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CLIMATE EFFECTS ON MAMMALIAN BODY SIZE AND GRASSLAND
COMPOSITION INFERRED FROM LATE QUATERNARY GRAZERS IN THE
GREAT PLAINS OF NORTH AMERICA

by

Tom Baldvins

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CLIMATE EFFECTS ON MAMMALIAN BODY SIZE AND GRASSLAND
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University of Nebraska, 2015

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Several mammalian taxa exhibited a diminution during the Pleistocene-Holocene transition. Two hypotheses have been proposed to explain this phenomenon: (1) human hunting and (2) climate change along with its effects on grasslands. I use stable isotopes from a variety of Quaternary grazing mammals to measure grassland changes following the Last Glacial Maximum (LGM) in Nebraska and to develop a climate proxy to compare with mammalian body size. Results indicate that latest Pleistocene equids and mammoths have $\delta^{13}\text{C}$ values indicative of a C_3 or mixed C_3/C_4 diet. However, Holocene bison have greatly elevated $\delta^{13}\text{C}$ values, indicating a diet dominated by C_4 vegetation, suggesting a northerly expansion of C_4 grasses with the warm conditions following the LGM. High $\delta^{13}\text{C}$ values from *Bison bison* sampled in this study suggest a greater abundance of C_4 grasses in Nebraska than today, and may indicate that these bison lived during the Holocene thermal maximum. *Bison bison* sampled in this study display a significant but weak correlation ($r^2=0.20$, $p=0.004$, $n=39$) between $\delta^{13}\text{C}$ and first molar occlusal area, which acts as a proxy for body size, indicating that size decreased as dietary C_4 increased and climate warmed; however, weakness of the correlation does not support previous hypotheses that attribute bison diminution solely to increased dietary C_4 .

These data indicate that other factors, such as temperature, aridity, and/or human hunting, are needed to explain the decrease in bison body size. On the other hand, a strong significant relationship ($r^2=0.83$, $p=0.011$, $n=6$) between $\delta^{13}\text{C}$ and equid metacarpal length of middle Pleistocene equids spanning both warm and cold intervals suggests that an increase in body size occurred with warming. I propose that both of these trends in body size were driven by changes in productivity. C_4 dominated habitats of the Holocene provided less primary productivity than mixed C_3/C_4 habitats contributing to bison diminution, while increased productivity during warmer intervals of the Pleistocene allowed equids to increase in size.

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INTRODUCTION

The Pleistocene Epoch was marked by dramatic shifts in climate between glacial and interglacial intervals. On the basis of evidence from $\delta^{18}\text{O}$ values of planktonic foraminifera, orbital cycles appear to drive the onset and termination of many glacial cycles (Hays et al. 1976, Imbrie et al. 1992, Hernandez-Almeida et al. 2012). The Last Glacial Maximum (LGM), dated approximately 18,000 calendar years before present (cal. yr BP), was distinguished by increased aridity during cold periods in the Northern and Central Great Plains (Mahowald et al. 1999, Wang et al. 2012). The increased aridity and decreased temperature caused flora and fauna to dramatically reduce their range boundaries across North America during glacial periods. Mammals at higher latitudes shifted their range to more equable environments, known as glacial refugia, south of the Laurentide ice sheet (Kurten and Anderson 1980, Sommer and Nadachowski 2006, Shafer et al. 2010) and floras at higher altitudes shifted to lower altitudes (Cowling 1999). During the LGM the maximum extent of the Laurentide ice sheet reached the northern border of Nebraska (Dyke and Prest 1987, Dyke et al. 2002, Mickelson and Colgan 2003).

Extreme climate changes during the Pleistocene relative to contemporary times offer an opportunity to study how mammalian body size may have been affected by relatively rapid fluctuations in temperature and vegetation. Over 50% of modern mammals follow a positive correlation between body size and latitude (Blackburn et al. 1999, Ashton et al. 2000, Rodríguez et al. 2008), known as Bergmann's rule, which has been attributed to temperature and/or primary productivity (McNab 2010). Temperature may have a direct influence on body size through heat loss. Larger animals lose

relatively less heat than smaller animals due to a decreased surface area to volume ratio, so large body size may be adaptive for colder climates (Gardner et al. 2011).

Temperature may also have an indirect effect on body size by controlling the distribution of plants and growing season length (Peñuelas and Filella 2001). Longer growing seasons create more available forage, which may allow animals to reach their maximum body size.

At the time of Euramerican settlement, the Great Plains was covered by a mix of grasses that use both the C_4 and C_3 photosynthetic pathways. C_4 plants thrive in warm, arid environments and are the dominant grasses south of 50° N latitude in North America; above this latitude C_3 grasses comprise $>50\%$ of grasslands (Teeri and Stowe 1976). Modern C_4 distribution is correlated primarily with two factors: summer precipitation and temperature (Teeri and Stowe 1976, Collatz et al. 1998). The temperature crossover model predicts that C_4 plants will be more competitive in areas where mean monthly temperatures are above 22°C (Ehleringer et al. 1997); however, there are known locations where C_4 plants thrive in temperatures below this threshold, which implies that temperature is not always the controlling factor in C_4 distribution (Naidu and Long 2004, Pau et al. 2013). It appears that differences in water-use efficiency between C_3 and C_4 plants coupled with regional precipitation patterns control C_4 distribution in some cases (Pau et al. 2013). It has also been suggested that C_4 grasses expanded their range during glacial cycles because of lower atmospheric CO_2 concentrations (Cerling et al. 1997, Collatz et al. 1998). A study involving controlled CO_2 concentrations suggest that C_4 grasses should be able to outcompete C_3 grasses under low CO_2 conditions due to the enzyme PEP carboxylase (Gerhart and Ward 2010).

This enzyme has a greater affinity for CO₂ than RuBisCO, the primary photosynthetic enzyme in C₃ plants, which potentially allows C₄ plants to survive in conditions unfavorable to C₃ plants. Although low CO₂ concentrations during glacial intervals (180 ppm, Luthi et al. 2008) would be expected to foster C₄ expansion, carbon isotope studies using mammalian herbivores from Florida, Wyoming, and California suggest that grazers and mixed feeders were consuming primarily C₃ vegetation during these intervals (Coltrain et al. 2004, DeSantis et al. 2009, Kohn and McKay 2012). It appears that, at least in these locations, C₄ grasses were not able to overcome the low temperatures of glacial periods to expand their range even during periods of low atmospheric CO₂.

