Sexing Bison Metapodials Using Principal Component Analysis

Patrick J. Lewis, Briggs Buchanan, and Eileen Johnson

Bison remains are a common and important component of many North American archaeological and paleontological sites. Interpretations of bison remains, however, are often hampered by the inability to determine sex reliably in this dimorphic taxon. Metapodials are among the most common bison element recovered in archaeological assemblages, but have proven difficult to sex. The methods currently in use to estimate sex range from those using only bivariate plots and ratios of various metapodial measurements to those using discriminant function analysis. Each method has advantages and disadvantages, with no one method producing certain, unambiguous results. The designation of sex in borderline specimens remains uncertain in all current methods and must be determined subjectively. By reducing data through the use of ratios, the current bivariate methods fail to make full use of the size variation present between male and female bison. The requirements of discriminant function analysis likewise limit this method's utility for sexing metapodials, particularly for assemblages containing small sample sizes. The use of principal component analysis utilizing several of the most dimorphic, commonly measured variables produces a more confident assessment of sex for both complete and partial specimens of modern bison metapodials.

Keywords: Bison, sexual dimorphism, metapodials, principal component analysis

The importance of discerning male and female skeletal elements in archaeological faunal assemblages and the inherent problems that arise from improper identification has produced several methods of sexing large herd animals (d’Errico and Vanhaeren 2002; Morrison and Whitridge 1997; Weinstock 2000, 2002), particularly late Quaternary members of the genus *Bison* (Bedord 1974, 1978; Brink et al. 1986; Duffield 1973; Morlan 1991; Reher and Frison 1980; Skinner and Kaisen 1947; Speth 1983; Todd 1986, 1987; Walde 1985; Wilson 1974). While obvious cranial features allow a distinction between males and females, postcranial elements exhibit overlap in metric variables and are more ambiguous in attempts to determine sex. Skeletal remains recovered from archaeological localities commonly are disarticulated due to cultural and natural pre-depositional and post-depositional processes (Lyman 1994). Although male and female bison clearly differ in size in this highly dimorphic taxon, no single variable generally is sufficient to separate all individuals in an assemblage (Bedord 1974). This paper focuses on the use of a multivariate method using principal component analysis to sex both complete and incomplete bison metapodials and to evaluate the success of this method.

The lack of reliable sexing data hampers studies such as the minimum number of individuals (MNI) represented in an assemblage, herd composition, seasonality, taphonomic processes, and the reconstruction of hunting strategies (e.g., Binford 1984; Speth 1983; Wheat 1972). The MNI estimates tabulated from faunal assemblages are
made after the most abundant element is tallied within a taxon for a given aggregate (Grayson 1984). Modifiers such as side, age, and sex of each element are used to adjust the MNI estimate. Modern observations of bison behavior indicate that sex-ratios within a herd fluctuate predictably during the course of the year (McHugh 1972). The differential representation of bulls and cows in bison assemblages, therefore, may suggest the time of year a kill was made or season of death in a natural die-off. Sex-ratios likewise provide important data on hunting strategies by indicating if one sex was targeted over the other (Speth 1983; Spiess 1979; Weinstock 2000, 2002).

When a sufficient number are recovered, bison skulls and mandibles are preferred for sexing due to their reliability and obvious distinguishing traits (Reher 1970; Speth 1983). Post-cranial remains have proven more difficult to sex, and many methods have been proposed and used to determine the sex of bison post-cranial elements. For example, only 80% of carpal and tarsal bones, abundant and well preserved at many archaeological sites, can be assigned correctly to bulls or cows/calves using bivariate plots (Morlan 1991). Astragali volume is apparently more effective at separating the sexes, as demonstrated at several Paleoindian kills on the Northern Plains (Zeimens 1982; Zeimens and Zeimens 1974), and fully fused calcanea have been used to estimate the sex of bison at kill sites. The relatively high marrow content within metapodials (Binford 1978:23; Emerson 1990, 1993), however, increases the probability these elements may be broken more often to extract marrow. Furthermore, metapodials commonly occur as expediency tools in butchering sites, particularly during the Paleoindian period on the Great Plains of North America (e.g., Frison 1974; Johnson 1982, 1987; Wheat 1972, 1979). These factors emphasize the need for a method that can discern the sex of portions of elements.

