distal anteroposterior and mediolateral width measurements were collected at the extremes on complete metapodials at the proximal and distal ends using sliding calipers. Unfused metapodials were not included in the study. Overall element length was taken at the extreme using an osteometric measuring board. Shaft diameters in the anteroposterior view and the mediolateral view also were collected from X-rays using sliding calipers. Robusticity (relative cortical bone thickness) was calculated using a published formula incorporating medullary cavity area, cortical bone thickness, and element size adjusted for estimated body mass (Trinkaus et al. 1994). Data were tested using ANOVA and Pairwise post-hoc Bonferroni/Dunn tests. A confidence level of 0.05 was set for all statistical tests.

RESULTS

Data from the Southern Plains indicate a different pattern of size change than that seen on the Northern Plains. The Southern Plains pattern is one of relative stasis in body size before 8,000 B.P. and following 6,500 B.P. (Figure 2). A rapid decrease in size occurs between 8,000 and 6,500 B.P. This pattern is found in both sexes and for both metatarsals and metacarpals. No statistically significant difference exists between the populations 8,000 years old and older, nor does a significant difference occur between those populations 6,500 years old and more recent. Pairwise tests find that the only significant difference between the bison populations is between the population dating to 8,000 B.P. and the population dating to 6,500 B.P.

A slight shift in metapodial shape appears to accompany this size decrease (Figure 3). Metapodials of similar length vary significantly by width (at the midshaft) when specimens from the group dating to 8,000 years and older are compared to specimens dating 6,500 years old and more recent (see Figure 3). A decrease in bone robusticity also is found, using a standard robusticity index adjusted for body size referred to as J/stand (Trinkaus et al. 1994). Again, this decrease in bone robusticity, or gracilization, of the metapodials occurs between 8,000 B.P. and 6,500 B.P. in concert with the change in body size and metapodial shape (Figure 4).

DISCUSSION

In general, the pattern of morphological change on the Southern Plains is quite different than that reported on the Northern Plains. The Southern Plains pattern is best summarized as relative stasis before 8,000 B.P., a rapid change in size, shape, and robusticity between 8,000 B.P. and 6,500 B.P., followed by stasis after 6,500 B.P. Bison reach their modern form on the Southern Plains, then, sometime in the 1,500 year period between 8,000 B.P. and 6,500 B.P., well before the appearance of modern morphology in Northern Plains bison at ca. 5,000 B.P. (McDonald 1981; Wilson 1975). The extremely rapid shift in Southern Plains metapodial morphology also contrasts starkly with the gradual pattern of change reported for Northern Plains bison (Wilson 1974a). With the pattern of morphological change on the Southern Plains established, variables associated with both the human hunting hypothesis and the climatic change hypothesis can be examined.

The period of rapid change in bison did not correlate with an increase in population pressure (Haynes 2002; Meltzer 2000). Bison were hunted intensively on the Southern Plains both before and after this change without any significant change in bison morphology. Also, no selection against
large animals occurred during the period of change, as kills continue to have females, juveniles, and males, and exhibit similar standard deviation levels for metric variables. Selection against large individuals also would not explain why a change in shape and robusticity of the metapodials occurs.

McDonald (1981) suggests that the change in size was not driven by selection of large animals, but that smaller bison would have had an advantage over larger bison. Smaller bison supposedly would be better able to escape and to breed more quickly. At issue with this hypothesis, however, is the fact that humans were not the primary predator of bison (Fuller 1959; Lott 2002; McHugh 1972). While humans were hunting bison during the period of rapid morphological change in the lineage, wolves remained their primary predator. It does not follow from a natural selection point of view for bison to become smaller in order to escape their secondary predator if such a change increased the likelihood of their being killed by their primary predator.

No major shift in hunting strategy precedes the change in bison morphology, nor does a dramatic change occur in tool technology (Frison et al. 1976; Johnson 1997). While it may be argued that the change from Paleoindian to Early Archaic tools constitutes a major change in technology, when undeniable paradigmatic shifts in hunting strategy and tool type do occur (e.g., the introduction of the bow and arrow, guns, and horses) no change in bison morphology is found. Likewise, increased predation from humans should be associated with increased herd movements. Such increases in movement would increase the bending forces and, therefore, be associated with more robust bones. Just the opposite is found, as bone robusticity decreases sharply with the decrease in body size. No obvious mechanism is apparent that would connect changes in bison morphology with human hunting based on the variables examined here.

In general, the changes in bison morphology appear to be explained better by the changing climate. Body size does decrease with warming temperatures, as would be expected (Wilson 1975). A correlation exists between metapodial shape and vegetation density in modern bovids, whereby...
species associated with denser vegetation typically have relatively wider metapodials than those in areas where vegetation is sparse (Scott 1985). As the amount of brushy vegetation on the Southern Plains decreased, bison metapodials become thinner. Lastly, given the earlier date of modern morphology on the Southern Plains than on the Northern Plains, the pattern of morphological change spreads south to north along with the temperature gradient.