There are few clear examples of body size trends that follow temperature or productivity changes in the geologic record. Nevertheless, many carnivores and ungulates, including horses and bison, decreased in body size during the Pleistocene-Holocene transition, about 12 to 8 thousand years ago (yr BP), but authors contribute this diminution to a variety of factors including human hunting and climate (Kurten 1965, Davis 1981, Klein and Scott 1989, Wolverson and Lyman 1998, Guthrie 2003, Lyman 2006, Smith and Betancourt 2006, Hill et al. 2008, Lyman 2010). Horses in Alaska decreased in body size following the LGM until their extinction at ~12.5 thousand radiocarbon years before present (¹⁴C yr BP) (Guthrie 2003). Bison in the Great Plains during the Pleistocene are thought to be a single evolutionary lineage from the larger *Bison antiquus* to the smaller *Bison bison* (McDonald 1981, Shapiro et al. 2004, Wilson et al. 2008). This lineage underwent a total size reduction of approximately 15-20% over two different time periods near the Pleistocene-Holocene transition and again at ~8,000 yr BP (Hill et al. 2008). As mentioned above, these diminutions are hypothesized to be

either human or climate induced (Hill et al. 2008). Knowledge of how mammals may react to the effects of temperature and changing grasslands is essential for predicting faunal changes in the near future due to climate change.

The primary goal of this study is to investigate the impact of climate and associated grassland composition on body size in large mammalian grazers during the Quaternary through a comparison of stable carbon and oxygen isotopes in teeth to body size proxies such as first molar occlusal area and metacarpal length in bison and horses. Fossils used in this study come primarily from the Red Willow fauna in southern Nebraska, which spans the Pleistocene-Holocene boundary, and from several late Pleistocene localities in Sheridan County in northern Nebraska. In order to estimate the percentage of C_3/C_4 vegetation present in these faunas, stable carbon isotopes were sampled in the teeth of horses, camels, and mammoths in the Sheridan fauna, which occurs before bison entered North America, and horses, bison, and mammoths in the Red Willow fauna. I demonstrate that Nebraska vegetation was composed primarily of C_3 plants during glacial intervals and mixed C_3/C_4 or C_4 vegetation during interglacial intervals by comparing stable carbon isotopes from glacial and interglacial faunas. I then use the carbon isotope composition of grazers as a proxy for climate change that can be compared with body size.

BACKGROUND

Geologic and biochronologic context

Teeth sampled for this study are from twenty localities in Nebraska (Fig. 1). Age estimates for localities are provided in Table 1. Six of the localities are located in

northern Nebraska along the Niobrara River (Fig. 1). These six localities are quarries in Sheridan County: Hay Springs (Sh-1, Sh-2), Rushville (Sh-3, Sh-4), and Gordon (Sh-5, Sh-6) (Table 1). The U.S. Army engineers were the first to collect fossils at this site in 1857 (Schultz and Tanner 1957). Since then, Harvard University, Princeton University, and the American Museum of Natural History all collected fossils between 1880 and 1930 (Schultz and Tanner 1957). The University of Nebraska State Museum (UNSM), which houses the samples included in this study, worked the quarries heavily in the 1930's and 1940's (LaGarry-Guyon and Myers 1993).

Specimens at the Sheridan County quarries were located in a river terrace complex below the Loveland loess (Schultz and Tanner 1957, Hintlian 1975, LaGarry-Guyon and Meyers 1993). Schultz and Stout (1948) identified these faunal assemblages to be medial Pleistocene, and this has been supported and refined by more recent work using North American Land Mammal age biochrons. These quarries have been assigned to the Irvingtonian NALMA (1.9-0.2 million years ago [Ma]), specifically biochron Ir-3 (0.4-0.2 Ma) due to the presence of *Ondatra nebrascensis* rather than *O. annectens*, *Microtus pennsylvanicus* rather than *M. paroperarius*, *Microtus ochrogaster* rather than *M. illanensis*, and *Smilodon fatalis* rather than *S. gracilis* (Kurten and Anderson 1980, Lundelius 1987, Bell et al. 2004). Furthermore, these localities lie below the Loveland loess, which was dated to approximately 162,000 yr BP by thermal luminescence and 159,000 \pm 14,000 yr BP by infrared luminescence (Forman et al. 1992, Maat and Johnson 1996, Forman and Pierson 2002). Hintlian (1975) suggested that these quarries are all the same age; however, LaGarry-Guyon and Myers (1993) showed different taphonomic conditions for the Rushville and Gordon quarries, suggesting that they sample different

time intervals. There are three different species of horse in these localities identified by Howe (1979): *Equus niobrarensis*, *E. francisci*, and *E. calobatus*. However, 98% of the fossils were identified as *Equus niobrarensis*.

Other Irvingtonian localities include the Albert Ahrens (No-104) and Fr-104 localities (Fig. 1, Table 1). The Albert Ahrens locality is a paludal deposit. It has been assigned to the middle Irvingtonian (Ir-2)(0.85-0.4 Ma) based on the Lava Creek volcanic ash dated at 0.602 ± 0.004 Ma using $^{40}\text{Ar}/^{39}\text{Ar}$, which is located at approximately the same stratigraphic level ~100 m from the quarry (Gansecki et al. 1998). This locality is inferred to be a glacial interval as indicated by the presence of caribou (*Rangifer tarandus*) and musk ox (*Ovibos* sp.), which today live only in cold climates. Historic records indicate that caribou ranged throughout Canada with the southernmost populations reaching New England; however, modern populations have been reduced to only occurring in latitudes above 50°N (Festa-Bianchet et al. 2011). Musk oxen naturally inhabit latitudes above 60°N with most of the population occurring in northern Canada (Gunn and Forchhammer 2008). Fr-104 occurs in fluvial channel deposits and has been assigned to the early Irvingtonian biochron (Ir-1)(1.9-0.85 Ma) based on the presence of *Tapirus copei* and *Equus scotti*, both of which are associated with the earliest Irvingtonian (Dalquest 1977, Diffendal and Corner 1983). Based on the presence a tapir (*Tapirus copei*) this locality almost certainly represents a warm interval such as an interglacial or an interstadial interval. Tapirs reside solely in warm regions today and have difficulty living in temperatures below 10°C with *Tapirus bairdii* ranging only into southern Mexico (Castellanos et al. 2008, AZA Tapir TAG 2013).

