

**Reassessment of late quaternary bison diminution on the Great Plains of North America**

by

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## ABSTRACT

The sex of animal remains from paleozoological contexts can offer information of prehistoric faunal exploitation and spatiotemporal changes in body size. Traditional approaches to sex determination use multiple univariate statistical analysis of bone measurements to distinguish males, females, and subadult individuals. Multivariate statistical analyses offer an alternative, quantitative method to capture the same information that is not dependent on relatively subjective analysts' assessments. A large sample of published bison data published illustrate the potential of this method for future research.

The proximate cause of reduction in the overall size of late Quaternary bison is the focus of continued debate. Some researchers contend that size reduction did not occur despite well documented changes in climate and vegetation, while others link directional change in body size to changes in forage quality and availability or human predation. Historically, assessments of bison size have used standard measurements, ratio diagrams, univariate and bivariate plots, and summary statistics 1) to distinguish males and females; and 2) to generate mean body size data. Application of various multivariate methods to 1,600+ calcanea from 40+ localities is used to eliminate the subjectivity of sex determination and, in turn, supply a refined understanding of spatio-temporal patterns in bison body size. Results confirm that late Pleistocene animals were substantially larger than their late Holocene counterparts.

## CHAPTER 1. GENERAL INTRODUCTION

Interpreting early human behavior in the New World is greatly dependent on understanding paleoecology. Bison on the Great Plains were among the dominant mammals and a focal prey for many human foragers (Frison 1982, 1991a; Frison, et al. 1976:53-55; Hill, 2007; Widga 2006a:4-5; Wilson 1975). In particular, the utilization of bison by Great Plains foragers was integral to their persistence. Research regarding the diminution of bison during the Holocene is a frequent topic of research with greatly varying conclusions (Frison, et al. 1976:55; Lyman 2004:81; Wilson 1978:22). An integral work by (Hill, et al., 2008) regarding bison concluded a dramatic decrease in body size over the last 37,000 years. Studies directly connecting diminution to human predation fails to be sufficient and it is suggested climate produced a more profound effect (Hill, et al., 2008:1766-1767; Lyman 2004:81). In direct contrast, a work by (Raymond and Prothero 2011) put forward that bison from Rancho La Brea show no significant diminution over the last 35,000 years (Raymond and Prothero 2011:637-638). Building on the analysis by (Hill, et al., 2008) a recent study suggests that bison body mass decreased by as much as 37% ( $910 \pm 50$  kg) over the last 40,000 years and predict a decrease of 46% ( $357 \pm 54$  kg) in response to increasing air temperature (Martin, et al. 2018:4564). A case of multiple studies utilizing many identical specimens, and their corresponding measurements, yet arriving at drastically different conclusions has surfaced. To reconcile questions regarding bison size change, a deeper analysis of body size change and the associated ecological drivers is necessary.

Bison kill sites provide a unique snapshot into extant herds and some characteristics of their dynamics. Indiscriminate killings of bison capture unique samples of bison populations from prehistory (McDonald 1981:258). Site based comparisons suggest that significant differences in the size of bison are measurable in their remains, with changes in size occurring at



irregular frequencies (Wilson 1978:22). Early studies quickly acknowledged a decrease in the size of bison bones relative to their place in time and attempted to connect ecological drivers to such changes (Frison, et al. 1976; Hanson 1984; Hill, et al., 2008; Hofman and Todd 2001; Martin, et al. 2018; Speth 1983; Widga 2006a; Wilson 1975). Numerous studies of bison body size make direct connections to Bergmann's Rule (increased latitude and body size are correlated) as a potential driver for size variability (Breslawski and Byers 2014:865; Hill, et al., 2008:1755; Martin, et al. 2018:4566; Raymond and Prothero 2011:636). Other studies incorporate ecological drivers like changing food sources as major contributors (Lewis, et al. 2010; Lyman 2004:83; Wilson 1974:96). The effect human predation would have on diminution in bison is frequently considered, yet poorly demonstrated (McDonald 1981:248-250). The degree of predation necessary to select for decreased body size would have to be immense and fails to be demonstrated convincingly in the literature. Effectively identifying a significantly covarying effect between body size and human predation has proven elusive, given the difficulties in measuring human predation in the archaeological record. However, measurements of bison bones and paleoclimate records are more available and can provide insight regarding climate as a driver for diminution.

Drivers for size diminution understood in the paleoecological record have escaped high resolution for decades. Traditional methods for analyzing body size change rely on relatively simple comparisons, in conjunction with univariate and bivariate plots (Bedord 1974; Todd 1986; Wilson 1978:12-13). The North American bison offers a unique specimen for identifying body size change from elemental metrics, given the large and diverse samples preserved in a kill site. Previous studies utilize the calcaneus for body size estimation (Breslawski and Byers 2014; Hill, et al., 2008; Martin, et al. 2018; Raymond and Prothero 2011). As many as nine

measurements are recordable on a complete calcaneus (Hill 1996:Appendix 3), effectively capturing a significantly greater amount of size and potentially shape variability. Univariate and bivariate analyses limit the potential for analyzing size variability. Furthermore, an effective method for identifying sex is integral for discussing changes in size over time. Earlier methods have demonstrated that sex is relatively identifiable in bison remains using a number of post-cranial elements (Duffield 1973:138; Todd 1986:117-118). Multidimensional analyses offer a powerful suite of additional tools to discriminate between male and female bison using skeletal elements. Limiting identifications to only a few measurements potentially reduces the amount of variability present to identify sex. To capture within sample variation, using more measurements will better capture differences between elements. Applying more sophisticated quantitative methods allows a deeper analysis to identify minute changes in size change, potentially informing on ecological and climate effects.

Understanding the causes driving changes in body size has important implications for reconstructing size-related relationships in ancient faunal communities, size selection, and modeling extinction probabilities in contemporary settings (Peters 1983; Tomiya 2013:E196). Significant study is being directed at body size studies to answer questions even outside of the paleoecological context. Body size change has been attributed to fluctuations in a number of environmental variables including dietary access, climate variability, and disease (Demment and Van Soest 1958:663-664; McCain and King 2014:1766; Sheridan and Bickford 2011:402-403). Extant fauna thus serve as proxies for their respective environmental drivers altering body size (Cerling, et al. 2009:893). Effectively identifying which body size changes in a given species correlates to a known environmental change offers an effective source of data for reconstructing the paleo world (Hayes, et al. 1990:1126-1127).

Important ecological characteristics regarding bison may be considered as well. If body size in bison is decreasing the question of equal sex diminution needs to be made. Ecological contributions for unequal changes in size by sex may include the effects of predation (Beckerman, et al. 2010:1075), differential land use and distribution by sex (Berger and Cunningham 1994:84-87), changes in gestation times (Berger and Cunningham 1994:122-123; Blue, et al. 2012:495), or the relationship between body size and maturation (Lee, et al. 2011:3307-3308). I hypothesize that the presence of differential diminution in bison is likely selection for quicker maturation times and shorter gestation times during a period of resource restriction. Female bison who mature quickly in times of intense resource restriction will have a greater chance of reproducing before they die than ones who mature slowly. When the risk of early death is particularly high, as it would be when resource access is low, reproducing sooner offers a substantial advantage towards an individual's fitness.

It is clear the problem of bison diminution is far from resolved, and several fundamental questions persist. Did the taxon experience size diminution, and if so, how much, when did it occur, and most importantly, why did it occur. Considering bison were an essential prey for human foragers it needs to be established what effect, if any, they had on bison populations in the Great Plains. This research addresses these questions through application of more robust statistical methods than those used by (Hill, et al., 2008), (Raymond and Prothero 2011), and (Martin, et al. 2018) to address sex and size change. In doing so, I established a robust method for reducing the noise captured by bison kill sites and evaluate the test implications of the hypothesis that climate change is the prime mover of size reduction.

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## **CHAPTER 2. SEX DETERMINATION OF BISON CALCANEAE USING MULTIVARIATE ANALYSES**

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### **Introduction**

Species may exhibit differences in phenotypic expression between sexes for various reasons. When the environment is geographically variable between sexes differences in selection can occur (Connallon 2015:2341). This phenomenon is a product of the differences in local adaptations specific to each sex. Male and female bison remain separated in sex specific herds for the majority of the year (Berger and Cunningham 1994:84-87). Segregated herds will drive differences in the selective pressures between the two groups of sexes when variation in their presiding environments is present. Any change that may affect one group's (sexes') fitness differently from the other will likely produce some change in favorable traits within that group independent of the other. Hence, variability in traits by sex is possible within species exhibiting geographic variability.

Sex-specific selection accounts for differences in the body size of adult males and adult females in many taxa (Fairbairn 2007:1-15). In mammals, the former are often larger than the latter, particularly in large, gregarious taxa like bison (Shine 1989:419-420). In geographically diverse environments such as on the Great Plains, differences in sex selection can occur (Connallon 2015:2341). In bison, sexual dimorphism appears to be the product of local adaptations specific to each sex since males and females are segregated for most of the year (Berger and Cunningham 1994; McHugh 1958; Meagher 1973; Roe 1951). Sexual segregation thus drives differences in the selective pressures on males and females because the sexes occupy

different habitats for most of the year. Observations of bison in Custer National Park, South Dakota, exemplify this pattern. Here, “[m]ales...either in all male groups or when solitary, were more than one hundred times as common in breaks, wood draws, and ravines than were females....In one exceptionally rugged 10 km<sup>2</sup> area...we never saw females although at least forty different males regularly used it” (Berger and Cunningham 1994:84). Intrasexual selection is frequently observed in sexually dimorphic species and can be quite profound. In a study of Alpine ibex (Brivio, et al. 2014) found large body mass correlated with better foraging strategies (Brivio, et al. 2014:1654-1655), thus favoring large body size selection in males and not females. In sum, variability in traits by sex is possible in taxa that exhibit geographical segregation.

Sexual dimorphism in bison is well established for both modern and extant populations. In theory, identification of sex should be readily observable from bison remains. Traditionally, the identification of sex from bison remains was largely dependent on “eye-ball” identifications. Researchers analyzing the material recovered from a bison kill site would compare the relative sizes for each skeletal element and identify sex according to differences in size (males being relatively larger than females) (Duffield 1973:133-134; Speth and Parry 1980:81). Later, skeletal element size identifications were performed using bivariate comparisons of postcranial elements providing a more quantitative method for identifications (Todd 1986). Relative size comparisons of skeletal elements, or “eye-ball” identifications, do retain some merit as it is predicated on the principle that bison are sexually dimorphic. However, much amount of the information captured in the variability of a given skeletal element is missed when only a few measurements are used.

Historically, researchers have used measurements on bison postcranial skeletal remains coupled with presentation of these data in univariate and bivariate plots to infer the sex of bison remains recovered from paleozoological contexts (Bedord 1974; Hillerud 1970; Morlan 1991;



Speth 1983). In general, the “eye-ball” method works well because of the high degree of sexual dimorphism in bison. However, while it is easy to confidently infer the sex of the largest and smallest specimens (inferred males and females, respectively), this becomes increasingly difficult (i.e., subjective) for specimens that fall between the two ends of the size spectrum, or that lack a complete or minimally adequate constellation of standardized measurements for comparison. Thus, most samples include specimens whose sex cannot be confidently inferred, which, not unexpectedly, varies among researchers. The generally arbitrary nature of this method therefore makes results derived from its application a challenge to replicate. Thus, one objective of this research is to develop and apply statistically robust methods – LDA, Hierarchical Cluster Analysis, and PCA – to remedy this problem.

Using a greater number of measurements from the calcaneus, will capture a greater proportion of the variability between each element. Different statistical methods can provide significant insight regarding the nature of variation between calcanea. Principal component analysis generates a dimensionally reduced linear combination of uncorrelated variables (Hotelling 1933; Pearson 1901). The principal components of measurements on the calcaneus identify the amount of contribution each variable provides towards the variability within the sample. It is expected that the first component of the principal components analysis (PCA) should capture the dominant contributor towards variation in size. The second and third components of the PCA may provide insight regarding the significance of shape. From the output of the PCA performed on a modern known sample (i.e., the control sample of bison), it can be determined which measurements contribute to the variability in size and shape for each sex.

To maximize the amount of variability between skeletal elements, multidimensional scaling (MDS) can be applied. Multidimensional scaling calculates a dissimilarity matrix for the

given data and generates a scaled distance matrix preserving the original dissimilarities, given some measure of distance (Borg and Groenen 2005; Kruskal and Wish 1978; Torgerson 1952). Components of multidimensionally scaled measurements can then be analyzed for easier interpretations of high dimensional data. MDS offers an effective mode to visualize and identify patterns and groupings between points in multidimensional space. Another advantage of MDS is the method is uninformed, meaning the scaling does not account for groups, hence clustering of points in multidimensional space may suggest strong similarities between those specimens. Given bison are sexually dimorphic, and that dimorphism is preserved in the measurements of the calcaneus, clear separations between the scaled values of calcaneal measurements are expected between male and female bison for each site.

An informed clustering approach may be taken using the MDS data. Hierarchical cluster analysis takes some measure of distances or dissimilarities between observations and identifies which observations are closest to one another (Ward 1963). A variety of methods are applicable to identifying the clustering of two groups (or more) of observations given their dissimilarities, including: single, complete and average linkages, Ward's Method, and K-means. Single linkage starts with all observations, identifying the closest pair among all points and proceeding to group upwards (Sibson 1973). In complete linkage each observation is individually clustered, and recombined into new clusters based on their dissimilarities (bottom up approach) (Defays 1976). Average linkage identifies initial pairs and averages the differences between each subsequent pair to identify clusters (Sokal and Michener 1958). Ward's Method uses the optimal value for minimizing the variance between clusters (Ward 1963). Another method for separating relatively close groups is using K-means clustering. K-means separates multidimensional data into (k) clusters that minimize the within-class variance for a conditional mean (MacQueen 1967).