Sexing bison skeletal remains is based primarily on the observation of pronounced dimorphism in overall body size (McHugh 1972; Wheat 1972). Compared to other mammals, dimorphism in modern bison is prominent, with males weighing up to twice as much as females (Halloran 1957; McHugh 1972; Nowak 1991). A problem is created, however, if immature males are unrecognized and analyzed with mature individuals, as the size of immature males may overlap with mature females. In order to judge sex reliably, the age of skeletal elements, identified usually on the basis of epiphyseal fusion stages (Bement and Basmajian 1996; Koch 1935), must be determined.

Duffield (1973) defined a method for separating the metapodials of modern male and female wisent (*Bison bonasus*) based on distal width and a ratio of maximum element length and mid-shaft width (utilizing data from Empel and Roskosz 1963). This method used a bivariate plot of the two variables and attempts to identify two clusters presumably representing males and females. Bedord (1974) subsequently applied Duffield’s method to sexing adult bison elements from several archaeological sites. This metapodial sexing method has remained the standard since its introduction.

Several questions concerning Duffield’s sexing method, however, remain unanswered. Tests of the method on substantial samples of modern North American bison are absent, although Todd (1986) used a number of comparative bison skeletons of known sex in his study of dimorphism in...
the upper limb bones. While two clusters generally are produced when distal width (mediolateral) is plotted against the ratio of length over mid-shaft width (referred to as “ratio 6” (Dibble and Lorrain 1968; Bedord 1974)), the division between the clusters is dependent on subjective visual identification. Individual specimens often fall between the two main clusters that are assumed to represent males (those with the larger overall measurements) and females, thereby leaving their affiliation with either cluster in doubt. This problem is exacerbated when assemblages composed of individuals from populations separated by time are plotted together, as may occur with archaeological and paleontological samples. Likewise, Duffield’s method does not address the sexing of incomplete specimens.

While the three measurements Duffield (1973) uses generally appear effective in separating the sexes of complete metapodials, the use of a ratio unnecessarily eliminates data pertinent to the objective. Bedord’s (1974) test of this method using archaeological specimens from several sites demonstrated that most of the separation between males and females is due to size and that considerable overlap is found in shape (Bedord 1974; Figures 6.4–6.19). If the primary distinction between male and female bison is size, then by reducing the length and mid-shaft width measurements to a ratio, the size information available in these measurements is lost in favor of a unitless shape index.

Speth (1983) also proposed a method for sexing bison metapodials that relied on bivariate plots. By plotting various measurements against each other, male and female bison metapodials again clustered into groups. While Speth’s method produced discrete groups representing male and female elements, the groups overlapped and the sex of some individual specimens was again left in doubt. Large female metapodials are likely to be indiscernible from small males. While the measurements Speth (1983) used to separate male and female metapodials appear to separate the sexes better compared to those used in Duffield’s method, Speth’s method suffers from many of the same drawbacks. In general, the methods proposed by Speth (1983) and Duffield (1973) both separate the specimens already easily identified into male and female categories by experienced researchers, without providing an unambiguous identification for the more problematic smaller males and larger females.

To overcome the problems of the bivariate and ratio-based sexing methods, a multivariate method for sexing bison metapodials was introduced (Walde 1985; Brink et al. 1986). This method uses those measurements suggested by Speth (1983) in a discriminant function analysis (DFA). The method appears to identify accurately the sex of known specimens ca. 95% of the time, still leaving the small male and large female specimens with uncertain sex. In addition, the DFA requires a normally distributed population and homogeneity of variance (Manly 1994), although the studies employing this method did not test for these requirements (Walde 1985; Brink et al. 1986). While the use of multiple variables in assigning sex to bison metapodials appears preferable to bivariate methods, the principal component analysis (PCA) may be even more appropriate. PCA is an exploratory technique that does not require normality or homogeneity of variance of the data (Manly 1994).