Glacial and interglacial periods were solely recognized by the faunal assemblage present at the Albert Ahrens and Fr-104 localities because there is a paucity of knowledge concerning Pleistocene stratigraphy. Most Pleistocene stratigraphy in Nebraska utilizes three different loess deposits: Loveland, Gilman Canyon, and Peoria (Mason et al. 2007). These loess units are often thinner, especially the Peoria loess, and more difficult to identify in Nebraska because it is relatively distant from the Laurentide Ice Sheet (Muhs et al. 2008). Additionally, Pleistocene loess units older than the late middle Pleistocene are rarely preserved (Mason et al. 2007). The Loveland loess is recognized as the oldest unit dating to ~160,000 yr BP based on infrared and thermal luminescence (Forman et al. 1992, Maat and Johnson 1996, Forman and Pierson 2002). The Gilman Canyon loess is late Pleistocene, and the Peoria loess was deposited during the LGM (~25,000 yr BP) (Muhs et al. 2008). In addition to loess units, there are a multitude of ashes that can be dated: Lave Creek B, Hartford, Bishop, Tsankawi Pumice, Cerro Toledo Rhyolite, Mesa Falls Ash, etc, but only the Lava Creek B Ash is present at one of the studied localities, Albert Ahrens (Bell et al. 2004).

The Red Willow fauna includes localities in Red Willow, Hitchcock, and Hayes counties in southern Nebraska (Fig. 1, Table 1). Fossils were recovered from commercial gravel pits along the Republican River (Corner 1977). Since these fossils were brought up using a hydraulic pump, there is poor stratigraphic control and many are damaged. The fauna is partly latest Rancholabrean (0.2 Ma- 11,700 yr BP) in age based on radiocarbon dates from mammoth teeth, ranging from 33,670 to 10,650 ^{14}C yr BP (Enk 2014, Fig. 2). The fauna also contains *Bison bison*, which other studies have shown first occurs in the Holocene at approximately 8,000 yr BP in the southern Great Plains and

5,000 yr BP in the northern Great Plains (McDonald 1981, Lewis et al. 2007), indicating that some of the Red Willow taxa are almost certainly Holocene in age (Fig. 2). The Red Willow fauna is diverse containing more than 24 different species (Corner 1977); however, bison fossils dominate the assemblage.

Stable Isotopes

Stable carbon and oxygen isotopes are useful for constructing ancient ecosystems and climates, respectively. Stable carbon isotope values ($\delta^{13}\text{C}$) in the teeth of herbivorous mammals record an individual's diet with predictable offsets (Koch 1998). Stable oxygen isotope values ($\delta^{18}\text{O}$) on the other hand, act as a proxy for local changes in the composition of surface water, which is influenced by meteoric water. Mammals incorporate carbon isotopes into their enamel through their diet. Enamel is composed of bioapatite [$\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})$] with a few weight percent CO_3 substituting at PO_4 and OH sites (Dalconi et al. 2003). Plants incorporate isotopes by fixing atmospheric CO_2 during photosynthesis. Plants preferentially uptake ^{12}C , giving their tissues a more negative $\delta^{13}\text{C}$ value than the surrounding atmosphere. C_3 and C_4 plants have non over-lapping $\delta^{13}\text{C}$ values due to differences in fractionation, which allows for the measurement of past diet of an herbivorous mammal (Cerling et al. 1997). The average global value is $\sim -27.4\text{‰} \pm 1.6\text{‰}$ (1 SD) for modern C_3 plants and $\sim -12.7\text{‰} \pm 1.1\text{‰}$ (1 SD) for C_4 plants (Passey et al. 2002). Diet–enamel $\delta^{13}\text{C}$ enrichment in domestic large mammalian ruminants is $14.6\text{‰} \pm 0.3\text{‰}$ (Passey et al. 2005) and $14.1\text{‰} \pm 0.5\text{‰}$ for a variety of both ruminant and non-ruminant herbivores including one African elephant (*Loxodonta africana*) (Cerling and Harris 1999, Cerling et al. 1999). Thus, a pure C_3 herbivore would have stable carbon isotope values of $\sim -13\text{‰}$ while a pure C_4 grazer of $\sim -1\text{‰}$

(Cerling and Harris 1999). Water availability, vegetation density, amount of solar radiation, and soil nutrients also influence $\delta^{13}\text{C}$ values in plant tissues—although the first factor appears to have the greatest influence (Kohn 2010, Diefendorf et al. 2010). A water stressed plant will have $\delta^{13}\text{C}$ values more elevated than those of an unstressed plant. Vegetation density influences $\delta^{13}\text{C}$ values in plants due to amount of solar radiation, retained moisture, and the recycling of CO_2 in dense forests, resulting in more negative values for closed areas (Van de Merwe and Medina 1991). Because this study is based primarily on grazers or mixed feeders known to preferentially occupy open areas, it is unlikely that vegetation density would have much of an effect on the results presented herein.

Stable oxygen isotopes in mammal teeth are commonly used as a proxy for local water values and as a proxy for relative water evaporation among taxa due to differing physiologies and water sources (Kohn 2006, Levin et al. 2006). Local water values may also reflect meteoric water values, which are sensitive to atmospheric temperature. However, shifts in meteoric water values between glacial and interglacial intervals in the Quaternary are complicated by dramatic changes in ice volume causing changes in the $\delta^{18}\text{O}$ composition of ocean water and possible changes in vapor circulation patterns, complicating paleoclimate interpretations. Thus, $\delta^{18}\text{O}$ values in Quaternary mammals are probably most useful for making relative comparisons of water use among contemporaneous mammals or mammals from the same area through time.

The $\delta^{18}\text{O}$ signature in modern mammals is derived from ingested water either through diet or drinking in addition to taxon specific fractionation (Kohn 1996, Kohn et al. 1998). Water obtained through diet may be influenced by the type of plant consumed.

Modern studies show that C₄ grasses are more ¹⁸O-enriched than C₃ grasses leading to more positive $\delta^{18}\text{O}$ values in C₄ grasses (Helliker and Ehleringer 2000, Kohn and Law 2006). Aridity may affect plant $\delta^{18}\text{O}$ composition even more so than its photosynthetic pathway; as an environment becomes more arid ¹⁶O will preferentially be lost through evapotranspiration at the leaf surface, elevating the leaf $\delta^{18}\text{O}$ value (Yakir et al. 1990).

Water ingested through drinking may be influenced by the source water and temperature. $\delta^{18}\text{O}$ values differ from one body of water to another. Rivers obtain their water mainly through meteoric precipitation, and the $\delta^{18}\text{O}$ values of precipitation are strongly correlated with temperature (Dansgaard 1964, Sharp 2007). However, local rivers may have different isotopic signatures based on where their headwaters are located (Dutton et al. 2005). The faunas used in this study are located near three different rivers in Nebraska: Niobrara River, Platte River, and Republican River. The Niobrara River has a mean annual $\delta^{18}\text{O}$ value of $-10.1 \pm 0.60\text{‰}$, the Platte River has a mean annual $\delta^{18}\text{O}$ value of $-9.1 \pm 0.66\text{‰}$, and the Republican River has a mean annual $\delta^{18}\text{O}$ value of $-6.8 \pm 0.98\text{‰}$ (Coplen and Kendall 2000).