Selecting the appropriate clustering method is largely dependent on the underlying structure of the data, which can be analyzed from the PCA, and how well dissimilarities are attributed to the groupings. In the case of bison calcaneal measurements, the effectiveness of hierarchical clustering depends on the variability within each sex. The overall difference, or lack of, between calcanea from their variance in multidimensional space will be reflected in the effectiveness of hierarchical clustering.

An additional multivariate statistical method for sex identification is linear discriminant analysis (LDA). When the data are continuous with multiple variables it can be difficult to best identify closeness in multidimensional space. LDA uses linear combinations of variables and discriminates for specified members of known groups (Fisher 1936; McLachlan 2004). This method differs from hierarchical clustering in that the groupings must already be identified. Using a modern sample of bison, a model may be constructed from the LDA using the known sex and corresponding measurements. From the LDA model, the probability for a given individual to be male or female for each site (with unknown sex) can be quantified. Assuming relative size differences between modern male and female bison and ancient bison are proportional it is expected that LDA predictions can identify bison sex. Where LDA is expected to fail is when the relative differences between sexes in modern bison are not proportionally different to ancient bison, which may provide insight regarding dimorphism between ancient and modern bison populations.

Improving methods for effectively identifying sex are essential to tackling the issues regarding bison size change and its associated drivers. Using the metric data published by (Hill, et al., 2008) for bison calcanea, a thorough investigation of multidimensional methods using a swath of cluster analyses, LDA, and MDS is applicable. This incorporation of more sophisticated

statistical methods for identification of groupings and change through time will provide enhanced methods for furthering our understanding of the North American bison.

### **Methods**

Measurements of modern bison serve as an interesting control group for comparisons with extant bison. Assuming a modern sample of bison is representative of contemporary bison populations, deviations, or correspondences with linear trends in measurements offer a fascinating source of comparisons for studying change through time. The calcanea of 27 modern bison with known age and sex (Hill 1994:Appendix VII) were used as a test case to evaluate the feasibility of applying LDA, MDS, and Hierarchical Clustering methods to securely isolate and distinguish specimens belonging to male and female bison in the prehistoric samples.

Measurements CL1 through CL9 were recorded for 25 of the 27 specimens and the two with missing measurements were excluded from the analysis (Figure 2.1). One specimen (catalog number 8505B) was remeasured due to a measurement error and updated in the data set. MDS was used to account for greater dimensionality in the size of bison calcanea so as to utilize the variability captured within upwards of nine measurements. Though all nine measurements are present for this modern sample, other measurement combinations (constellations) are also assessed to establish an effective number of measurements for identifying sex. All analytical analyses were performed using R version 3.6.3 (R 2020).

To first establish differences in the contribution to elemental size variability principal components analysis is applied to the modern sample of bison calcanea. Out of the respective components from PCA identify the amount of contribution each variable provides towards the variability in the overall data. Scree diagrams are constructed to evaluate the minimum number of components necessary to capture a sufficient amount of the variability. From the output of the PCA performed on a modern known sample (effectively the control sample of bison), it can be

determined how many and which measurements contribute importantly to the variability in size and sex.

Multidimensional scaling (MDS) is applied to both the modern and archaeological samples. MDS calculates a dissimilarity matrix for the given data and generates a scaled distance matrix preserving the original dissimilarities, given some measure of distance (Borg and Groenen 2005; Kruskal and Wish 1978; Torgerson 1952). Multidimensionally scaled measurement data can then be analyzed individually for easier interpretations of high dimensional data. MDS offers an effective mode to visualize and identify patterns and groupings between points in multidimensional space. Another advantage of MDS is the method is uninformed, meaning the scaling does not account for groups, hence clustering of points in multidimensional space may suggest strong associations. Given bison are sexually dimorphic, and that dimorphism is preserved in the measurements of the calcaneus, clear separations between the scaled values of calcaneal measurements are expected between male and female bison for each site. MDS is applied to first the modern sample and archaeological samples.

Hierarchical cluster analysis is applied to the multidimensionally scaled data for modern and archaeological samples. Hierarchical cluster analysis takes some measure of distances or dissimilarities between observations and identifies which observations are closest to one another (Ward 1963). A variety of methods are applied to identify the effectiveness of each method for identifying sex, including: single, complete and average linkages, Ward's Method, and K-means. Single linkage starts with all observations, identifying the closest pair among all points and proceeding to group upwards (Sibson 1973). In complete linkage each observation is individually clustered, and recombined into new clusters based on their dissimilarities (bottom up approach) (Defays 1976). Average linkage identifies initial pairs and averages the differences

between each subsequent pair to identify clusters (Sokal and Michener 1958). Ward's Method uses the optimal value for minimizing the variance between clusters (Ward 1963). Another method for separating relatively close groups is using K-means clustering. K-means separates multidimensional data into (k) clusters that minimize the within-class variance for a conditional mean (MacQueen 1967). Provided there are a maximum of nine dimensions in a measurement constellation, three arbitrary groupings high (from seven to nine measurements), medium (four to six), and low (less than four) are assigned to compare the effects of dimensionality. Each clustering method is applied to modern sample and compared to the known sex. Clustering methods are analyzed and plotted to check for bimodality in the MDS coordinates.

LDA was also applied to the modern sample of bison. When the data are continuous with multiple variables it can be difficult to best identify closeness in multidimensional space. LDA uses linear combinations of variables and discriminates for specified members of known groups (Fisher 1936; McLachlan 2004). This method differs from hierarchical clustering in that the groupings must already be identified. Using a modern sample of bison, a model may be constructed from the LDA using the known sex and corresponding measurements. From the LDA model, the posterior probability for a given individual to be of sex male or female for each site (with unknown sex) can be estimated.

Complete fusion on the proximal calcaneus was used to separate adults from juveniles. Modern bison with known sexes are used as an initial test for identifying sex. Analyses were performed using R statistical software (R 2020). The modern bison are first assessed to identify the effects of calcaneal measurement combinations and various clustering methods against a known sex. Data are scaled and centered, and principal components analysis is performed for each combination of measurements. The loadings of the principal components are output and

analyzed from scree diagrams to identify the contribution of each measurement towards the variability.

An effective number of samples is established for each site. The effect on the number of samples with the greatest number of measurements is assessed for each site individually. Ultimately, the combination which maximized the number of calcaneal measurements while minimizing the number of removed samples was selected. Sites that proved to have too few samples (less than five calcanea) after maximizing the count of measurements were not pursued following the cluster analysis.

Bison are notably sexual dimorphic, and dimorphism is preserved in the size of their bones, thus after applying MDS, LDA, and hierarchical clustering methods a bimodal distribution of their measurements should be observed. Size was addressed to identify dimorphism by applying LDA and hierarchical clustering methods to the multidimensionally scaled data at each site. Density plots are outputted to observe the presence or absence of bimodality given each method. To assess variation in shape differences a function to convert raw measurements into log mean differences (LMD) is constructed using the equation

eq. 1) 
$$\tilde{\mu}_{ij} = \ln(\mu_i) - \ln(x_{ij})$$

where  $\tilde{\mu}_{ij}$  is the log mean difference for individual (i) at measurement (j),  $\mu_i$  is the log mean of all available measurements for individual (i), and  $x_{ij}$  is the value for individual (i) at measurement (j). The log mean differences offer a method for analyzing the effectiveness of shape for sex identification.

Multidimensional scaling is applied for each site using their effective set of samples. The data are transformed into natural logs then scaled and centered to assess size. Both size data using transformed measurements of the calcaneus and shaped data from the log mean differences

are used. Dissimilarity indices for the data are first computed for each site using Euclidean distances. From the dissimilarity matrix, the indices are multidimensionally scaled and the respective eigenvalues are calculated. The PM1 criterion is calculated from the cumulative sum of the absolute values of the eigenvalues. Identification of the minimum number of components that capture a significant amount of the variability is noted from PM1. Plots of the multidimensionally scaled components capturing the greatest proportion of the variability are produced to compare the known sex to identified sex. Plots using the first two components of the MDS values and three-dimensional plots using the first three components are generated for each site.

Distances between points in multidimensional space are represented by the dissimilarity indices. Using the previously calculated dissimilarity matrices clusters are constructed using a variety of methods. To perform hierarchical cluster analysis, the dissimilarity matrices are clustered using single, average and complete linkages in addition to Ward's method and K-means, searching for two distinct clusters. Individual specimens are then assigned to a male or female group and compared against the researcher identified sex. Plots of the canonical discriminants and cluster dendrograms are constructed to identify if clusters are distinct (Figure 2.2). Results for the modern sample are compared against the known sex and summary tables are constructed. Counts of the differences between the sex initially reported in (Hill, et al., 2008) are compared to the newly identified sex using these clustering methods. Clusters and MDS components are each plotted to compare the final results for sex identification.

Linear discriminant analysis is performed on the modern sample using all calcanea with nine measurements ( $n = 25$ ). Measurements are transformed into natural logs then scaled and centered to assess size and log mean differences are calculated for shape. Results of the modern



LDA are outputted and graphs plotting the posterior probabilities of male against female are constructed. An iterative function is assembled to recognize the number of effective measurements for a given site and compute a new LDA model from the modern sample using the same set of measurements. From the newly constructed LDA model sex is predicted for each calcanea at the site and the associated probabilities are analyzed. Identified sexes from the LDA model are then compared to the initial researcher identified sex.

A final sex is assigned to each element on a site by site basis. Each site is individually analyzed using density plots for Single, Average, and Complete linkage, Ward's method, K-means, and LDA against CL1 through CL9 and the first coordinate of the multidimensionally scaled data. Density plots where there are clear separations between sexes, and when there is agreement between methods, are used to identify sex for a given site. The newly identified sexes are recorded and added to the data for comparisons.

## **Results**

Results of sexing analyses on modern bison calcanea using several clustering methods are provided in Table 2.1. It appears that single and average linkage and K-means often fail to correctly differentiate males and females whereas complete linkage and Ward's method typically do, and often in different combinations of dimensions. Complete linkage identifies the correct sex more frequently when it is performed on high dimensional data (i.e.,  $\geq 7$  dimensions). Complete linkage and Ward's method produce similar results with medium (i.e.,  $\geq 4 \leq 7$  dimensions) and low (i.e.,  $\leq 4$ ) dimensional data (Table 2.1). Using LMD did not provide improvement to sex identification (Table 2.2).

Using Ward's method for hierarchical cluster analysis, two distinct groups are identified for each site using a combination of measurements which minimizes loss of sample size.

Separation indicated by the canonical discriminants suggest that using an informed clustering method often could identify two unique clusters separated at zero. The multidimensionally scaled data, when compared with the groupings from the canonicals, suggest nearly identical groups with generally ideal separation at zero. Generally, all sites produced very clear separations from both the canonicals and multidimensionally scaled data (MDSd) (Figure 2.3). The only clear example of poor separation from the canonical discriminates and MDSd is the Milburn site.

Results between the identified sex using Ward's method and MDS are variable. Of the 24 sites which retain a large enough number of measurable calcanea, 13 share complete or nearly complete agreement on sex (Table 2.2). Among the 13 sites in agreement, six originally reported calcanea that could not be identified to sex and are identifiable using hierarchical clustering. Of the calcanea identified as females by the initial researchers, 48 are identified as males using hierarchical clustering. Among the males identified by the initial researchers, 13 are identified as females from the cluster analysis and 41 previously unidentified specimens are assigned a sex. Disagreements between the initial sex identifications and clustering identifications are dominated by two sites, Glenrock (28 incorrect females) and Bonfire Shelter (10 incorrect males). Overall, there appears to be a tendency for disagreement between researcher sex identification of males and cluster sex identification of females (Table 2.2). However, both the researchers and clustering methods generally agree on male identifications.

Plots of the multidimensionally scaled data and dendrograms of the cluster selections using Ward's method show precisely where data points are clustering. All sites that agree between previously identified sex and sex assigned by hierarchical clustering produced distinct clusters, like those at Olsen Chubbuck (Figure 2.3b). Sites with specimen unidentified to sex by

the initial researchers fall into distinct clusters identified from Ward's method. All unidentified specimens from Glenrock fall quite clearly into the male group, with 28 originally identified as females who instead cluster as males (Figure 2.3a). Most misidentifications occur with specimens identified as females who instead cluster as males.

Principal components analysis (PCA) suggests that for nearly every site the first two components capture a significant portion of the variability in these data. Plots of the scree diagrams, showing the sums of the eigenvalues, agree that two components capture variability quite nicely among these data. Notable exceptions include Hawken and Rourke, which seem to require at least the first three components to sufficiently capture their variability. The significance of each calcaneal measurement is approximately the same, and their directions are always the same for the first component. Differences in the proportion of variability captured by each measurement are negligible for the first component, suggesting each measurement contributes similarly to the variability in size. The second component of the PCA shows CL8 individually is strongly correlated and CL1, CL3, and CL9 are negatively correlated. Contrary to CL1, CL3, and CL9, CL8 is not frequently recorded across all sites and assessment of its significance is difficult.

Using modern bison as a model for predicting sex via LDA in the archaeological samples produced mixed results. For relatively small and recent sites two distinct groups were identifiable with significant posterior probabilities ( $\sim 0.90$ ). In earlier and larger sites more calcanea produced posterior probabilities close to 0.50 suggesting poorer confidence regarding their fit as male or female. Calcanea with unidentified sexes, as prescribed the initial researchers, often produced high posterior probabilities for being male across all sites. The results from linear

discriminant analysis showed one female bison in the modern sample who frequently plotted as a male and was thus removed as an outlier.