This research tests the reliability of PCA to separate male and female metapodials using a sample of modern bison metapodials of known sex. The results are compared to Duffield’s method. The objective of the current analysis is to produce a reliable method of sexing bison metapodials that can be employed with samples recovered from archaeological and paleontological localities dating from the late Quaternary. Researchers using any method of sexing bison based on the analysis of modern elements, however, must be aware that documented evolutionary changes in the size of bison over the late Quaternary (McDonald 1981; Wyckoff and Dalquest 1997) may lead to the misidentification of males and females in temporally mixed assemblages, as metapodial size changes dramatically during this period (McDonald 1981; Lewis et al. 2003). A primary assumption in the use of dimorphic characteristics of modern bison is that these characteristics also were present in past populations.

METHODS

A total of 78 metapodials of known sex are used in the test (Table 1). They are composed of the following: adult Bison bison bison (30 metac-
Figure 1. Measurements taken on metacarpals: 1) distal width; 2) mid-shaft width; 3) proximal width; 4) distal breadth; 5) length; 6) mid-shaft breadth; 7) proximal breadth. Metatarsal measurements: 8) distal width; 9) mid-shaft width; 10) proximal width; 11) distal breadth; 12) length; 13) mid-shaft breadth; 14) proximal breadth (Figure adapted from Bedord 1974).

Table 1. Descriptive statistics for modern bison metapodials for males and females.

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<th>Females</th>
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<tr>
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</tr>
<tr>
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<td>Shaft Width</td>
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arpals, comprised of 20 males and 10 females; 23 metatarsals, comprised of 12 males and 11 females) and *B. b. athabascae* (8 metacarpals, comprised of 5 males and 3 females; 9 metatarsals, comprised of 5 males and 4 females); and adult *B. bonasus* (4 metacarpals, comprised of 3 males and 1 female; 3 metatarsals comprised of 2 males and 1 female).

The *B. bison* sample comes from several localities, primarily Northern Plains and zoo specimens. *Bison bonasus* is considered conspecific with *B. bison* by some researchers (e.g., Kurtén and Anderson 1980; Nowak 1991). While four female subadult specimens were used with ages of three to four years, very young juveniles aged at one to two years old have not been included. Specimens exhibiting excessive pathologies likewise were eliminated from analysis.

One side of each element was used per individual to avoid weighting those individuals with both sides present, with right elements used when both were available. Seven measurements were generated, six for each specimen using sliding digital calipers, and one using an osteometric measuring board. The measurements taken were: distal width; mid-shaft width; proximal width; distal breadth; length; mid-shaft breadth; and proximal breadth (Figure 1). Due to damage to various areas of some bones, all measurements were not available for each specimen. While all available measurements were used in the univariate and bivariate analyses, only complete specimens could be used in the multivariate analysis due to the requirements of the tests. By using both modern North American subspecies, several subadults, and the European form, variation expressed in the data set should approximate or exceed that encountered in an archaeological or paleontological assemblage.

Univariate statistics and boxplots were generated for each variable of both elements and tested with analysis of variance (ANOVA) to determine if male and female bison metapodials differed significantly. Univariate statistics identified variables best suited for the multivariate analysis by revealing those with the least overlap in range between males and females. Bivariate plots then were generated for each element using Duffield’s method to compare its accuracy with known-sex specimens of modern bison.

Principal component analysis (PCA) is used to examine size and shape variation between male and female metapodials. PCA is an exploratory data reduction technique used to identify a small set of uncorrelated variables (components) that account for a large proportion of the total variance in the original variables (Manly 1994). The objective of PCA is to reduce the dimensionality of a data set containing a large number of interrelated variables without losing the variation present in the data (Sokol and Rohlf 1995). This reduction is achieved by creating a new set of variables (the principal components) that are not correlated and are ordered so that the first few contain the majority of the variation present in all of the original variables (Jolliffe 1986). Principal component scores of an individual on a component are weighted averages of all the individual’s characteristic states. Score plots for the first two principal components, therefore, graphically portray how each element clusters based on all variables between the groups.

While PCA does not ignore correlation and covariance, it focuses on variance. The first principal component (PC1) generally accounts for the largest amount of variation, with each successive PC accounting for the majority of variation not accounted for by the previous PCs (Jolliffe 1986). The best results are found in highly correlated data sets (Manly 1994). The PCA involves finding the eigenvectors (the major and minor axes) and corresponding eigenvalues (the variances of the principal components) of the sample covariance matrix (Manly 1994). Eigenvectors and eigenvalues produced by the PCA indicate the polarity and magnitude of variation in each variable and the relative percentages of variation accounted for in each component respectively. As this method is exploratory, assumptions about normality are not necessary (Manly 1994). Interpretation of PCA is based on the vector coefficients for individual variables, and eigenvalues for amount of among-group variance accounted for by each PC.