The body mass of mammals may also influence their $\delta^{18}\text{O}$ values. Smaller mammals typically obtain the majority of their ingested water through dietary vegetation (Bryant et al. 1995); however, larger mammals need a greater amount of water than their diet alone can provide, so large mammals rely upon drinking to obtain their ingested water (Bryant et al. 1995). Based on this, it is thought that $\delta^{18}\text{O}$ values in large mammals better record local fluctuations in meteoric water values (Bryant et al. 1995).

Body Size

After the Last Glacial Maximum, many taxa decreased in body size: American black bears (*Ursus americana*), aurochs (*Bos primigenis*), badger (*Meles meles*), beech marten (*Martes foina*), bison (*Bison*), brown bear (*Ursus arctos*), elk (*Cervus canadensis*), gazelle (*Gazella gazelle*), horses (*Equus* spp.), jackal (*Canis lupaster*), jungle cat (*Felis chaus*), leopard (*Felis pardus*), marbled polecat (*Vormela peregusna*), raccoon dog (*Nyctereutes vinetorum*), red fox (*Vulpes vulpes*), spotted hyena (*Crocuta crocuta*), striped hyena (*Hyaena hyaena*), wild boar (*Sus scrofa*), wild cat (*Felis silvestris*), wild goat (*Capra aegagrus*), wolf (*Canis lupus*) (Kurten 1965, Davis 1981, Klein and Scott 1989, Wolverson and Lyman 1998, Guthrie 2003, Lyman 2006, Hill et al. 2008, Lyman 2010). Two competing hypotheses explaining diminution are climate change and human hunting.

Distribution of some 60-70% of modern mammals at the species level conforms to a latitudinal gradient by body size, with smaller bodied forms at low latitudes and larger bodied forms at high latitudes (Ashton et al. 2000, Meiri and Dayan 2003, Meiri et al. 2004). This phenomenon is often called “Bergmann’s Rule,” and is commonly attributed to differences in ambient temperature. Larger animals have a greater surface-area-to-volume ratio and therefore retain more heat than smaller animals. It has also been observed that mammals in colder climates often have smaller extremities such as ears and limbs (Serrat et al. 2008); this is sometimes called “Allen’s Rule.” Similar to Bergmann’s Rule, it is thought that the reduced appendages diminish surface area, allowing the animal to retain greater body heat (Serrat et al. 2008). However, heat

conservation does not seem to adequately explain the latitudinal gradient of body size (Ashton et al. 2000, Prothero et al. 2012).

Another explanation for Bergmann's Rule suggests that primary productivity plays an important role in body size distribution (McNab 2010). Animals require proper nutrition to reach maximum body size; without adequate food, individuals will reduce their growth rate and be unable to attain maximum body size (Hilderbrand et al. 1999, McNab 2010). The tropics generally have nutrient poor, acidic soils due to constant weathering while higher latitude soils are often nutrient rich, partially from glacial disturbances tilling the landscape and from lower rates of weathering (Huston and Wolverton 2009). The productive environments that mid latitude ecosystems offer allow animals to eat more nutrient rich food, likely contributing to an increase in overall body size (McNab 2010).

Human hunting has also been evoked to explain bison diminution, exclusive of changing climate or primary productivity. Dated archaeological remains provide evidence that humans first entered North America through the Bering land bridge ~13,600 yr BP (Goebel et al 2008). Shortly thereafter (~12,000 yr BP) several examples of butchered fossils and mass kill sites are found in the Great Plains (Kenady et al. 2011, Driver et al. 2013). Humans may influence the size of animals through hunting practices; for example, humans have affected body size among extant bighorn sheep (Coltman et al. 2003). By selecting the animals with the largest horns for trophy hunting, horn and body size have decreased in big horn sheep populations over the past 30 years (Coltman et al. 2003). If ancient hunters killed the largest bison with the most meat, they could potentially have artificially selected for a smaller body size.

The fossil record may be used to test whether or not temperature or vegetation influenced body size change. Though rare, there are examples present in the fossil record where average mammal body size rapidly changed during periods of intense warming. During the Paleocene-Eocene Thermal Maximum (PETM), stable isotopes and other lines of evidence show that a rapid increase in temperature corresponded with a decrease in body size for several mammal groups including perissodactyls, euprimates, creodonts and others, with some taxa decreasing more than 60% in size (Gingerich 1989, Clyde and Gingerich 1998, Secord et al. 2012). When temperatures decreased at the end of the PETM, a rapid rebound in body size occurred (Secord et al. 2012). Another study found that the wood rat (*Neotoma cinerea*) decreased in size, based on fecal pellet size, with warming during the deglaciation after the LGM; furthermore, the wood rat increased in size during glacial conditions (Smith and Betancourt 1998, Smith and Betancourt 2006). To test whether or not climate affected the body size of horses and bison, I compare the changes in mammalian body size with stable carbon and oxygen isotope values, which are used as proxies for changes in local vegetation and temperature/aridity, respectively.

Bison Evolution

The phylogeny of North American bison is controversial because of multiple possible immigration events (McDonald 1981). The genus *Bison* arose in Eurasia and immigrated into North America during the late middle Pleistocene around 160,000 yr BP (Guthrie 1970, Bell et al. 2004). By the LGM, *Bison* split into two genetically distinct groups: a northern Beringian population and a southern population (Shapiro et al. 2004). The southern population is hypothesized to comprise a single continuous population that displayed different morphologies temporally and spatially (Hill et. al., 2008). This

evolutionary bison lineage ranges from the large, late Pleistocene *Bison antiquus* to the small, modern *B. bison* (McDonald 1981). The first occurrence of *B. antiquus* is not well resolved; however, the oldest well constrained occurrence appears to be from New Mexico ~60,000 yr BP (Drakos et al. 2007). Bison decreased in size from 12,000 yr BP to ~5,000 yr BP based on horn core, metapodial, humeral, and calcanei lengths with the periods of most rapid decline occurring at 12,000 yr BP and 8,000 yr BP (McDonald 1981, Hill et al. 2008). During this transition the intermediate form between *B. antiquus* and *B. bison* is identified as *B. occidentalis* or *B. antiquus occidentalis*, which is thought to have first occurred between 10,500 yr BP and 9,000 yr BP based morphology and mitochondrial DNA of radiocarbon dated fossils (McDonald 1981, Wilson et al. 2008). *B. bison* is identified from fossil localities younger than 5,000 yr BP in the northern Great Plains and 8,000 yr BP in the southern Great Plains (Lewis et al. 2007). The two modern subspecies of *Bison bison* are *B. b. bison* and *B. b. athabasca* (McDonald 1981). *Bison b. athabasca* historically lived in forested areas north of the plains and is slightly larger than *B. b. bison* (McDonald 1981). *B. b. bison* is better adapted to grasslands and is the smallest subspecies of bison (McDonald 1981). These different subspecies follow Bergmann's Rule in that the more northern *B. b. athabasca* is larger than the southern *B. b. bison*, which suggests that these animals may react to climate changes with a change in body size (Raymond and Prothero 2011).