Density plots produced mixed but interesting results regarding clear separations between male and female bison (Figures 3.4-3.5). In recent sites, namely Glenrock and Garnsey, separation between males and females was effective using LDA and hierarchical clustering. For earlier sites cluster analysis performed notably better than LDA, with the exception of the oldest site Lipscomb and sites with small samples (less than 10) (Table 2.3). LDA produced good separation in density plots for 33% of sites while K-mean and Ward's method produced good separation in 78% and 63% of sites respectively. When sites had relatively few calcanea identification of sex between all methods including the initial researcher identification were common (19% of sites). There were no instances when Single, Average, or Complete linkage produced clear separation independently (Table 2.3). These results differ somewhat from modern bison analysis where K-mean performed very poorly and Ward's and LDA appeared to be ideal methods for identifying sex.

### **Discussion**

Clustering methods offer a powerful tool for identify unique groups given a set of measurements. Single, average, and complete linkages prove to be poor clustering methods for sex identification (Table 2.2). Single linkage almost exclusively identifies a single large male and groups all remaining calcanea as females. Average linkage follows a similar pattern to single linkage. Complete linkage often identifies unique clusters given high dimensional data, but quickly fails given fewer dimensions (Table 2.2). Having many dimensions simply provides more information for linkage methods to work on and reduces the pull of an individual measurement. Ward's method and K-means intuitively and practically prove to be better clustering methods. Considering the processes of both methods, Ward's method and K-means,

their effectiveness is not particularly surprising. Ward's method operates on minimizing variance between pairs to ultimately identify unique clusters (Ward 1963). Optimizing variance as opposed to taking raw distances will prevent any particular measurement from dominating the clustering. When the variance is driving which points cluster together, having a large number of dimensions is not as significant. Ward's method provides a better overall approach to clustering identification of two distinct groups when approaching data where the true sex is unknown. K-means' effectiveness is attributed similarly to Ward's method where optimizing the mean can reduce the variance within each cluster (Table 2.2).

The modern sample of bison provides an interesting comparison for the effectiveness of hierarchical clustering and sex identification. While the sex was known among the modern bison identifying unique groups using clustering methods proved rather poor (Table 2.2). Ward's method and Complete linkage performed the best, but often did not cluster males and females perfectly. Results from the modern sample suggest that distances in multidimensional space given most sets of measurements struggle to identify the correct groups for this sample of modern bison. It should be noted that only 27 modern bison were recorded and only 25 retained all nine measurements on the calcaneus. Of the 25 modern bison eight are males and 17 are females. It very well may be that this modern set is not easily differentiable by sex given the relatively small sample. However, modern bison also persist under notable different environmental conditions than extant bison. Further understandings regarding changes in sexual dimorphism are necessary to establish the relationship between time and dimorphism.

Applying Ward's minimum variance method and K-means to each individual site produced surprising results. Most sites separated into very distinct clusters using both the canonical discriminants (from the hierarchical clustering) and the multidimensionally scaled

data. Clusters produced from hierarchical clustering are “forced” to identify a set number of groups (in this case two), however MDS simply plots points in multidimensional space with no *a posteriori* knowledge. Thus, clear separation of distinct groups among the MDS strongly supports the presence of two unique clusters, like those seen at Olsen-Chubbuck (Figure 2.3b). Considering nearly all utilized methods, including principal components, hierarchical clustering analysis, and the MDS, identify two unique groups from measurements of bison calcanea, and given that the presence of sexual dimorphism, though not the degree, is well documented in bison, these methods show that sex can be identified from the calcaneus.

Initial difficulties in identifying sex using purely clustering methods among modern bison prompted use of LDA to identify sex. Within the modern sample LDA performed acceptably with the exception of one specimen which was ultimately removed from the analysis. Unless the data were particularly poorly separable it is not expected that LDA would fail to identify sex for the modern sample of bison (since sex is known). Using the constructed model from modern bison to predict for sex in archaeological sites only performed well in relatively recent sites (Table 2.3). LDA affectively identified sex at Glenrock, which dates to 298 cal. B. P., but performed quite poorly for sites ranging from ~4,000 cal B. P. to ~11,000 cal B. P. This gives some argument that modern bison are not equally variable in sexual dimorphism through time. The effectiveness of LDA to identify sex at Glenrock suggests that the males and females discriminate similarly for those relatively close in time (Table 2.3). In other words, dimorphism between modern male and female bison is similar to dimorphism in relatively recent male and female bison. Earlier sites discriminate very poorly using LDA and appear to improve substantially using clustering methods, particularly K-means. The comparison between LDA and clustering methods gives some argument that the relative differences between sexes is not the

same through time. An outlier to this inference is Lipscomb which dates to 12,799 cal B. P. and separated well using LDA (Table 2.3). Perhaps contemporary environmental drivers of sexual dimorphism more closely emulate those ~13,000 years ago than through the greater part of the Holocene.

It is worth noting that agreement between the original researchers' identification of sex and these clustering methods is substantial (Table 2.3). Except for Glenrock and Bonfire Shelter, discrepancies between sex identifications are minimal. Clustering methods for sex identification offer a more effective route for dealing with bison calcanea that appear close in size. While "eye-ball" methods and simple bivariate comparisons can separate the extremes, they do not offer effective identifications of similarly sized specimens. Additionally, clustering methods offer a quantitative approach to sex identification where there is visual improvement in newly identified sexes (Figure 3.3). Applying quantitative methods offers both future improvement and roads for measurably critiquing results. While the results of this analysis are convincing, future development in cluster identification and continued recording of bison anatomical measurements may offer improved methods for sex identification.

Interestingly all sites appear to produce at least a single individual of each sex (Table 2.3). This phenomena is observed by both initial researchers and here using various discriminant functions and cluster analyses to identify sex. Studies of modern bison suggest that mixed groups are uncommon during the greater part of the year (Berger and Cunningham 1994:84). Only during the rut, which occurs in late Fall, do male and female bison congregate in large numbers then generally separate thereafter. In the case of Badlands National Park male and female bison even inhabit different landscapes during the majority of the year staying relatively separated (Berger and Cunningham 1994:84-89). The observation of mixed herds in virtually all bison kill

sites beacons the question why more unisex kill sites are not discovered. Separations identified by initial researchers and using these detailed methods for identifying sex strongly suggest that two discernable size groups exist in these sites. It is difficult to discern whether this is evidence that mixed herds were more common in previous bison populations or if Great Plains hunters were targeting bison herds during periods of mixed populations. Regardless, an interesting dynamic regarding differences in bison population dynamics between contemporary and extant bison may be detectable.

### **Conclusions**

Identifying sex using hierarchical cluster analysis and multidimensional scaling on the calcanea of North American bison can be performed effectively. While miss-identifications do occur in the modern sample for all hierarchical clustering methods, they provide a quantitative approach to sex identification. Modeling ancient bison using modern bison may not be sufficient as the time gap increases. It does appear that clustering methods are useful tool for identifying two unique clusters of bison calcanea in multidimensional space. Such clustering appears to be a good representation of sex. Much agreement exists between researcher identified sex and clustering identified sex, though cluster analysis and MDS provide tools for dealing with similarly sized specimens. Previous methods regarding sex identification depend on simple and sometimes difficult to replicate techniques. A quantitative approach to sex identification offers comparative methods which can effectively be improved upon and compare to future methods. Developing a more substantial database of modern bison and studying their variability may provide improvements in modeling ancient bison.



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Table 2.1. Summary of cluster methods that produce statistically significant results for inferring sex of bison calcanea.

| Calcaneus              |                |          |
|------------------------|----------------|----------|
| Measurements           | Cluster Method | %Correct |
| High ( $d > 7$ )       | Complete       | 100.0    |
| High ( $d > 7$ )       | Ward's         | 81.0     |
| Medium ( $4 < d < 7$ ) | Complete       | 81.0     |
| Medium ( $4 < d < 7$ ) | Ward's         | 89.0     |
| Low ( $d < 4$ )        | Complete       | 84.0     |
| Low ( $d < 4$ )        | Ward's         | 79.0     |

Table 2.2. Results of applications of cluster analyses to a sample of skeletally mature bison calcanea of known age and sex.

| Calcaneus<br>Measurements<br>Constellation, nos.: | Cluster Method<br>(perfect separation) | Incorrect Determinations |        |        | Shape Error (LMD)<br>(see eq. 1) |        |
|---|--|--------------------------|--------|--------|----------------------------------|--------|
|   |  | n                        | F as M | M as F | F as M                           | M as F |
| 1-9   | no                                     | 6                        | 0      | 6      | 0                                | 6      |
| 1-8   | no                                     | 6                        | 0      | 6      | 0                                | 6      |
| 1-6   | no                                     | 6                        | 0      | 6      | 0                                | 6      |
| 1-3, 7-8  | no                                     | 6                        | 0      | 6      | 0                                | 6      |
| 1-5   | no                                     | 6                        | 0      | 6      | 0                                | 6      |
| 1-3   | no                                     | 5                        | 0      | 5      | 0                                | 5      |
| 1, 4-8  | no                                     | 6                        | 0      | 6      | 0                                | 6      |
| 1, 4-5  | no                                     | 6                        | 0      | 6      | 0                                | 6      |
| 2-9   | no                                     | 6                        | 0      | 6      | 0                                | 6      |
| 2-4, 5, 9   | no                                     | 6                        | 0      | 6      | 0                                | 6      |
| 2-3, 7-9  | no                                     | 6                        | 0      | 6      | 0                                | 6      |
| 2, 3, 9   | no                                     | 5                        | 0      | 5      | 0                                | 5      |
| 4-5, 7-9  | no                                     | 6                        | 0      | 6      | 0                                | 6      |
| 4, 5, 9   | no                                     | 6                        | 0      | 6      | 0                                | 6      |
|   | $\Sigma$                               | 82                       | 0      | 82     | 0                                | 82     |
|   | Average Linkage                        | n                        | F as M | M as F | F as M                           | M as F |
| 1-9   | no                                     | 7                        | 7      | 0      | 7                                | 0      |
| 1-8   | no                                     | 7                        | 7      | 0      | 6                                | 0      |
| 1-6   | no                                     | 5                        | 5      | 0      | 11                               | 0      |
| 1-3, 7-8  | no                                     | 8                        | 8      | 0      | 6                                | 0      |
| 1-5   | no                                     | 5                        | 5      | 0      | 4                                | 0      |
| 1-3   | no                                     | 7                        | 7      | 0      | 14                               | 0      |
| 1, 4-8  | no                                     | 7                        | 7      | 0      | 7                                | 0      |
| 1, 4-5  | no                                     | 4                        | 4      | 0      | 16                               | 0      |
| 2-9   | no                                     | 6                        | 0      | 6      | 7                                | 0      |
| 2-4, 5, 9   | no                                     | 6                        | 0      | 6      | 4                                | 0      |
| 2-3, 7-9**  | yes                                    | 0                        | 0      | 0      | 0                                | 0      |
| 2, 3, 9*  | yes                                    | 0                        | 0      | 0      | 2                                | 0      |
| 4-5, 7-9  | no                                     | 6                        | 0      | 6      | 7                                | 0      |
| 4, 5, 9   | no                                     | 6                        | 0      | 6      | 0                                | 6      |
|   | $\Sigma$                               | 74                       | 50     | 24     | 91                               | 6      |
|   | Complete Linkage                       | n                        | F as M | M as F | F as M                           | M as F |
| 1-9   | yes                                    | 0                        | 0      | 0      | 7                                | 0      |
| 1-8   | yes                                    | 0                        | 0      | 0      | 7                                | 0      |
| 1-6   | yes                                    | 0                        | 0      | 0      | 2                                | 0      |
| 1-3, 7-8  | no                                     | 9                        | 9      | 0      | 6                                | 0      |
| 1-5   | yes                                    | 0                        | 0      | 0      | 4                                | 0      |
| 1-3   | no                                     | 8                        | 8      | 0      | 7                                | 0      |
| 1, 4-8  | no                                     | 11                       | 11     | 0      | 7                                | 0      |
| 1, 4-5  | no                                     | 4                        | 4      | 0      | 10                               | 0      |
| 2-9*  | yes                                    | 0                        | 0      | 0      | 5                                | 0      |
| 2-4, 5, 9*  | yes                                    | 0                        | 0      | 0      | 4                                | 0      |
| 2-3, 7-9**  | yes                                    | 0                        | 0      | 0      | 6                                | 0      |
| 2, 3, 9*  | yes                                    | 0                        | 0      | 0      | 0                                | 0      |
| 4-5, 7-9  | no                                     | 5                        | 5      | 0      | 0                                | 0      |
| 4, 5, 9   | no                                     | 4                        | 4      | 0      | 4                                | 0      |
|   | $\Sigma$                               | 41                       | 41     | 0      | 69                               | 0      |

Table 2.2, continued.