Plots of the first two components were generated using scores from male and female elements. Initially, the PCA was performed using only the three variables of the Duffield method. A subsequent analysis utilizing the measurements identified by the univariate statistics as the most appropriate for discerning between males and females also was performed. All univariate and bivariate
tests were run with StatView 5.0, while multivariate tests were run with Minitab 11.2. An α of 0.05 was used for all tests.

RESULTS

Univariate

As expected, descriptive statistics found the average male measurements to be larger for all variables taken (Table 1). ANOVA tests found significant differences between males and females for all variables of both elements (P< 0.02 for all tests). Boxplots of each variable (Figures 2, 3) graphically displayed the overlap between males and females for each element. While all breadth measurements other than proximal breadth overlapped considerably (Figures 2a, 3a), all width measurements exhibited little overlap (Figures 2b, 3b). Overall length likewise had considerable overlap (Figures 2c, 3c). These results suggest that, based on size, measurements other than length and distal breadth (i.e., five of the seven measurements) may be helpful in distinguishing between males and females. As predicted by Duffield's method, bivariate plots of distal width and ratio 6 produced two distinct clusters representing males and females with no overlap (Figure 4). Without prior knowledge of the sex of the bison, however, where to make the division between clusters was arbitrary. Most likely, at least two of the males would have been identified as female for both elements.

Multivariate

PCA score plots using the three variables from Duffield's method (length, mid-shaft width, and distal width) also produced two distinct groups (Figure 5). While greater separation was apparent between males and females, ambiguity for large females and small males (those along/adjacent to the zero line) still was a problem, with from 5% to 10% of specimens misidentified (Figures 5a, 6a). Eigenvalues indicated that the majority of variation in metacarpals (79%) was contained in PC1, a general component interpreted as representing size (Table 2). Shape data contained in the bipolar vector of PC2 accounted for 19% of overall metacarpal variation. Metatarsals had 84% of their variation contained in PC1 and 13% in PC2. Loadings indicated that shape variation was driven by width variables decreasing more rapidly relative to length in the metacarpals (Table 2). Just the opposite was found for the metatarsals, where length decreased rapidly relative to the width variables.

Complete Specimens. A second PCA (Table 3) was executed for both metapodials using only variables found in the boxplots that were judged to have the least overlap (all width measurements and proximal breadth; Figure 1). These variables further separated the groups and accentuated dif-

Figure 2. Boxplots of the three metacarpal breadth (a), width (b), and length (c) measurements (males white, females gray) in cm. Medians, 75th percentiles, and 90th percentiles are shown.
ferences along PC1 (Figures 5b, 6b). In addition, distinctive patterns along PC2 were uncovered, where males exhibited greater variation along this axis and females were clustered more tightly. As in the preceding analysis, PC1 was interpreted as a size vector and PC2 as a shape vector. PC1 accounted for 92% of the metacarpal variation and PC2 for 4%. For the metatarsal, PC1 accounted for 91% of the variation while PC2 accounted for 5%. The minor amount of shape variation in the metacarpal was due to the relatively rapid decrease in distal width as compared to the much slower decrease in proximal width. Shape variation in the metatarsal, however, was due to the relatively rapid decrease in mid-shaft width and proximal breadth as compared to the slower change in proximal width (Table 3). A line drawn from zero on the X-axis (PC1) easily separates males from females for both elements (Figures 5b, 6b).

Incomplete Specimens. As many archaeological and paleontological specimens recovered are incomplete, several PCAs were run to ascertain the feasibility of determining sex from partial specimens. For metacarpals, proximal width and breadth and mid-shaft breadth produced two distinct clusters (Figure 7a). Both proximal measurements combined with both mid-shaft measurements separated male and female metatarsals (Figure 7b). Again, the sexes were separated by males demonstrating negative values along PC1 and females having only
positive values. The difference between males and females was along the X-axis, indicating that size was the principal discriminator. PC1, interpreted as a size vector, accounted for 93% of the variation for metacarpals, with only 4% accounted for by PC2, interpreted as a shape vector (Table 4). For metatarsals, 91% of the variation was accounted for by PC1, interpreted as a size vector, while 6% was accounted for by the shape vector PC2. The shape variation was due to the decrease in proximal breadth relative to the remaining variables.