METHODS

Sampling, Pretreatment, and Isotope Analysis

Tooth enamel was bulk sampled from 54 bison, 14 mammoth, 52 equid, and 14 camel specimens for a total of 134 samples from 20 localities. Approximately six specimens per taxon per locality were sampled. If six specimens were not present at a locality, all of the individuals of that taxon were sampled. Samples were taken along the entire length of the tooth from the crown apex to the cervical margin in order to average seasonal fluctuation in isotopes during tooth formation. Soft decalcified enamel was avoided because it may contain diagenetically altered carbonate, and only hard enamel was sampled.

Third molars were preferentially sampled because they form after weaning in most mammals and are easy to distinguish from other tooth positions. Modern equid third molars erupt 3.5 years after birth and are the last tooth to begin mineralization at approximately 21 months (Hoppe et al. 2004). Bison third molars begin to form at about 10 months, which occurs after weaning (Green et al. 1993), and they erupt 3 years after birth (Gadbury et al. 2000). In the extant genus *Camelus*, which is a close relative of *Camelops* based on morphology and genetics, third molars erupt at 5 years after birth (Silver 1969, Humpala et al. 2007). Mammoths do not erupt all of their teeth early in ontogeny like other mammals but rather have only one functional cheek tooth in each quadrant at a time (Roth and Shoshani 1988). I sampled both second and third molars from mammoths for this reason. The second and third molars erupt at about 13 and 34

years in the closely related Indian elephant, *Elephas maximus*, respectively, well after the weaning period (Roth and Shoshani 1988).

Enamel was removed from the tooth using a diamond burr attached to a variable speed mounted dental drill in order to obtain 4-6 mg of enamel per specimen. Powdered enamel samples were pretreated following the method of Koch et al. (1997) except that samples were dried using a drying oven instead of being lyophilized. For the elimination of organic matter, >0.04 ml/mg of 2-3% reagent grade sodium hypochlorite was added. After 24 hours, the samples were rinsed by adding deionized water to each microcentrifuge tube with a plastic syringe. Samples were vibrated using a Vortex Genie until all the material was suspended. The samples were spun in a centrifuge at 10,000 rpm for 5 minutes. After centrifuging, water was removed from the samples with a different plastic syringe, and the rinsing process was repeated 5 times. Upon completion of the final rinse, samples were placed uncapped in a drying oven overnight to remove any excess water. The next day, an excess of 0.04 ml/mg sample of a 1 M acetic acid buffered solution was added and allowed to react for 24 hours. Each rinse process was repeated 5 times, and samples were placed in a drying oven at 60°C after the last rinse. These were then shipped to the University of Michigan Stable Isotope Laboratory (UMSIL) for measurement of isotope ratios.

Isotopes were measured at UMSIL using a Finnigan MAT 251 triple-collector gas source mass spectrometer coupled to a Finnigan Kiel automated preparation device.

Isotope values are reported in standard δ - notation in parts per thousand (‰): $X =$

$([R_{\text{sample}}/R_{\text{standard}}]-1) \times 10^3$. $\delta^{13}\text{C}$ values are reported relative to the Vienna PeeDee

Belemnite International Standard (vPDB), and $\delta^{18}\text{O}$ values relative to the Vienna

Standard Mean Ocean Water (vSMOW). For every eight samples, two internal lab enamel standards were measured: LOX and MES. LOX was made from modern *Loxodonta africana*, courtesy of David L. Fox at the University of Minnesota, and MES was made from enamel fragments of a mammoth from New Mexico. The mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for the LOX standard were $-5.6 \pm 0.16\text{‰}$ and $32.0 \pm 0.04\text{‰}$ respectively, and the mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for the MES standard were $-9.6 \pm 0.06\text{‰}$ and $23.2 \pm 0.34\text{‰}$ respectively; error for standards is 2 standard deviations (SD). All additional error reported in this paper for stable isotopes is 1.96 standard errors (95% confidence of mean) unless stated otherwise.

Interpretation of $\delta^{13}\text{C}$

The maximum $\delta^{13}\text{C}$ value of tooth enamel for a diet of water stressed C_3 vegetation was estimated to be -8.4‰ and a pure C_4 grass diet was calculated to be 3.5‰ . This number was calculated based on the method developed in Kita et al. (2014), using an enrichment factor of $14.1 \pm 0.5\text{‰}$ (Cerling and Harris 1999) and an atmospheric offset of $+1.0\text{‰}$ for the late Pleistocene and early Holocene, based on Tipple et al. (2010). The burning of hydrocarbons such as coal associated with the industrial revolution lowered atmospheric $\delta^{13}\text{C}$ by $\sim 1.5\text{‰}$ making the late 20th Century value $\sim -7.8\text{‰}$ compared to Pleistocene $\delta^{13}\text{C}$ values of $\sim -6.9\text{‰}$ inferred from benthic foraminifera (Friedli et al. 1986, Francey et al. 1999, Tipple et al. 2010). Since modern plant values are affected by the lower atmospheric $\delta^{13}\text{C}$, an atmospheric correction needs to be applied when interpreting past stable carbon isotopes.

Percent C₄ in mammalian diet was calculated using the formula in Koch et al. (1998): $\delta^{13}\text{C}_{\text{apatite}} = (\delta^{13}\text{C}_{\text{pure C4 feeder}})(X) + (\delta^{13}\text{C}_{\text{pure C3 feeder}})(1-X)$ where X is the percent C₄ vegetation consumed. The values for a pure C₄ feeder and pure C₃ feeder were obtained by using C₄ and C₃ values of modern plants reported by Passey et al. (2002), mammalian enrichment factor of 14.1‰ from Cerling and Harris (1999), and an atmospheric correction from Tipple et al. (2010) discussed above.

Determination of Body size

As a proxy for body mass, lower first molar occlusal crown area (length x maximum width, Fig. 3) for both bison and equids was used, and measurements and dimensional ratios from equid metacarpals such as metacarpal length and metacarpal width (Fig. 3) were used. Lower first molar area is strongly correlated with body size among extant ungulates (Janis 1990). Additionally, mean body size and molar occlusal area are correlated in both sexes of *Bison bison* (McDonald 1981). Metacarpal length and width measurements were taken according to Eisenmann (1979) (Fig. 3). Since limb bones are subjected to strain associated with locomotion, they need to be robust enough to support the body mass of the animal, especially in large ungulates, creating a strong relationship between body mass and limb dimensions (Scott 1990). From the nine modern bison sampled one m1 was not measured for a body size proxy (specimen number C50) because the m1 was too damaged to accurately measure occlusal area.