| Calcaneus<br>Measurements<br>Constellation, nos.: | Cluster Method<br>(perfect separation) | Incorrect Determinations |        |        | Shape Error (LMD)<br>(see eq. 1) |        |
|---|--|--------------------------|--------|--------|----------------------------------|--------|
|   |  | n                        | F as M | M as F | F as M                           | M as F |
| 1-9   | no                                     | 7                        | 7      | 0      | 7                                | 0      |
| 1-8   | no                                     | 7                        | 7      | 0      | 7                                | 0      |
| 1-6   | no                                     | 11                       | 11     | 0      | 4                                | 0      |
| 1-3, 7-8  | yes                                    | 0                        | 0      | 0      | 4                                | 0      |
| 1-5   | no                                     | 4                        | 4      | 0      | 4                                | 0      |
| 1-3   | no                                     | 8                        | 8      | 0      | 0                                | 2      |
| 1, 4-8  | no                                     | 7                        | 7      | 0      | 7                                | 0      |
| 1, 4-5  | no                                     | 4                        | 4      | 0      | 4                                | 0      |
| 2-9*  | yes                                    | 0                        | 0      | 0      | 7                                | 0      |
| 2-4, 5, 9   | no                                     | 4                        | 4      | 0      | 4                                | 0      |
| 2-3, 7-9**  | yes                                    | 0                        | 0      | 0      | 6                                | 0      |
| 2, 3, 9   | no                                     | 5                        | 5      | 0      | 0                                | 0      |
| 4-5, 7-9  | no                                     | 5                        | 5      | 0      | 8                                | 0      |
| 4, 5, 9   | no                                     | 4                        | 4      | 0      | 4                                | 0      |
|   | $\Sigma$                               | 66                       | 66     | 0      | 66                               | 2      |
|   | K-means                                | n                        | F as M | M as F | F as M                           | M as F |
| 1-9   | no                                     | 6                        | 6      | 0      | 6                                | 0      |
| 1-8   | no                                     | 6                        | 6      | 0      | 7                                | 0      |
| 1-6   | no                                     | 7                        | 7      | 0      | 7                                | 0      |
| 1-3, 7-8  | no                                     | 6                        | 6      | 0      | 6                                | 0      |
| 1-5   | no                                     | 5                        | 5      | 0      | 5                                | 0      |
| 1-3   | no                                     | 5                        | 5      | 0      | 5                                | 0      |
| 1, 4-8  | no                                     | 7                        | 7      | 0      | 7                                | 0      |
| 1, 4-5  | no                                     | 5                        | 5      | 0      | 12                               | 0      |
| 2-9   | no                                     | 6                        | 6      | 0      | 6                                | 0      |
| 2-4, 5, 9   | no                                     | 4                        | 4      | 0      | 4                                | 0      |
| 2-3, 7-9  | no                                     | 6                        | 6      | 0      | 6                                | 0      |
| 2, 3, 9   | no                                     | 2                        | 2      | 0      | 2                                | 0      |
| 4-5, 7-9  | no                                     | 6                        | 6      | 0      | 6                                | 0      |
| 4, 5, 9   | no                                     | 4                        | 4      | 0      | 4                                | 0      |
|   | $\Sigma$                               | 75                       | 75     | 0      | 83                               | 0      |

Note: <sup>1</sup>\*(indicates two different clustering methods produced correct identifications for males and females), \*\* (three different clustering methods perfectly separated males and females).

Table 2.3. Results of sex determination analysis compared with previous results. iSex provides the number of males, females or unknown for each site. “Method” provides the corresponding method(s) for identifying sex at each site. Methods for sex identification were identified from the density plots.

| Sample               | Calcaneus<br>Measurements<br>Constellation, nos: | iSex<br>(Hill, et al., 2008) |     |     | iSex<br>(this study) |     | Method (this study) |
|----------------------|--|------------------------------|-----|-----|----------------------|-----|---------------------|
|                      |  | F                            | M   | ?   | F                    | M   |                     |
| Agate Basin          |  |                              |     |     |                      |     |                     |
| <i>Agate Basin</i>   | 1, 4, 5  | 10                           | 2   | 0   | 10                   | 2   | Any method          |
| <i>Folsom</i>        | Insufficient Samples                             |                              |     |     |                      |     |                     |
| <i>Hell Gap</i>      | Insufficient Samples                             |                              |     |     |                      |     |                     |
| Big Bone Lick        | 1-9  | 20                           | 3   | 2   | 20                   | 5   | Ward's              |
| Big Goose Creek      | 4-5, 9   | 4                            | 2   | 1   | 4                    | 3   | Any cluster method  |
| Black Water Draw     |  |                              |     |     |                      |     |                     |
| <i>Brown Sand</i>    | Insufficient Samples                             | 1                            | 1   | 0   |                      |     |                     |
| <i>Gray Sand</i>     | Insufficient Samples                             | 3                            | 0   | 0   |                      |     |                     |
| Bonfire Shelter      |  |                              |     |     |                      |     |                     |
| <i>Bonebed 2</i>     | Insufficient Samples                             | 0                            | 2   | 0   |                      |     |                     |
| <i>Bonebed 3</i>     | 4-5, 9   | 16                           | 2   | 0   | 6                    | 12  | Any cluster method  |
| Casper               | 1-8  | 18                           | 2   | 2   | 19                   | 3   | Ward's              |
| Clary Ranch          | 1, 4-5   | 4                            | 1   | 3   | 4                    | 4   | K-means             |
| Finley               | 1, 4-5, 7, 9                                     | 6                            | 7   | 2   | 4                    | 11  | K-means             |
| Folsom               | 1-5  | 4                            | 2   | 1   | 3                    | 4   | Any method          |
| Frasca               | 2, 4-5, 8-9                                      | 8                            | 5   | 0   | 8                    | 5   | Any method          |
| Frazier              | 1, 7-9   | 4                            | 0   | 1   | 2                    | 3   | Any cluster method  |
| Garnsey              | 1-4  | 3                            | 2   | 0   | 3                    | 2   | Any method          |
| Glenrock             | 1, 4, 5, 9                                       | 103                          | 26  | 91  | 161                  | 59  | Ward's              |
| Hawken               | 2-5, 8-9   | 8                            | 2   | 1   | 8                    | 3   | Any cluster method  |
| Hudson-Meng          | 3-4, 5, 9  | 12                           | 3   | 0   | 10                   | 5   | K-means             |
| Interstate Park      | 1, 3-9   | 3                            | 2   | 0   | 3                    | 2   | Any cluster method  |
| Itasca               | 1-9  | 3                            | 2   | 0   | 2                    | 3   | K-means             |
| Jurgens              | 1, 4, 5, 7, 9                                    | 4                            | 6   | 0   | 7                    | 3   | Any cluster method  |
| Lindenmeier          | 1, 5, 9  | 2                            | 6   | 0   | 2                    | 6   | Any cluster method  |
| Lipscomb             | 3-4, 5, 9  | 12                           | 2   | 1   | 12                   | 3   | LDA                 |
| Lubbock Lake         |  |                              |     |     |                      |     |                     |
| <i>FA5-6</i>         | Insufficient Samples                             | 3                            | 1   | 0   |                      |     |                     |
| <i>E, Strata 3</i>   | 1-5  | 3                            | 3   | 0   | 2                    | 4   | Any cluster method  |
| MBR                  | 1, 4-5, 8-9                                      | 15                           | 2   | 2   | 14                   | 5   | K-means             |
| Milburn              | 1, 4-5, 9  | 12                           | 2   | 42  | 17                   | 39  | K-means             |
| Nye                  | 1, 4-5, 9  | 6                            | 3   | 0   | 6                    | 3   | Any cluster method  |
| Olsen-Chubbuck       | 1-5, 7-9   | 19                           | 10  | 0   | 19                   | 10  | Any cluster method  |
| Rancho La Brea       | 1-9  | 20                           | 16  | 4   | 22                   | 17  | Ward's              |
| <i>Pit 13</i>        | 1-2, 4-5, 8-9                                    | 8                            | 2   | 0   |                      |     |                     |
| <i>Pit 3 - Lower</i> | Insufficient Samples                             | 0                            | 4   | 0   |                      |     |                     |
| <i>Pit 3 - Upper</i> | Insufficient Samples                             | 9                            | 3   | 1   | 9                    | 4   | Ward's              |
| <i>Pit 61/67</i>     | Insufficient Samples                             | 3                            | 3   | 0   |                      |     |                     |
| <i>Pit 77</i>        | Insufficient Samples                             | 5                            | 3   | 0   |                      |     |                     |
| <i>Pit 81</i>        | Insufficient Samples                             | 1                            | 0   | 0   |                      |     |                     |
| <i>Pit 91</i>        | Insufficient Samples                             | 2                            | 2   | 0   |                      |     |                     |
| Rourke               | 1, 3-9   | 4                            | 1   | 0   | 4                    | 1   | Any cluster method  |
| Rustad               | 2-3, 6-8   | 3                            | 3   | 1   | 5                    | 2   | LDA                 |
| Simonsen             | 1-9  | 2                            | 12  | 3   | 6                    | 11  | Ward's              |
| Σ                    |  | 328                          | 129 | 157 | 383                  | 230 |                     |

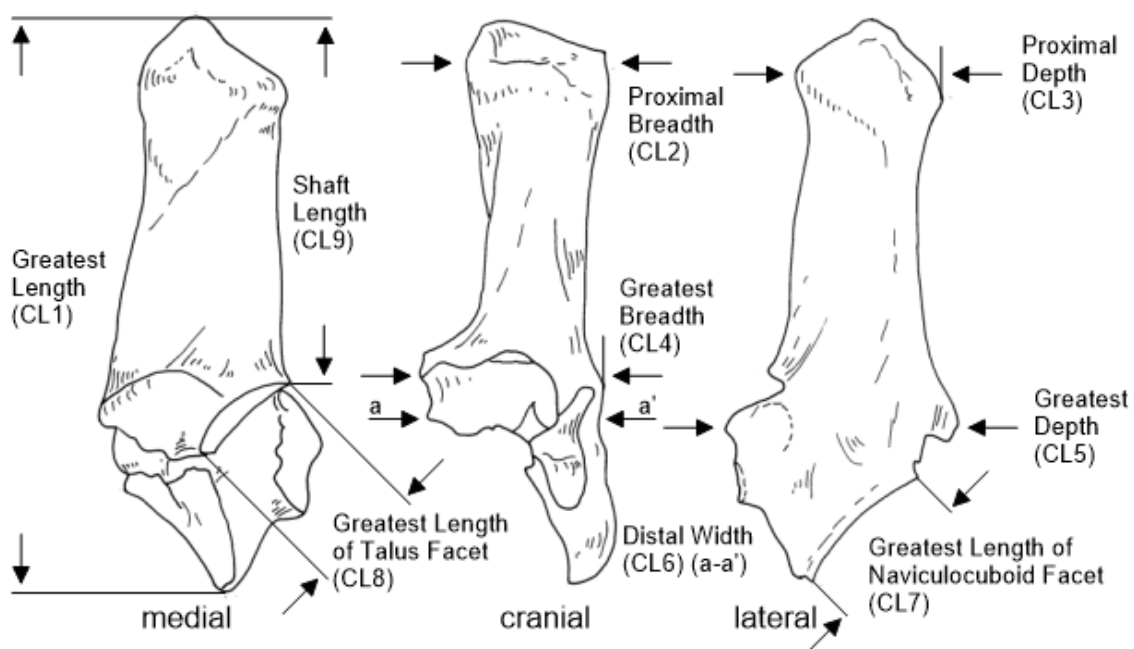


Figure 2.1. Measurement locations for bison calcanea (after Hill 1996).



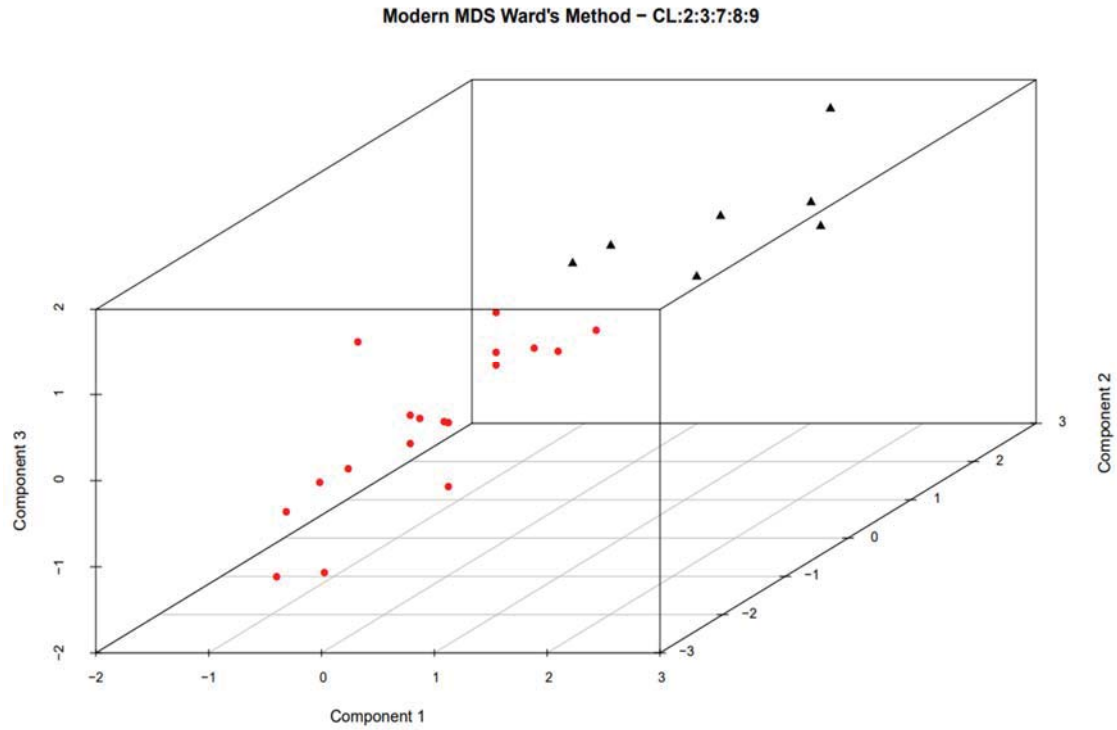


Figure 2.2 Three-dimensional plot of the first three components from the MDS of the modern bison sample. Red indicates females identified using Ward's method and black indicates males. Circles indicate known females and triangles indicate known males.