Distal measurements likewise were useful in discerning sex (Figure 8). Distinct clusters were produced using distal width and breadth and mid-shaft width and breadth for the metacarpals (Figure 8a). The separation between male and female metatarsals, however, was ambiguous and not separated by any non-arbitrary line along a single axis for the metatarsals (Figure 8b). A single four year-old female was misidentified as a male in the analysis. Metacarpals again were separated by the zero axis along the X-axis. PC1, interpreted as a size vector, accounted for 84% of the variation in the metacarpals, while the shape vector PC2 accounted for 11% (Table 5). The shape variation was driven by an increase in distal breadth relative to the remaining variables. For metatarsals, only 63% of the variation was accounted for by size and PC1, with PC2 and PC3, both shape vectors, accounting for 24% and 10% respectively. The shape variation in PC2 was driven by a relative increase in mid-shaft breadth relative to other variables, while the variation in PC3 was a result of a relative increase in distal and mid-shaft width relative to both breadth variables.
DISCUSSION

Bivariate and ratio-based sexing methods attempt to separate male from female bison metapodials utilizing both size and shape data (Figure 4). The break point between the two clusters produced by these methods, however, is ambiguous in an analysis lacking a priori knowledge of sex, as no obvious and distinctive gap occurs between male and female elements. Similarly, samples containing only a few individuals may present a comparable problem. While Bedord (1974) generated arbitrary lines to divide proposed male and female metapodial clusters, this accommodation has not been done here, as sex was known a priori. No distinctive shift occurs in the relationship between ratio 6 and distal width for males and females. Rather, the ratio appears to change on a continuum until leveling off with very large males. This characteristic makes defining any line to divide the sexes based on this subjective line technique suspect.

In bivariate plots of modern bison metapodials, male and female variables do not overlap along the size axis (distal width), although overlap along the shape axis (ratio 6) is apparent for both elements (Figure 4). The PCA using variables from the Duffield method further indicates that size is the principal factor working to distinguish males from females and that the two sexes have very similar and overlapping shapes for both elements. The use of a ratio along the X-axis in Duffield's method, therefore, fails to utilize fully the size variation in the overall length and mid-shaft width measurements. Element shape changes along a continuum, whereby small males and large
### Table 2. PCA loadings and eigenvalues for tests of the measurements used in Duffield’s method.

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### Table 3. PCA loadings and eigenvalues for tests of the measurements used in proposed multivariate method.

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### Table 4. PCA loadings and eigenvalues for tests of the proximal and mid-shaft measurements.

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<td>Eigenvalue %</td>
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### Table 5. PCA loadings and eigenvalues for tests of the distal and mid-shaft measurements.

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<td>Eigenvalue %</td>
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females are indistinguishable. While little variation exists in element shape, this aspect of variation is given equal weight with size variation in a ratio-based approach.

Better separation between male and female elements is gained by utilizing a multivariate space and the combined variation of size found in all measurements used while still utilizing the minor variation in shape. The X-axis (PC1) is interpreted as the size axis and, again, contains the majority of variation. But the size axis differs from that used in Duffield’s method by utilizing the size variation in all variables rather than only distal width. Furthermore, results from the attempt to determine sex on distal portions indicate distal width could not separate the sexes completely for metatarsals. The Y-axis (PC2) accounts for the shape variation. Little separation along this axis is discernable for any group and males appear more variable than females. The proposed method also presents a non-arbitrary breakpoint between males and females for modern *Bison bison* along the X-axis, with males demonstrating negative values and females positive values. Although the sample contained representatives of both modern species (*B. bison* and *B. bonasus*) and both modern North American subspecies (*B. b. bison* and *B. b. athabascae*), males and females could be discerned easily.