Identification of Bison species

Species in the evolutionary lineage of *Bison antiquus* to *B. occidentalis* to *B. bison* are usually distinguished by size. Generally, *B. antiquus* has been reported only

from localities older than 5,000 yr BP in the northern Great Plains (Lewis et al. 2007). McDonald (1981) created a set of cranial measurements that may be used to identify *Bison* species. Since the Red Willow specimens were found in gravel pits, the skulls are broken and disarticulated making traditional cranial measurements difficult. For identification in this study, the natural log of the lower third molar (M/3) occlusal area was used (Fig. 4). A sample of wild *Bison bison bison* from a kill site in Highwood Montana were used as a standard for modern body size. These modern bison from Montana have a mean $\text{Ln}(\text{M/3 Area})$ of 6.5 ± 0.11 (SD)(Table 2), and bison from Red Willow that were greater than 3 SD above the mean were identified as *B. antiquus*. The majority of the specimens in the Red Willow fauna are within three SD of the mean, but five are above this range: UNSM 49806, 49236, 49237, 49238, 132521.

RESULTS

Descriptive statistics such as mean, median, range, standard error, and standard deviation for the various taxa sampled are reported in Table 3. Stable carbon isotope values from the Irvingtonian faunas range from -11.0‰ to -3.6‰ (Table 3), and stable oxygen isotopes ($\delta^{18}\text{O}$) range from 20.1‰ to 25.3‰ (Table 3). The Red Willow fauna, which is Rancholabrean to Holocene in age, ranges in $\delta^{13}\text{C}$ values from -11.1‰ to 3.7‰ and in $\delta^{18}\text{O}$ values from 20.8‰ to 32.2‰. The mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values between the Irvingtonian and Rancholabrean isotopes are significantly different from one another using a standard T-test ($\delta^{13}\text{C}$ $p < 0.001$, $\delta^{18}\text{O}$ $p < 0.001$). Modern bison from Nebraska have $\delta^{13}\text{C}$ values ranging from -6.2‰ to 1.8‰ with a mean value of $-3.1 \pm 1.92\text{‰}$ ($n=9$), and $\delta^{18}\text{O}$ values range from 20.3‰ to 27.2‰ with a mean of $23.1\text{‰} \pm 1.60\text{‰}$ ($n=9$).

Irvingtonian localities

The mean $\delta^{13}\text{C}$ values for late Irvingtonian horses from the Sheridan County localities range from -8.9‰ (13% C_4) to -6.4‰ (30% C_4)(Fig. 6). Mean $\delta^{13}\text{C}$ values of equids from No-104 ($-9.3 \pm 0.94\text{‰}$)(10% C_4)($n=6$) are significantly more negative than those from Fr-104 ($p=0.036$), Sh-3 ($p=0.013$), and Sh-5 ($p<0.001$; T-test) (Table 3, Fig. 6). The Fr-104 mean $\delta^{13}\text{C}$ value ($-6.3 \pm 2.72\text{‰}$)(31% C_4)($n=3$) is significantly more positive than No-104 ($p=0.036$), Sh-1 ($p=0.036$), and Sh-2 ($p=0.045$) (Table 3, Fig. 6). In No-104, mammoths have similar mean $\delta^{13}\text{C}$ values ($-9.5\text{‰} \pm 0.64\text{‰}$; $n=2$) to equids (-9.3 ± 0.94 ; $n=6$). However, the site contained only two mammoth molars, so the sample size is very small. Mammoths from Sheridan County range from -9.5‰ (8% C_4) in Sh-5 to -4.9‰ (41% C_4) in Sh-1. *Camelops* sp. from locality Sh-1 exhibits a wide range of $\delta^{13}\text{C}$ values from -8.5‰ (15% C_4) to -3.9‰ (48% C_4)(Table 3). Two out of the six samples have elevated $\delta^{13}\text{C}$ values of -3.9‰ (48% C_4) and -4.8‰ (42% C_4)(Fig. 5). These teeth are a different color (dull gray) than other teeth from this site (white), so they may sample another time interval. However, the enamel was hard, so it was most likely not decalcified. Other camels from Sheridan County had $\delta^{13}\text{C}$ values ranging from -8.9‰ to -7.8‰ (Fig. 5). There is a significant correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for equids from the Sheridan County localities ($r^2=0.41$, $p<0.001$, $n=33$)(Fig. 5).

Rancholabrean/Holocene localities

$\delta^{13}\text{C}$ isotope values in the Red Willow fauna range from -11.1‰ to 3.7‰ (0% and 100% C_4 grass respectively). The large range is due to bison. The *Bison* spp. mean value is $0.5\text{‰} \pm 0.66\text{‰}$ (79% C_4)($n=40$) with the majority of the $\delta^{13}\text{C}$ values falling between -

1.6‰ and 3.7‰ (Fig. 7). The mean values of modern bison ($-3.1 \pm 1.92\text{‰}$, $n=9$)(54% C_4) are significantly more negative ($p<0.001$) than those of the Red Willow bison. Other taxa sampled within the Red Willow fauna do not show strong positive values like those of the bison. The mean $\delta^{13}\text{C}$ values for *Mammuthus* sp. and *Equus* sp. are $-8.5 \pm 1.46\text{‰}$ (-8.5% C_4)($n=7$) and $-8.3 \pm 0.50\text{‰}$ (17% C_4)($n=10$), respectively. Maximum values are -6.3‰ (31% C_4) and -7.4‰ (23% C_4), respectively.

The mean $\delta^{18}\text{O}$ value of bison from the Red Willow fauna is $26.4 \pm 0.96\text{‰}$ ($n=40$), and the $\delta^{18}\text{O}$ values range from 21.2‰ to 32.2‰ (Fig. 8). Modern bison $\delta^{18}\text{O}$ values fall within the range of the Red Willow bison, but the $\delta^{18}\text{O}$ mean value ($23.1 \pm 1.60\text{‰}$, $n=9$) is significantly lower in the Red Willow bison ($p<0.01$). Mammoth and equid $\delta^{18}\text{O}$ mean values are also lower than in the Red Willow bison with mean $\delta^{18}\text{O}$ values of $22.7 \pm 1.12\text{‰}$ ($n=6$) and $22.5 \pm 0.48\text{‰}$ ($n=10$) respectively.