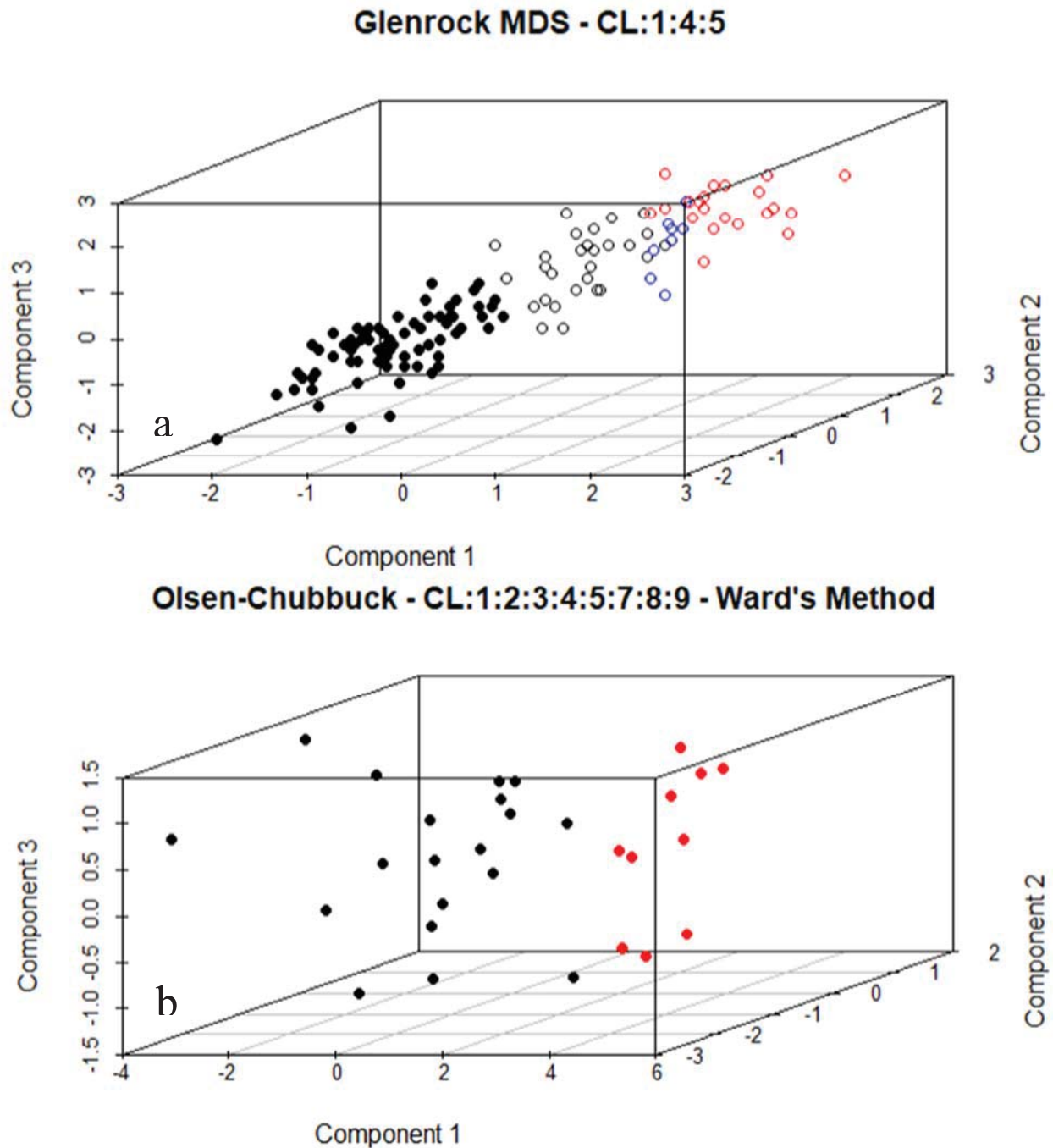


Figure 2.3. Three-dimensional plot of the first three components of the multidimensionally scaled data for a) Glenrock where black indicates females, red males, and blue unknown as identified by the initial researchers. Filled circles indicate females and open circles males as identified by this study. b) Olsen-Chubbuck where black indicates females and red males (same for both initial researchers and this study). For both sites Ward's method was implemented to identify sex.

### **CHAPTER 3. REASSESSMENT OF LATE QUATERNARY BISON DIMINUTION ON THE GREAT PLAINS OF NORTH AMERICA**

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#### **Introduction**

Bison are an ideal taxon to investigate questions about mammalian body size. The evolutionary history is relatively well documented, and includes longstanding recognition that ancient bison are larger than the modern form in terms of overall body size and the distance between the tips of the horn cores (McDonald 1981). Second, for nearly 11,000 years, human foragers on the Great Plains regularly hunted bison for food as well as for a source of raw material for the manufacture of an assortment of items (Ewers 1958; Frison 1991b; Kehoe and Kehoe 1960; Verbicky-Todd 1984; Wheat 1972). In most instances, kills probably involved only several animals in order to meet short-term needs. However, there are also many examples of kill-butcher sites that include the remains of upwards of 10-20 individuals and, occasionally, many times those numbers. Third, on account of a long history of interest in bison kill-butcher sites by archaeologists and vertebrate paleontologists, the distribution of the taxon in space and time is firmly established, and large samples of remains are available for analysis, including many published data sets. Bison thus afford an opportunity to evaluate competing ideas about the drivers of body size in a large herbivore.

The topic of bison diminution was built upon with a benchmark study by (Hill, et al., 2008), who concluded that environmental change, as opposed to human hunting, is the main driver of size reduction. However, more recent research, using the data provided by (Hill, et al., 2008), produced very different findings. (Raymond and Prothero 2011) concluded that the taxon

did not experience size reduction over the past 40,000 years, while in dramatic contrast, (Martin, et al. 2018) concluded that late Holocene bison ( $665 \pm 21$  kg) weighed upwards of 37% less than their late Pleistocene ancestors ( $910 \pm 50$  kg) (Martin, et al. 2018:4564). Such drastically different conclusions from identical data suggests further attention is greatly needed.

Studies connecting climate variability to body size change have been established for other species. Several, recent noteworthy examples include island dwarfism (Vartanyan, et al. 1993) and reductions in the size of modern deer (Wolverton, et al. 2007) and bison (e.g. Big Bone Lick, Kentucky) (Widga 2006b), the latter of which is focus of this research. Bison were among the dominant mammals in North America and a focal prey for foragers (Frison 1982). In particular, the utilization of bison by Great Plains foragers was integral their persistence. While direct study of paleo people in the Great Plains is both difficult and minute their behavioral “foot print” left behind at bison kill sites is vast. Kill sites can retain massive amounts of faunal material and are widely distributed across the Great Plains region (Figure 3.1). Bison kill sites in turn provide a unique snapshot into the paleo world. Both human exploitation of bison for subsistence and ecological factors that may drive body size change in bison can be evaluated from kill sites.

To this point, considerations regarding bison size change overtime specifically identify body size as the measure of interest. In fact, many studies regarding body size directly associate it with body mass and may use size to estimate the mass directly (Christiansen 2002:688; Martin, et al. 2018:4567). While body size and body mass can provide some important information regarding a number of ecological and physiological factors (Damuth and MacFadden 1990:1) they are not always essential to estimate, and depend on the question being answered. Ungulates who practice rutting behaviors experience wild fluctuations in body mass in response to high energy reproductive behavior (Berger and Cunningham 1994:8-9; Forsyth, et al. 2005:2159-

2160). Between the effects on body weight due to both rutting and pregnancy a single estimate of body weight should come with a large amount of variability. Even to estimate a lifetime average body weight for a single animal is difficult given it should depend on multiple noisy predictors (e.g., forage quality and availability, fecundity, disease). A better approach to assessing size change in the archaeological record is to simply address the size of the bones.

From the measurements of an animal's bones the size of its skeleton should reflect a more stable estimate of its body size given fluctuations in bone size respond more slowly to sources of variation. It has been shown that bone density and size can respond to use in life among humans (Haapasalo, et al. 2000). Thus, it is not expected that two bison of equal size will remain equal allometrically should they experience different mobility behaviors over an extended duration of time. To account for differences in behavior that may influence bone size using a non-weightbearing element is ideal. Non-weight bearing elements should better capture skeletal differences that are most directly attributed to body size. Not only should elemental size be considered in a study of extant bison, but variation in shape as well. A bone like the calcaneus, that is well preserved in the archaeological record and whose size is a predominantly a product of relative body size is key for identifying bison sex.

At first glance, and provided the spectacular record of human exploitation of bison on the Great Plains, it is not unreasonable to think that hunting by human predators could lead to smaller-bodied bison over time. However, the probability of this happening is exceedingly low. For human predation to drive selection for smaller bison body size two phenomena should occur. One, human predation needs to be strong enough and focused (targeting large bodied bison) enough to reduce herds to the point that entire populations are shifting towards small body size. Two, bison kill sites should predominantly retain only large bison. It would require the same

(high) rate of sustained, intensive predation by an enormous human population on a metapopulation distributed relatively evenly across some 2,900,000 km sq. for a relatively long period of time. Additionally, bison kill sites retain animals of invariable size, especially when sex is not accounted for, which is demonstrated in this study (Figure 3.2). For these reasons, I do not consider human hunting as a driver in size reduction further. More probable is that the reduction in bison body size is tied to the shift to Holocene environments that commenced around 10,000 years ago and their concomitant effect on the overall quality and availability of forage.

Bison kill sites provide a unique snapshot into extant herds and some characteristics of their dynamics. Site based comparisons suggest that significant differences in the size of bison are measurable in their remains, with changes in size occurring at irregular frequencies (Wilson 1978:9). Early studies quickly acknowledged a decrease in the size of bison bones relative to their age and attempted to connect ecological drivers to such changes (Speth 1983). Numerous studies of bison body size make direct connections to Bergmann's Rule (increased latitude and body size are correlated) as a significant driver for size variability (Breslawski and Byers 2014; Butler, et al. 1971; Hill, et al., 2008; Martin, et al. 2018; Raymond and Prothero 2011). Other studies incorporate ecological drivers like changing food sources as major contributors (Lewis, et al. 2010; Lyman 2004:83; Wilson 1974:96). The effect human predation would have on diminution in bison is frequently considered, yet poorly demonstrated (McDonald 1981:248-250). Effectively identifying a significantly covarying effect between body size and human predation has proven elusive, given the difficulties in measuring human predation in the archaeological record. However, measurements of bison bones and paleoclimate records are more available and can provide insight regarding predation.

Interpreting early human behavior in the New World is greatly dependent on understanding the paleoecology. Bison were among the dominant mammals in North America and a focal prey for foragers. In particular, the utilization of bison by Great Plains foragers was integral their persistence. Research regarding the diminution of North American bison during the Holocene is a frequent topic of research with greatly varying conclusions. An integral work regarding bison body size by (Hill, et al., 2008) concluded a dramatic decrease in body size over the last 14,000 years (Hill, et al., 2008:1762). Using measurements on both the calcanea and humeri of bison spanning the last 37,000 years it is suggested that “Late Pleistocene *Bison* were 15-20% larger than modern forms if not more” (Hill, et al., 2008:1753). Provided the relative intensity of human hunting necessary to drive diminution, the known effects of environmental variables on body size, and the lack of evidence for intensive hunting on other extant Pleistocene fauna, directly connecting diminution to human predation fails to be significant and it is suggested climate produced a more profound effect (Hill, et al., 2008:1766-1767).

In direct contrast, a work by (Raymond and Prothero 2011) put forward that bison from Rancho La Brea show no significant diminution over the last 35,000 years (Raymond and Prothero 2011:637-638). Their study includes multiple elements including the calcanea and humeri measurements used by (Hill, et al., 2008). It is proposed that the results of (Raymond and Prothero 2011) reopen the question of whether human predation could drive bison diminution (Raymond and Prothero 2011:639). Two methodological considerations must be noted. Firstly, only samples from Rancho La Brea are considered for their study. While Rancho La Brea has a great time range it only includes up to eight time periods with fewer than 200 samples. Secondly, it was acknowledged that sexual dimorphism exists in bison, but due to a lack of bimodality in

their data sex was not treated separately (Raymond and Prothero 2011:637). Clearly both a methodological and interpretative discrepancy exists given these two studies.

Building on the analysis by (Hill, et al., 2008) a recent study suggests that bison body size decreased by an average of 37% ( $910 \pm 50$  kg) over the last 40,000 years as a response to increasing air temperature (Martin, et al. 2018:4564). Once again, using much of the same data originally published by (Hill, et al., 2008) a significantly different conclusion is drawn. Live body mass is estimated using a simple equation (Christiansen 2002:688) and measurements of the calcaneus (Martin, et al. 2018:4567). An average 37% decrease in body size differs from the estimate by (Hill, et al., 2008) of 20-15%, and greatly differs from the conclusions of (Raymond and Prothero 2011). A case of multiple studies utilizing many identical specimens, and their corresponding measurements, yet arriving at drastically different conclusions has surfaced. To reconcile questions regarding bison size change, a deeper analysis of body size change and the associated ecological drivers is necessary. Incorporating multivariate statistical methods can provide greater insight into identifying the drivers of bison size change over time.