Principal component analysis was used in this examination in order to separate size and shape variation and due to the relaxed requirements associated with exploratory techniques. Discriminant function analysis also was an effective tool for separating male and female metapodials. The use of DFA to separate male and female elements in prior research (Walde 1985), however, did not provide a non-arbitrary break point between male and female groups, was not as effective at predicting the sex of elements as this test of PCA, and failed to test the data for normality and homogeneity of variance as required by the test. Other multivariate methods, such as geometric means, may prove to be effective in discerning male and female bison metapodials. While standard and easily obtained measurements were used in this analysis, other variables may be as effective.

The attempt to determine the sex of incomplete specimens is successful for proximal portions. The proximal end of both elements appears to be the more diagnostic. Specimens lacking the distal end can be sexed reliably if the proximal end is undamaged and the specimen is complete at least to the mid-shaft. Sexing the proximal end, however, is based on specimens of known age and only adults were used here. Determining whether a proximal metapodial belongs to a juvenile or to an adult specimen may be difficult if not associated with a more age-diagnostic element or element portion. The use of the distal end of metapodials also is possible in separating males from females, although the test of distal metatarsals did not allow an unambiguous sorting of the sexes with the measurements used in this analysis. Nevertheless, clustering occurs with metatarsals so that the majority of specimens (98% in this case) can be sexed, although some specimens would remain vague. Fusion of the epiphysis indicates adult age for distal specimens, and vagaries in eliminating juvenile specimens, therefore, should be accomplished more easily with distal portions than with proximal portions.

A drawback of all sexing methods, including the method presented here, is for tests on small sample sizes. Duffield’s method relies on multiple specimens in order to form discernable clusters. The requirements of PCA and DFA likewise need reasonable sample sizes to perform well, with the differences between males and females less obvious in small samples. To test the sex of individual specimens or small assemblages of metapodials, measurements should be run with a known data set for the matrices to function optimally.

**SUMMARY**

Bison metapodials commonly are recovered in high numbers from archaeological assemblages based on their comparatively low food value (Emerson 1993) and relatively high bone density (Kreutzer 1992). Their density likewise preserves them deeper into the fossil record, and they frequently are encountered in paleontological contexts. When found as part of archaeological assemblages, however, they often are broken due to marrow processing. These elements are useful in the analyses of MNI, seasonality, demographic reconstructions, and hunting strategies. Reliable determination of metapodial sex can aid in the analysis of these archaeological concerns.
The statistical analysis (PCA) conducted with this research found that commonly collected measurements from the metapodials could discriminate reliably between modern male and female bison. The measurements that separate the sexes best are distal width, mid-shaft width, and proximal width and breadth. Partially preserved specimens also are sexed reliably, providing they are intact to at least the mid-shaft. While sensitive to sample size, the multivariate method described here is more accurate and less subjective than previous methods.

Larger sample sizes of modern bison would strengthen the confidence in the proposed method for sexing metapodials. The use of additional variables may uncover more subtle shape variation, allowing the identification of even more fragmentary specimens. Nevertheless, current research is attempting to test the multivariate sexing method presented here on extinct bison from the Cooper site (Bement 1999), where metapodials are associated with skulls and sex determined on that association.

This multivariate sexing method provides a reliable technique to determine the sex of bison metapodials recovered from archaeological sites and paleontological localities. Future research may extend the usefulness of this technique to other dimorphic bison elements (e.g., long bones, Todd 1986, 1987; carpals and tarsals, Morlan 1991) with the discovery of appropriate measures, and to other dimorphic species commonly found in late Quaternary faunal assemblages.

ACKNOWLEDGEMENTS

The authors would like to thank Dr. Leland Bement and Kent Buehler (Oklahoma Archeological Survey) for providing some of the modern bison samples and with assistance in data collection and comments that greatly improved the manuscript, and to thank Robert Fisher for providing access to modern bison samples in the Vertebrate Zoology Collections of the National Museum of Natural History. Dr. Richard Strauss (Biological Sciences, Texas Tech University) offered statistical advice on the analysis. Comments from Rob Bozell (Nebraska State Historical Society) and three anonymous reviewers helped improve the manuscript’s content. This study was funded by the Museum of Texas Tech University and represents part of the ongoing Lubbock Lake Landmark regional research program into late Quaternary adaptations to ecological, climatic, and landscape changes on the Southern Plains.

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