Body Size

There is a strong, significant correlation between mean equid metacarpal lengths from the various Sheridan localities and mean $\delta^{13}\text{C}$ values for teeth from each locality ($r^2=0.83$, $p=0.011$, $n=6$) (Fig. 9). However, metacarpal length is not significantly correlated with $\delta^{18}\text{O}$ ($r^2=0.40$, $p=0.179$, $n=6$). There is no significant relation between metacarpal width and either $\delta^{13}\text{C}$ ($r^2=0.44$, $p=0.152$, $n=6$) or $\delta^{18}\text{O}$ ($r^2=0.57$, $p=0.082$, $n=6$), nor is there a significant relationship between first molar occlusal area and $\delta^{13}\text{C}$ ($r^2<0.01$, $p=0.926$, $n=6$) or $\delta^{18}\text{O}$ ($r^2=0.45$, $p=0.148$, $n=6$).

Lower first molar (m1) occlusal areas in bison from the Red Willow localities were measured from the same jaws from which the lower third molars were sampled for

stable isotopes. Thus, individual body size and stable isotopes may be directly compared to one another. The m1 occlusal area for bison ranged from 328 mm² to 575 mm² with a mean of 408 \pm 15.40 mm² (n=39). There is a weak but statistically significant negative relationship between molar occlusal area and $\delta^{13}\text{C}$ values ($r^2=0.20$, $p=0.004$, $n=39$) (Fig. 10). Molar occlusal area is not correlated with $\delta^{18}\text{O}$ values ($r^2<0.01$, $p=0.612$, $n=39$). Modern bison m1 occlusal areas ranged from 335 mm² to 485 mm² with a mean of 388 \pm 35.68 mm² (n=8).

DISCUSSION

Rancholabrean/Holocene faunas

The range of isotopes from all the Rancholabrean/Holocene localities suggests that the majority of the individuals within the faunas had a mixed C₃/C₄ diet. The Red Willow fauna has a much higher number of mixed C₃/C₄ feeders than the Irvingtonian faunas, indicating a greater abundance of C₄ grasses in the latest Rancholabrean and/or Holocene. These sites span from the LGM to the Pleistocene-Holocene transition (33,000 -10,600 radiocarbon years) based on mammoth ¹⁴C dates (Enk 2014) (Fig. 2). However, the presence of *Bison bison* indicates that this site extends into the Holocene based on the known geologic range of this species, which is restricted to the Holocene. Mitochondrial DNA combined with carbon-14 dates suggests that *B. bison* first appeared in the northern Great Plains ~5,000 yr BP (Lewis et al. 2007). Bison from the Red Willow fauna have high $\delta^{13}\text{C}$ values (0.3 \pm 0.62‰) indicating a C₄ dominated diet for most of the individuals (Fig. 7). These carbon isotope values suggest that these bison were living in a C₄ dominated grassland. Modern bison living in Nebraska have

significantly lower $\delta^{13}\text{C}$ values ($-3.1 \pm 1.92\text{‰}$, $p < 0.001$) than the Red Willow bison, which is in accord with modern amounts of C_4 present in Nebraska (Teeri and Stowe 1976). Furthermore, elevated $\delta^{13}\text{C}$ values of Red Willow bison suggest that these bison lived during a period of higher temperatures and/or aridity than modern bison, which may indicate that they lived during the Holocene thermal maximum.

Climate during the Holocene thermal maximum, 9,000 – 5,000 yr BP, was warm and arid (Renssen et al. 2009). Dunes in the Sand Hills region of Nebraska were mobilized indicating an extremely arid environment (Loope and Swinehart 2000, Miao et al. 2005). $\delta^{13}\text{C}$ values of soil carbonates from sediments dated with optically stimulated luminescence (OSL) suggest that C_4 communities greatly expanded just prior to the arid conditions of the thermal maximum at about 9,000 yr BP (Feggestad et al. 2004). Although C_4 grasses do not thrive during droughts (Fawcett et al. 2011), precipitation was variable enough to allow for the survival of drought intolerant ragweed (*Ambrosia*), and a pollen record demonstrates a xeric grassland community during the middle Holocene ~6,000 yr BP, which should favor C_4 grasses (Grimm et al. 2011, Schmeider et al. 2013). Another pollen record from a lake in northern Nebraska contains more grass than herbaceous pollen during an arid period at ~5,000 yr BP (Schmeider et al. 2013). The warm and arid conditions should be conducive to a northern range expansion of C_4 grasses.

It is unlikely that the shift in $\delta^{13}\text{C}$ isotopes of modern bison relative to those of the Red Willow fauna indicated a change in diet from grazing to browsing because *Bison bison* are considered to be hypergrazers; modern plains bison actively avoid forbs and other herbaceous plants (Knapp et al. 1999, Fortin et al. 2003). Dental wear patterns

(mesowear) in both wood bison (*B. bison athabasca*) and *B. antiquus* from Big Bone Lick in Kentucky, however, suggest diets with >70% browse (Widga, 2006). *B. antiquus* from the central Great Plains consumed grasses like modern *B. bison*, as evidenced by carbon isotopes (Gadbury et al. 2000). Additionally, it is unlikely that bison would selectively feed solely on C₄ grasses over C₃ grasses because $\delta^{13}\text{C}$ from modern bison suggest a diet of ~54% C₄ vegetation. Gadbury et al. (2000) found that bison from the Hudson-Meng bonebed, dated to 9,500 ¹⁴C yr BP, had a mean enamel $\delta^{13}\text{C}$ value (-5.2 ± 0.26‰; n = 5), which was ~5‰ higher than one modern bison from the area (-10.7‰). They concluded that this indicated an arid, water-stressed environment. However, meaningful comparisons can't be made without a larger sample size. Additionally, the modern bison used by Gadbury et al. (2000) had its forage supplemented with hay during winter months.

Alternatively, Red Willow bison may have also migrated from warmer southerly C₄ grasslands; however this would require the bison to have lived in C₄ dominated habitats during the entire formation of the third molar (~1 year). Using ⁸⁷Sr/⁸⁶Sr isotopes, Widga et al. (2010) found no evidence for long distance seasonal migrations in bison from western Iowa and eastern Nebraska from localities dated between 8,930 and 6,980 cal. yr BP. Serial ⁸⁷Sr/⁸⁶Sr lack a seasonal pattern suggesting that these bison remained in the same relative area throughout the year (<50 km). Although, over the entire length of a tooth series (~4-5 years) several individuals show a much greater range of ⁸⁷Sr/⁸⁶Sr values suggesting that the herd moved a large distance (~500 km) but still did not migrate with the seasons (Widga et al. 2010). Widga et al. (2010) also sampled enamel carbonate for stable carbon and oxygen from bison in western Iowa and eastern Nebraska (mean

$\delta^{13}\text{C}$ $-3.5 \pm 1.24\text{‰}$, $n=16$) from localities dated between 8,930 and 6,980 cal. yr BP. They determined that C_4 composition in the tallgrass prairie was similar to modern composition, though some of their values do support a C_4 dominated grassland.