Drivers for size diminution understood in the paleoecological record have escaped high resolution for decades. In general, traditional methods for analyzing body size change rely on relatively simple comparisons, in conjunction with univariate and bivariate plots (Bedord 1974; Wilson 1978:12-13). The North American bison offers a unique specimen for identifying body size change from elemental metrics, given large and diverse samples preserved in a kill site. Previous studies utilize the calcaneus for body size estimation (Breslawski and Byers 2014; Hill, et al., 2008; Martin, et al. 2018; Raymond and Prothero 2011). As many as 11 measurements are recordable on a complete calcaneus (Hill 1996:Appendix 3), effectively capturing a significantly greater amount of size and potentially shape variability. Univariate and bivariate analyses limit



the potential for analyzing size variability. Furthermore, an effective method for identifying sex is integral for discussing changes in size over time. Earlier methods have demonstrated that sex is relatively identifiable in bison remains using a number of post-cranial elements (Duffield 1973:138; Todd 1986:117-118). To tackle the issue of size change in bison, multidimensional methods are applicable. Multidimensional analyses offer a powerful suite of tools to discriminate between male and female bison using skeletal elements. Limiting identifications, for either sex or size change, to only a few measurements potentially reduces the amount of variability explained by the data. To capture between sample variability using more measurements will better capture differences between elements. Applying more sophisticated quantitative methods allows a deeper analysis to identify minute changes in size change, potentially informing on ecological and climate effects.

Important ecological characteristics regarding bison may be considered as well. If body size in bison is decreasing the question of equal sex diminution needs to be made. Ecological contributions for unequal changes in body size by sex may include differential effects of predation (Beckerman, et al. 2010:1075), land use and foraging patterns (Berger and Cunningham 1994:84-87), gestation times (Berger and Cunningham 1994:122-123; Blue, et al. 2012:495), or maturation rates (Lee, et al. 2011:3307-3308). I hypothesize that the presence of differential diminution in bison is likely selection for quicker maturation times and shorter gestation times during a period of resource restriction. Female bison who mature quickly in times of intense resource restriction will have a greater chance of reproducing before they die than ones who mature slowly. When the risk of early death is particularly high, as it would be when resource access is low, reproducing sooner offers a substantial advantage towards an individual's fitness.

## Methods

To analyze the change in size over time, a series of plots are generated for each site, based on their calibrated radiocarbon age, and separated by the newly identified sex. Plots were constructed accounting for sex, site, and calibrated ages. Sex was identified using the methods described in (Dalmas, 2020). After accounting for the newly identified sex, plots of relative means and standard deviations for each sex at each site were assembled. To fill in missing measurements for a given site imputation methods are employed. Imputations are performed across all calcanea from all sites for measurements CL1 through CL9 using predictive mean matching. Sexed samples from the analysis of sexual dimorphism are matched to their corresponding imputed data and stored as a separate data set. Plots for CL1 through CL9 against climate were constructed to observe the relationship between mean difference in temperature and diminution.

Climate variability is also taken into account using climate data published by (Viau, et al. 2006a) acquired through NOAA (Viau, et al. 2006b). These data contain estimates from pollen records of average July temperatures for the last 14,000 years in North America. Additionally, regional temperature records for the Midwestern United States with mean differences from contemporary temperatures are provided. Meta-regressions were performed across all sites and for each sex, with sufficient sample sizes, using sample means and standard deviations for CL1, CL4, CL5, and CL9, against the mean temperature differences reported in (Viau, et al. 2006a). Comparisons between the two regression results for each set of size means are performed using Cohen's *d*. The standardized differences produced by Cohen's *d* at a level of 0.20 in the means for males and females indicates different mean sizes for each sex through time. Additionally, the fit of the meta-regression through time and against climate suggests if there is a significant relationship between each sex and changes in mean temperature difference relative to the

present. Results of the meta-regression are summarized and reported to address variation across time and within sites.

## Results

Plots of the calcaneal measurements against time and by sex are created, after accounting for sex using the previously detailed methods. Among all measurements of the calcaneus, there is a clear decreasing trend from ~13,000 cal B. P. until modern bison. After accounting for sex it is evident that body size changed notably over time (Figure 3.2b-c). It is clear that not accounting for sex, as was dismissed by Raymond and Prothero (2011), increases the variability greatly within a given site, thus muddying the observation of size diminution. There exists some autocorrelation within these data, most evident in CL4, CL5 and CL8, indicating a non-linear relationship between changes in bison calcanea through time. A notable instance of autocorrelation appears around 10,000 cal B. P., where a sharp dip can be seen among all three measurements and for both sexes. Immediately following the 10,000 cal B. P. dip there is a relative increase until 7304 cal B. P., where size dips yet again, though not as strongly in CL8.

From the imputed data estimates of the mean and standard deviations were estimated for model fitting. Standard deviations proved to be rather small across all sites with a mean variance for female bison of 4.96mm and for males 5.01mm. Two sites produced relatively high variability. The greatest standard deviation among all sites was observed in Milburn for both sexes ( $\sigma_F^2 = 12.4\text{mm}$  and  $\sigma_M^2 = 14.6\text{mm}$ ). High standard deviations are also present for males at Lipscomb and females at Finely (approximately  $\sigma^2 = 8\text{mm}$  for each). It should be noted that sample sizes for males ( $n_m = 168$ ) and females ( $n_f = 229$ ) are quite different. Two sites, Nye and Rourke, identified only a single male and thus could not compute a variance.

Variances between groups through time were computed to test if males and females varied significantly differently. The results of the F-test produced an F-value of 1.26 with a

corresponding p-value of 0.57. Asymptotic test for the equality of coefficients of variation were performed as well and produced a test statistic of 1.28 with corresponding p-value of 0.26. Both tests suggest that the differences in variability for each sex over time are not significantly different from one another.

Meta-regressions of the imputed data for size and temperature produced significant results. Not accounting for sex and regressing measurements against temperature for each site produced a statistically significant relationship (p-value < 0.001,  $R^2 = 0.64$ ) (Figure 3.6). The residual heterogeneity produced an  $I^2$  of 0.82 and corresponding  $\tau^2$  of 37.1, suggesting that a significant amount of unexplained variability exists between bison kill sites. After accounting for sex males failed to produce a significant relationship with temperature (p-value = 0.3009) with a large  $\tau^2$  of 51.8. Females failed to produce a statistically significant relationship (p-value < 0.9803) with an  $I^2$  of 0.87 and  $\tau^2$  of 26.6.

## Discussion

In North America the Great Plains offers a unique laboratory for studying archaeology. Use of the Great Plains and North American bison by native peoples has been extensive over the last ~13,000 years. Bison offer an interesting proxy for understanding humans and their behavior on the landscape. The Great Plains spans an enormous space with a wide distribution of bison kill sites. Though the spatial element of bison hunting on the Plains is expansive kill sites are quite similar. Radiocarbon dating of bison specimens on the plains are quite effective retaining multiple well dated individuals. Our understanding of the distribution and precision of bison kill sites across the Great Plains is notable and offers a unique opportunity to study changes over time.

Within a bison kill site a small sample of the local bison population is suddenly captured in time. Generally, prehistoric bison hunters employed methods that indiscriminately kill a group

of bison. These samples appear to be relatively unbiased given mass kill events capture an uncontrolled group and includes all individuals. Within a single hunting event we can treat that sample of bison as a snapshot of bison on the Great Plains. The discovery of bison kill sites is limited by preservation and discovery efforts which limits the available sample of bison metrics for analyses. Yet, if the variability in size change over time is significant enough and a given site captures the approximate size of bison then size change through time is detectable. Though the underlying assumptions to large scale studies of bison through time are broad some variability remains observable given appropriate methods.

A notable question concerning bison hunting and their paleoecology regards the effect, or absent of effect, of human predation. Researchers have correlated the relatively sudden and rapid diminution in bison size over the last 13,000 years to human predation (McDonald 1981:248-250). The precision of both diminution of bison and human arrival on the landscape are relatively well known suggesting that some correlation certainly exists. It must be addressed that a climate variability is also strongly correlated to diminution and human migration during this period. Temperatures in North America express some periodicity in climate variability ranging on about 1,100 year intervals (Viau, et al. 2006a:4). The significance of the periodicity of climate change throughout the Holocene appears to weaken towards the present. Comparing the significance in the variability of climate and bison diminution after accounting for sex are significantly correlated.

Resource limiting factors induced by changes in the climate will increase selection notably (McCain and King 2014). One variable influencing effective population size is age at maturity. In a study by (Lee, et al. 2011) they concluded that the ratio of effective population size to census population size is driven by the survival rate of juveniles, where lower survival

rate induces higher levels of directional selection favoring small bodies. In an environment where resources are limited and the climate is neither stable nor favorable to North American bison, we can expect that the survival rate of all animals, and especially juveniles, is low. Increased levels of directional selection could specifically increase the rate of body size reduction in such an environment as selection for small bodies intensifies. Hence, favorable selection for small animals should not only be stronger but be occurring at differential selective rates between males and females.

Not only do bison appear to be getting smaller as time progresses under fluctuating resources, but small-bodied females who reach reproductive capabilities sooner should be selected for. Similarly, if one female in the population is able to reach reproductive maturity before another female, she has shortened that period during which she could be killed by a predator or die from malnourishment. Thus, small bodied and quickly maturing females are strongly selected for under these climate-limiting conditions. Whereas males are not expected to receive as strong of a selective pressure to reach reproductive age quickly, given that their contribution to the next generation requires less time and resources than females. A single female contributes completely to the carrying of an offspring both during gestation and raising the young to maturity. Hence, the resource demand is greater for female bison than males, given males only directly contribute via insemination. Smaller male body size will receive selective pressure as smaller offspring require less resources and the resources expended in reproduction and raising offspring is less demanding. Female bison will also be selected for smaller body sizes but must be able to gestate and bring offspring to reproductive maturity in a resource restricted environment.

It appears that male and female bison are in fact decreasing in body size over time, as is evident from size plots over time and the meta-regression results (Figure 3.7). It is difficult to determine whether male or female bison are changing at relatively different rates. Variance in size over time between sexes suggests minimal overlap between males and females (Figure 3.7). The within sex variance on the other hand does suggest a lot of variability for any male or female population at a given point in time. Estimates of means from the sex identified individuals at each site also have relatively large variances given many are constructed using small samples. Though, sites with relatively large samples like Glenrock and Olsen Chubbuck produced similar variances to sites with fewer measurements ( $\sigma^2 = 5.9$  and  $\sigma^2 = 3.6$  respectively). Even when variances were large sexes did not overlap significantly except for Milburn. Another hurdle in estimating rates of size change are the irregular gaps in time between sites. When gaps are significantly large one sample with an associated mean and variance contributes to a larger proportion of the rate estimate. At this time it is difficult to effectively quantify rate changes for a given sex and produce a convincing estimate.

Establishing the presence of resource limiting factors can be difficult, with high spatial resolution, in the paleo record. Data measuring shifts in vegetation throughout the Holocene present promising methods for future analysis, though additional research is needed on the Plains. Analyzing fluctuations in the change of bison size (as estimated from changes in the measurements of the calcaneus) relative to changes in climate variability offers methods for potentially correlating such phenomena. It is clear from the results of the meta-regressions that the correlation between changes in calcaneal measurements and the mean difference in temperature are significant. Temperature variation offers insight regarding variability in the climate in North America during the Holocene. Millennial scale variability is commonly

observed in the Holocene for North America suggesting a notably noisy climate (Viau, et al. 2006a). Considering the changes in bison body size through time, assuming bison kill sites capture a representative sample of Great Plains bison, it appears that body size trends towards smaller bison but not linearly. Rather than observing a clear linear trend in the size of the calcaneus through time it appears that size changes variably with the climate (Figure 3.6). It should be expected that body size responds to climate fluctuations as the environment changes as well. Bison body size may be responding to the same millennial scale variability in the climate or more likely to the corresponding environmental shifts.

Comparisons of the forest plots between sexed and unsexed meta-regressions show a few notable trends. The differences between males and females appears to vary somewhat through time (Figure 3.7). While males are consistently observed as being significantly larger the gaps between male and female variability are not apparently constant. Analytical comparisons between these differences in variability between males and females suggest the variability between the two groups are not significantly different. There is not sufficient evidence from the results of this study to suggest significant differences in size change between male and female bison over time. Though, higher resolution data and improved methods for estimating parameters concerning bison size may better identify such phenomena. It is apparent that size is certainly variable and better understood when sex is accounted for, but additional data is needed to identify significant contributors.

Concerning the discrepancies of interpretation between (Martin, et al. 2018) and (Raymond and Prothero 2011) it is apparent that both methods could improve their analysis after better accounting for sex. In the study by Raymond and Prothero they are cited as suggesting that dimorphism is known in bison, yet they did not observe bimodal differences (Raymond and



Prothero 2011:637). Conversely, analyzing the multidimensionally scaled data and applying clustering methods and LDA shows that two distinct groups are observable among these data. Given a sufficient number of measurements or large enough sample size sex can be identified from the measurements of the calcaneus. When analyzing size change overtime without accounting for sex the variability for a given site is immense (Figure 3.2). Thus, the relative change in bison size over time may not appear to be significant when the significant covariate sex is not accounted for. Similarly, the study by (Martin, et al. 2018) does not account for sex when estimating body size change to compute body weight through time (Martin, et al. 2018:4570). While their methods do suggest body size is decreasing significantly, the degree can not be well estimated without accounting for the effects of sexual dimorphism (this is still difficult even when sex is accounted for). Additionally, estimating body weight from unsexed bison adds another significant layer of uncertainty.

### **Conclusions**

The lack of linearity between changes in bison calcaneus and time, after accounting for sex, suggest autocorrelation in these data. This autocorrelation may very well be ecological responses to millennial-scale climate changes throughout the Holocene. Accumulating higher resolution data for climate variability in the Great Plains can improve investigations into this autocorrelation. Additional studies for environmental change on the Great Plains over the last 14,000 years may also offer insight regarding forcings that affect bison body size. Further investigation to connect the autocorrelation in these data to specific climate variability offers a route for identifying drivers of body size change in North American bison.