When changes in temperature and rainfall are examined with the changes in bison morphology, however, several shortcomings of the climatic hypothesis become evident. Based on both floral and faunal changes (see Johnson 1987), the late Pleistocene and early Holocene are characterized by a warming and drying trend on the Southern Plains. This trend peaks at ca. 7,000 to 5,000 B.P., during the deposition of stratum 3 at Lubbock Lake (Figure 5), and is followed by a return to cooler, moister conditions. Bison morphological change, therefore, occurs as the climate reaches its warmest and driest conditions. But, if bison morphology were tracking closely with temperature and rainfall, then the decrease in body size would have begun much earlier when the climate first began to change. While the warming and drying trends appear to explain the progression toward relatively smaller bison in the late Quaternary, it does not explain the period of rapid change between 8,000 and 6,500 B.P.

Likewise, if the morphological changes during this period were strictly phenotypic responses to changing temperatures, then they should have reversed when the conditions cooled after ca. 4,500 B.P. (stratum 4 at Lubbock Lake). Also, the decrease in metapodial robusticity during the late Quaternary is inconsistent with a drying, degrading habitat where bison would have been forced to range further to find adequate food. This increased movement would have increased bending forces on the skeletal elements of the limbs and led to more robust metapodials, not less robust metapodials. The climatic model, as it stands, fails to address these inconsistencies.

Recent phytolith analyses from Southern Plains localities (Fredlund 2002; Fredlund et al. 2002, 2003) offer a possible explanation for both the decrease in body size and in robusticity. A dramatic and rapid shift from C₃ to C₄ grass occurs on the Southern Plains beginning at ca. 10,000 B.P. and completed by 8,000 B.P., just when changes in bison morphology begin to appear in the fossil record. C₄ short grasses have an advantage over C₂ long grasses under warm Holocene conditions, as C₂ grasses are less tolerant of warm, dry conditions. The decrease in bison body size begins at approximately the same time that tall grass (C₂) ecosystems begin to give way to short grass (C₄) ecosystems on the Southern High Plains in the early Holocene. Additionally, both C₄ grasses and smaller bison spread northward during the Holocene. Once C₄ grasses become dominant on the Southern High Plains ca. 8,000 to 7,500 B.P., C₂ grasses never rebound despite the cooling climate of the late Holocene (Fredlund 2002; Fredlund et al. 2002, 2003).

The timing and pattern of the short grass ecosystem’s spread follows that of all morphological changes in bison metapodials on the Southern Plains. The productivity and nutrition of C₄ grasses may explain why the transition in grass types would cause such a suite of changes in bison morphology. C₄ grasses are more productive per acre than are C₂ grasses (Howe 2000). With greater productivity, bison would not be required to range as far to find similar amounts of food. Such a
change in grass types may have led, therefore, to a decrease in herd movements and a subsequent reduction in range during the late Quaternary. This reduction in movement patterns would have led to decreased bending forces on the skeletal elements of the limbs and ultimately to less robust metapodials. The pattern of robusticity change would be a rapid shift during the period of transition from C₃ to C₄ grasses, followed and preceded by relative morphological stasis.

Despite higher productivity, C₄ grasses possess a larger cell wall and less protein than their C₃ counterparts, and are thus less nutritious (Howe 2000). Such a change in nutritional quality may have selected for bison with smaller body sizes, as smaller mammals generally require absolutely fewer calories and have reduced protein demands (Calder 1984). Larger mammals have higher total rates of metabolism than do smaller species, and the increase in metabolic rate is not proportional to mass (Calder 1984). A doubling of mass necessitates a 64% increase in basal metabolic rate, for example, while decreasing the mass by half reduces the basal metabolic rate by only 39% (McNab 1990). A mammal, therefore, can respond to decreases in available energy by either reducing mass or reducing the metabolic rate at a fixed mass (McNab 1990). Thus, change in bison body size would have been rapid during the transition from C₄ to C₃ grasses (and may have occurred passively, as bison fed on protein-poor C₄ grasses), and been followed and preceded by general morphological stasis.

NEW HYPOTHESIS

The new hypothesis proposed, therefore, is that the changing grasslands of the Southern Plains drove morphological changes in the late Quaternary bison lineage. This hypothesis, focused on the spread of an abundant but nutritionally poor primary food source for bison, explains both the decrease in bone robusticity and the decrease in body size. The timing of morphological changes and the earlier appearance of modern bison on the Southern Plains also are explained, as both modern bison morphology and C₄ grasses continued to spread northward as the late Quaternary climate dried and warmed. The effect of changing vegetation on late Quaternary bison provides increasing evidence that the dramatic changes in the North American fauna following the Wisconsin glaciation were driven primarily by the altering environment rather than hunting pressure from humans.

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