This hypothesis beckons the question; if the environment is so unfavorable for numerous megafauna presiding in North America, then why is it that bison did not go extinct while many similar species did? It may be supposed that environmental effects and selection for shorter

gestation time and earlier age at maturity were great enough in North American bison to respond to changes in the climate. It is evident that body size changed rapidly during the Early Holocene, suggesting that selection for body size was strong and an effective response to climate variability. It may also be posited that bison mobility allowed for more effective movement between resource patches in a resource-limited environment. Further investigation into the effects of mobility, climate variability, and the degree of body size change are necessary to develop this hypothesis.

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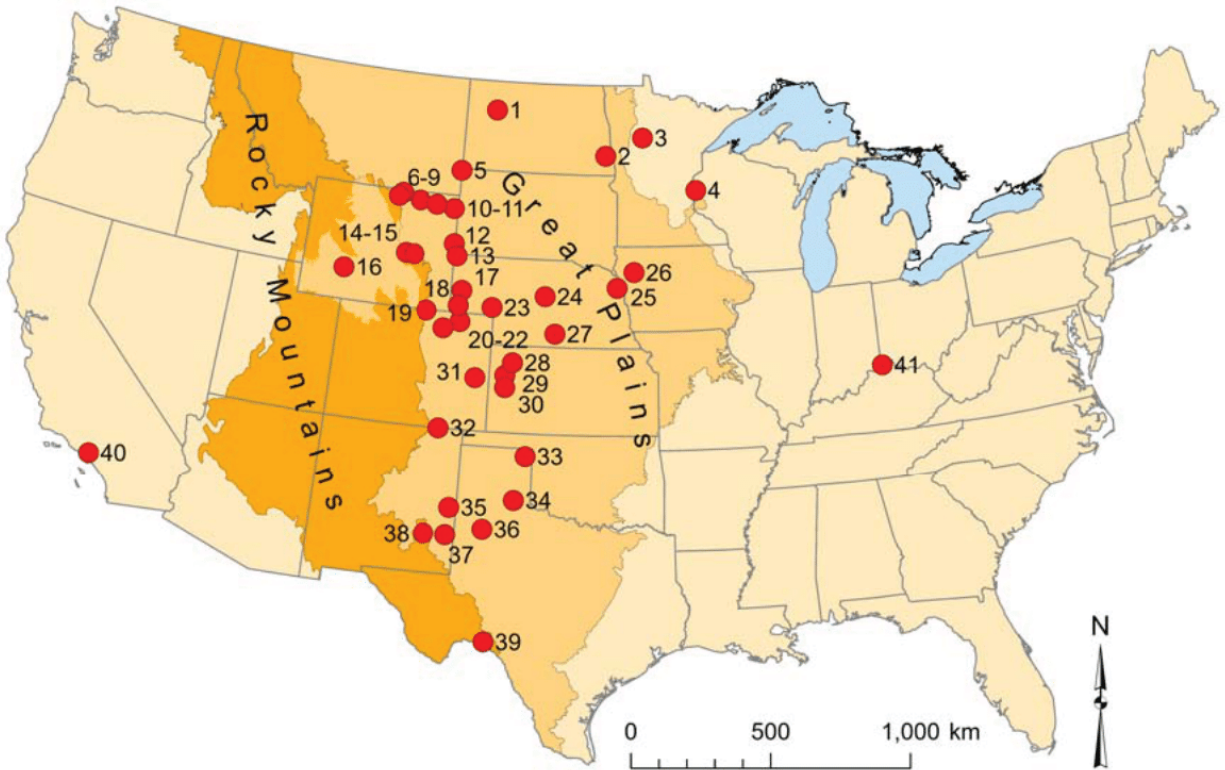


Figure 3.1. Map of the contiguous United States showing the location of the archaeological and paleontological sites from which calcaneus data in this study are derived. Site numbers: 1) Beacon Island, 2) Rustad, 3) Itasca, 4) Interstate Park and Nye, 5) Mill Iron, 6) Big Goose Creek, 7) Mavrakis-Bentzen-Roberts, 8) Cordero Mine, 9) Rourke, 10) Hawken, 11) Vore, 12) Agate Basin, 13) Hudson-Meng, 14) Glenrock, 15) Casper, 16) Finley, 17) Scottsbluff, 18) Lodgepole Creek, 19) Lindenmeier, 20) Frazier, 21) Jurgens, 22) Frasca, 23) Clary Ranch and O.V. Clary, 24) Milburn, 25) Logan Creek, 26) Simonsen, 27) Red Smoke, 28) Burntwood Creek, 29) 12 Mile Creek, 30) Scott County Pueblo, 31) Olsen-Chubbuck, 32) Folsom, 33) Lipscomb, 34) Rex Rodgers, 35) Blackwater Draw, 36) Lubbock Lake, 37) Milnesand, 38) Garnsey, 39) Bonfire Shelter, 40) Rancho La Brea, 41) Big Bone Lick.



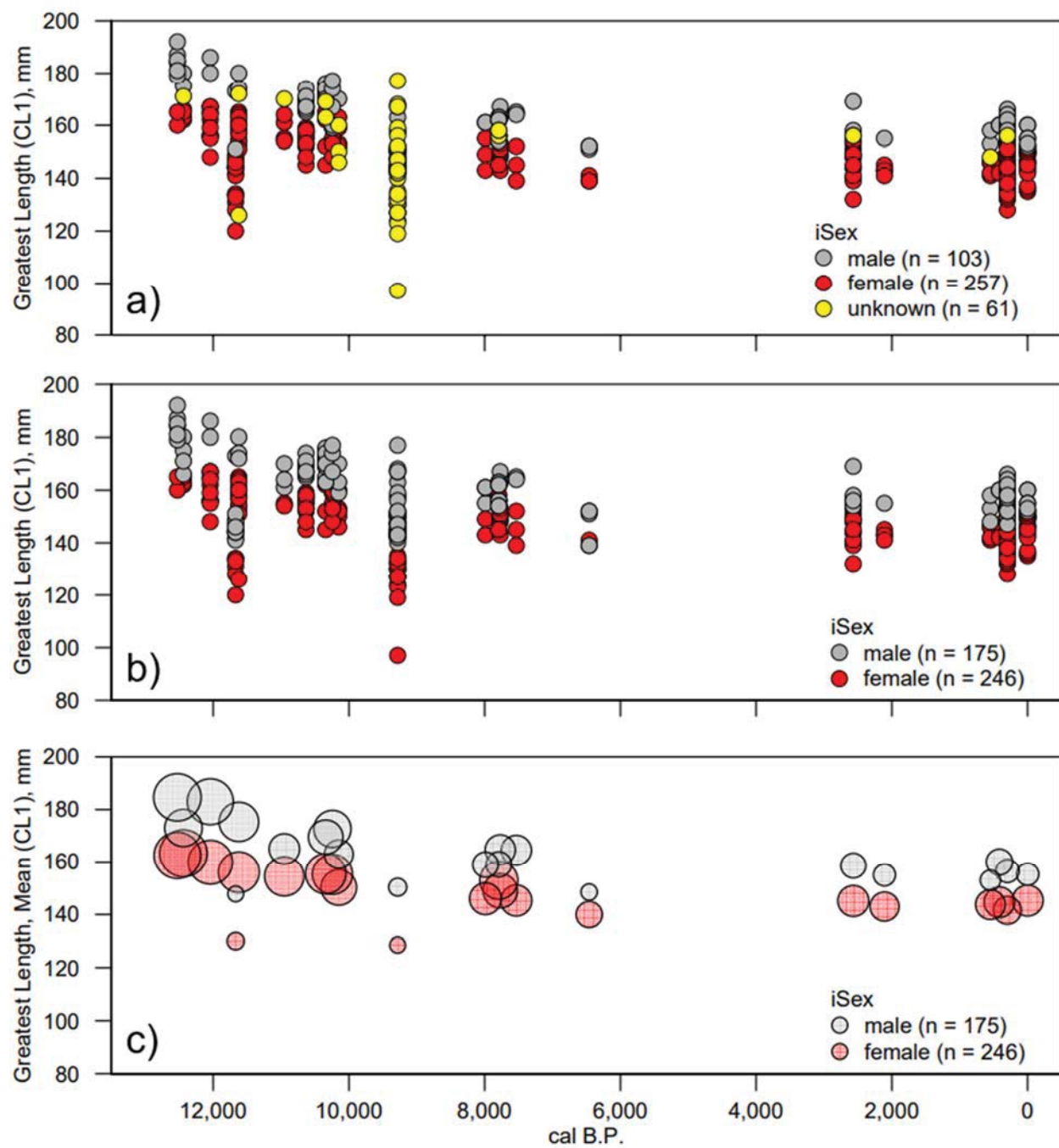


Figure 3.2. a) Change in CL1 through time grouped by initial researcher identified sex. b) Change in CL1 through time grouped by newly identified sex. c) Mean CL1 by sex using newly identified sex, circle size is relative to number of samples.

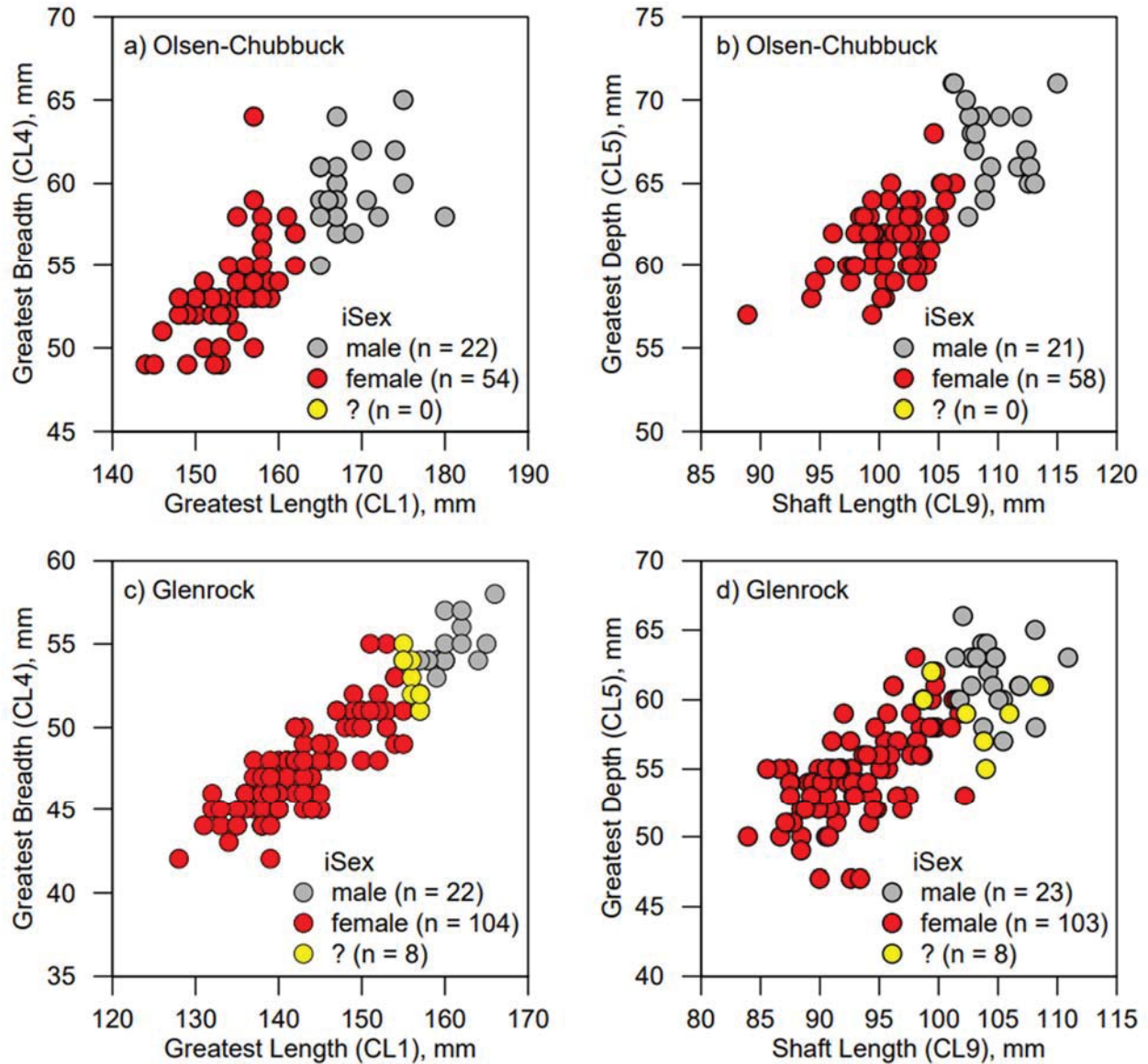


Figure 3.3. Bivariate plots of CL1 by CL4 grouped by sex. a & b) using newly identified sex versus c & d) using initial researcher identified sex.



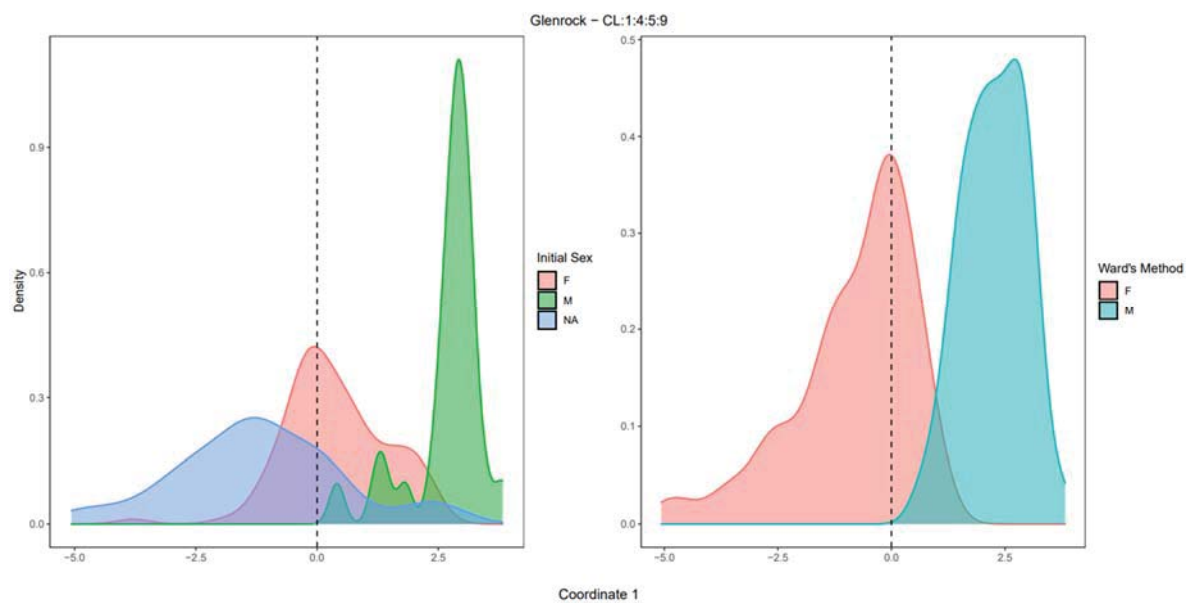


Figure 3.4. Density plots of the first MDS coordinate comparing the initial researcher sex against newly identified sex.

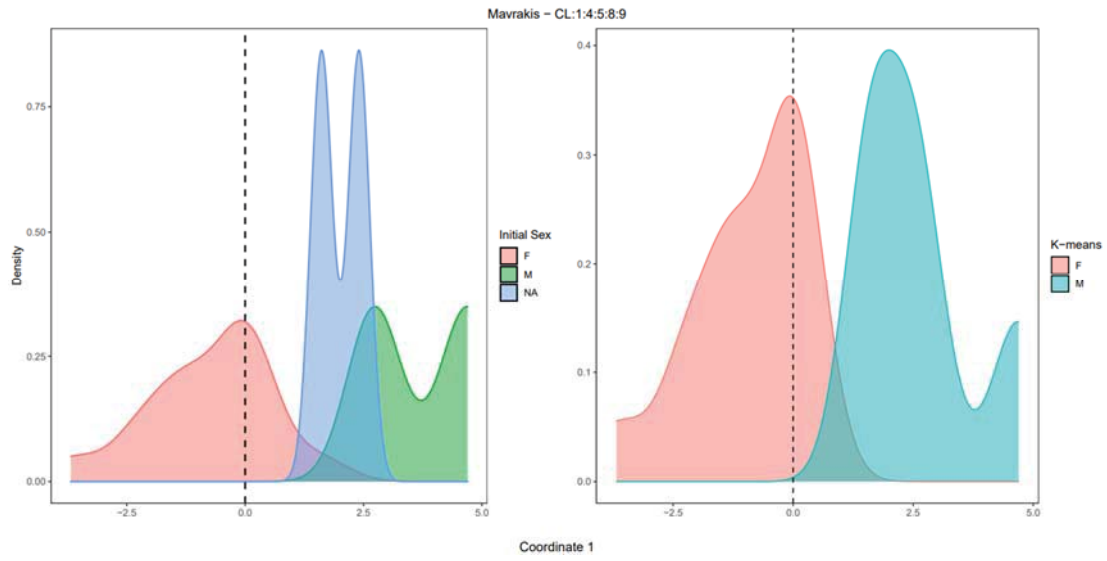


Figure 3.5. Density plots of the first MDS coordinate comparing the initial researcher sex against newly identified sex.

$Q = 32.5$ ,  $df = 1$ ,  $p\text{-value} = < 0.0001$ ,  $\tau = 5.3$

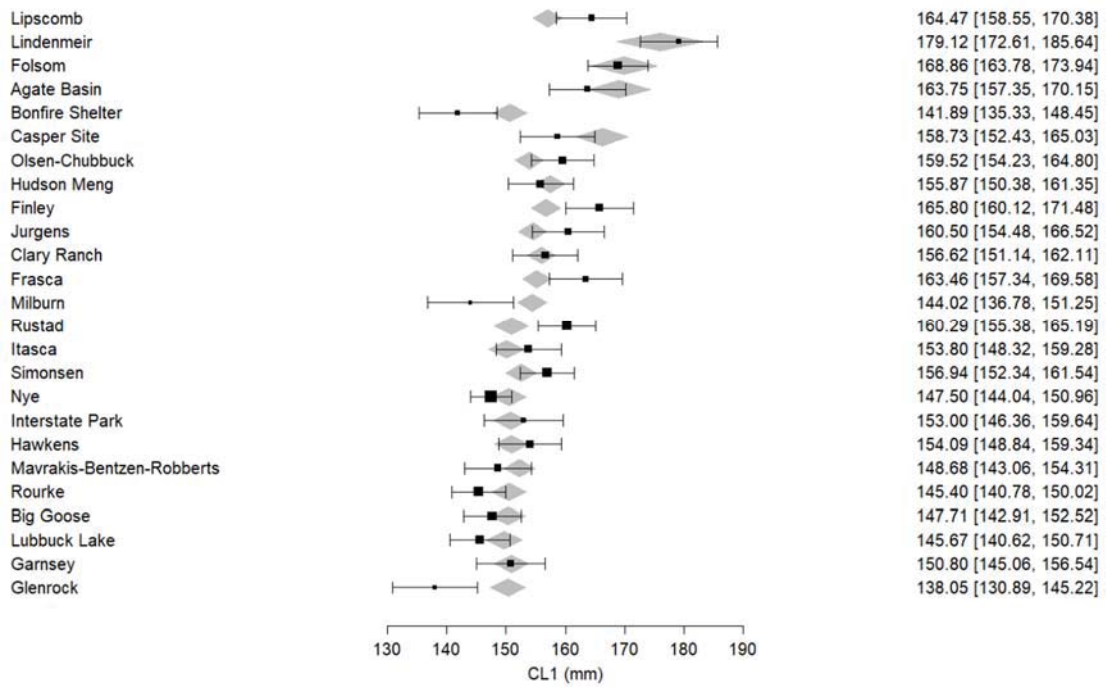


Figure 3.6. Results of the meta-regression for temperature using CL1 when not accounting for sex.

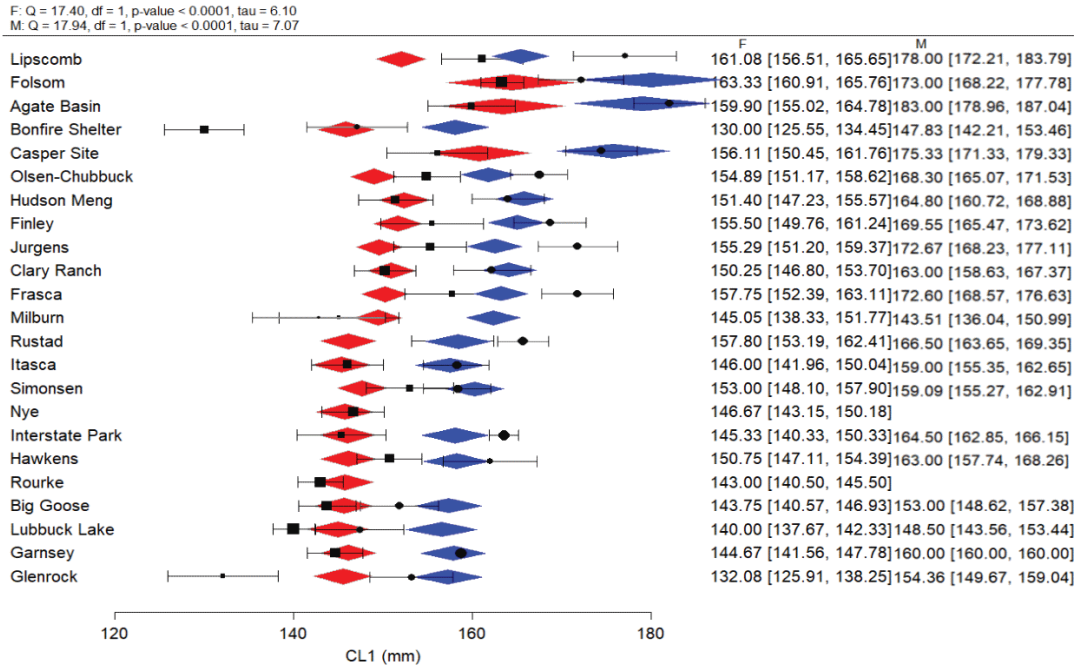


Figure 3.7. Results of the meta-regression for temperature using CL1 when accounting for sex. Red indicates the results of the within site fit for female bison and squares indicate the mean CL1 with corresponding 95% confidence intervals (values for intervals listed on the right). Blue indicates the within site fit for males and circles mean CL1 with confidence intervals.

## CHAPTER 4. GENERERAL CONCLUSIONS

### Conclusions

Research regarding changes in bison offer key information regarding early human foragers in the New World. Bison served as an integral source of food and materials and were clearly a persistent prey for foragers. Fluctuations in bison populations have been attributed to intense predation by humans. To date, convincing evidence that human predation was the primary driver of bison diminution remains elusive. To establish good studies of bison size change an abundance of data is necessary. Not only having ample data, but also rigorous and encompassing methods to capture as much information as is available is essential. Statistical methods offer a swath of powerful tools to handle many of the classic problems when dealing with archaeological remains. Working with relatively irregular or small samples is common but should not deter attempts to interpret such data. Applying multivariate approaches to identify sex from metrics of the calcanea provides an improved method for sex identification. Once sex is accounted for analysis of body size change over time and its potential drivers can be approached. The calcaneal data published by (Hill, et al., 2008) suggest that variability in the climate during the Holocene is strongly correlated with changes in bison body size. Not only does the archaeological data support climate driven diminution but so does the ecological theory.

Bison, similar to many large mammals, respond readily to environmental changes and prove to be rather plastic animals (Clifford 2010; Martin, et al. 2018). While studies of climate variability have largely been the focus of study for variability in bison body size, additional ecological drivers certainly should be considered. Bergmann's Rule suggests that mammals frequently respond to cold climates, often represented latitudinally, with increased body size (Bergmann 1847). For bison, it appears that Bergmann's Rule certainly holds true. During the

shift from the Younger Dryas, characterized as being dry and cold, into a warmer climate during the Holocene may have drove body size reduction in bison (Elmore and Wright 2011). Yet, teasing out specifically what environmental and ecological changes result from a cooling climate is necessary to further our understanding of changes in bison body size. While mean temperature differences correlate strongly with size change further investigations into potential climatic variables will further establish potential drivers.

Animal body size is a particularly fluid phenotype in ecological studies (McCain and King 2014; Rudolf and Singh 2013; Sheridan and Bickford 2011). Extensive research regarding body size variation among various taxonomic levels attempts to understand the associated drivers and responses to body size fluctuations. Potential drivers for size change in bison are often associated with the rapidly changing environment in North America during the early Holocene (Hill, et al., 2008; Lyman 2004; Martin, et al. 2018; Wilson 1978). North America, and much of the Northern hemisphere, experienced sways in the climate which were brought on by the end of the Last Glacial Maximum (LGM) (Higgins and MacFadden 2009). Climate changes are strongly associated with significant changes in the ecology and phenotypes of fauna, including body size and sex determination (Rudolf and Singh 2013; Sheridan and Bickford 2011). In response, many mammals became limited in their access to previously available resources and struggled to adapt to new climate conditions. Though the effects of climate and temperature on a number of modern species are well studied, how the body size of bison responded to such climate events requires further attention.

In environments with high predation and or limited resources, it has been observed that populations respond with smaller individuals at higher frequencies and earlier births for various species (Beckerman, et al. 2010; Lee, et al. 2011). The reasoning being that as resources become

limited or predation is increased the likelihood for a particular individual to reproduce will decrease as more are either killed prior to sexual maturity, die (from malnourishment or illness), or are incapable of birthing a healthy offspring. Thus, those individuals with traits that enable reproduction under limited conditions will be selected for. Those most capable of reproducing in this instance would be whomever can reproduce most quickly. Traits that shorten time to reach maturity or produce shorter gestation periods will increase reproductive rates. Gestation times are largely controlled by the size of the offspring (Bleu, et al. 2012; Kiltie 1982). Thus, those mothers producing smaller offspring will increase their fitness by decreasing the amount time during which they could die, from malnourishment or predation when resources are restricted, prior to birthing offspring. Additionally, smaller females often reach sexual maturity before larger animals. On the population scale, high predation and or resource limitations should favor smaller bodied bison and selection for small-bodied females should be greater. Further investigations regarding the specific ecological drivers possible in ancient bison populations will open numerous doors to understanding their past.

The theory that human predation may have led to the diminution of bison body size seems to depend on the correlation between the reduction of bison body size in conjunction with human arrival. However, measures of Holocene climate variability retain strong relationships with bison diminution. A major source of difficulty in assessing the potential effect human predation is simply acquiring good data to test such relationships. Continuing to build on the current understanding of bison in archaeological contexts with further studies of human use and effect. To properly establish compelling evidence of human use of megafauna continued discovery and methodological developments are necessary.

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