The $\delta^{18}\text{O}$ values of bison from the Red Willow fauna are more elevated than those of both the modern bison and other grazing taxa from the fauna (Fig. 8). The mean Red Willow bison $\delta^{18}\text{O}$ value ($26.2 \pm 0.88\text{‰}$) is 3.1‰ significantly higher ($p=0.005$) than modern bison ($23.1 \pm 1.60\text{‰}$). However, the modern bison from this study probably obtained much of their water from the Platte River watershed ($-9.1 \pm 0.66\text{‰}$), while Red Willow bison would have obtained their water from the Republican River watershed ($-6.8 \pm 0.98\text{‰}$). Since the Republican River is more positive ($\sim 2.3\text{‰}$) than the Platte River, the differences in $\delta^{18}\text{O}$ values between these bison are probably not meaningful.

Both modern bison and bison from the Red Willow fauna have higher $\delta^{13}\text{C}$ values than either Red Willow equids or mammoths ($-8.3 \pm 0.5\text{‰}$, $-8.5 \pm 1.46\text{‰}$ respectively). The mammoths and equids represent late Pleistocene conditions and the higher values in the younger bison indicate that C_4 grasses increased their range during warmer periods of the Holocene. This is opposite of what is expected if CO_2 concentrations were controlling C_4 distribution because CO_2 increased after the LGM (Luthi et al. 2008), so it appears that temperature was the primary influence on C_4 distribution in Nebraska during the Pleistocene. A previous hypothesis predicted an expansion of C_4 grasses during colder climates with low CO_2 atmospheric concentrations, which is not what is observed in the Red Willow fauna (Cerling et al. 1997, Collatz et al. 1998). The mean $\delta^{13}\text{C}$ value (0.5‰) of *B. bison* from this fauna suggests a diet of 79% C_4 compared to the 54% C_4 diet present of modern Nebraskan bison. Furthermore, the $\delta^{13}\text{C}$ values of radiocarbon dated

Mammuthus from this fauna indicate a diet of <35% C₄ vegetation. This demonstrates that as temperature increased in the Holocene, C₄ vegetation increased in abundance suggesting that temperature was the controlling factors in C₄ distribution in Nebraska.

Irvingtonian faunas

The majority of the $\delta^{13}\text{C}$ values from the Irvingtonian sites indicate that most individuals of *Equus*, *Camelops*, and *Mammuthus* were consuming a mix of C₃ and C₄ vegetation (Fig. 5), although many individuals consumed a pure, or nearly pure C₃ diet, including both mammoth samples from No-104 (Fig 5). The significant relationship between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in equids from Sheridan County suggests that as temperature increased C₄ grasses expanded northward, similar to trends interpreted in the Red Willow fauna (Fig. 5). C₄ grasses have higher $\delta^{18}\text{O}$ values than C₃ grasses, which could indicate that $\delta^{18}\text{O}$ is tracking the change in diet between C₃ and C₄ consumption and not warmer climates (Helliker and Ehleringer 2000). However, the range seen in the equid $\delta^{18}\text{O}$ values (20.2‰ – 25.2‰) is too great to be explained solely by the difference between C₃ and C₄ grasses. The Albert Ahrens (No-104) glacial locality and the Fr-104 interglacial locality do not fall on the correlation line of the Sheridan localities. Albert Ahrens and Fr-104 have similar mean $\delta^{18}\text{O}$ values ($23.1 \pm 0.40\text{‰}$ and $22.9 \pm 1.00\text{‰}$ respectively). Differences in $\delta^{18}\text{O}$ values between these sites and the Sheridan County sites may be partly explained by the differences between the Republican River and Niobrara River watersheds (Fig. 1). There is approximately a 3.3‰ positive difference in $\delta^{18}\text{O}$ values between the Niobrara River ($-10.1 \pm 0.60\text{‰}$) and the Republican River ($-6.8 \pm 0.98\text{‰}$) (Coplen and Kendall 2000), which originate in different areas in the Rocky Mountains of Wyoming and Colorado.

Furthermore, the mean $\delta^{13}\text{C}$ value of all taxa from the Albert Ahrens glacial ($-9.3 \pm 0.70\text{‰}$) locality is significantly lower ($p=0.013$) than that of Fr-104 interglacial ($-6.3 \pm 2.72\text{‰}$). Also, the mean $\delta^{13}\text{C}$ values of Sh-3, and Sh-5, and Fr-104 are significantly more positive than Albert Ahrens, Sh-1, and Sh-2. This demonstrates that the Sheridan localities may be a mix of warm and cool intervals with the warmer localities (Sh-3: 30% C_4 , Sh-5: 29% C_4) having greater amounts of C_4 grasses than the cooler localities (Sh-1: 14% C_4 , Sh-2: 13% C_4). DeSantis et al. (2009) found a similar pattern in glacial and interglacial $\delta^{13}\text{C}$ values in Florida. Mammalian herbivores in the interglacial locality were consuming a mixed C_3/C_4 vegetation, while herbivores at the glacial locality consumed primarily C_3 vegetation (DeSantis et al. 2009).

Based on modern observations, stable carbon isotopes, and mesowear, equids consume a wide variety of plants and may change their diet seasonally alternating between grasses, forbs, shrubs, and tree leaves (MacFadden et al. 1999, Feranec 2004, Hoppe et al. 2004, Kaiser and Franz-Odenaal 2004, Koch et al. 2004, Feranec et al. 2009, Mithlbackler et al. 2011, Kita et al. 2014). Although it is possible that horses switched their diets seasonally from C_4 grasses to C_3 plants, $\delta^{13}\text{C}$ values from other known grazers (*Mammuthus*, *Camelops*) in the Sheridan localities and Albert Ahrens are also indicative of diets high in C_3 vegetation. Moreover, based on plant macrofossils and pollen data, habitats in the central Great Plains, including Nebraska and Kansas, were relatively open during glacial periods (Baker et al. 2009). Plant macrofossils indicate a treeless prairie at ~50,000 yr BP (Baker et al. 2009). At 29,000 yr BP an open parkland is apparent due to the presence of poplar, spruce, and birch macrofossils and pollen, and near the LGM there is evidence of a spruce forest, but this only occurred in eastern

Nebraska and Kansas (Baker et al. 2009). After the deglaciation following the LGM, spruce forests moved northward creating an open grassland (Schmeider et al. 2013).

Mammoth $\delta^{13}\text{C}$ values ($-9.5 \pm 0.64\text{‰}$)(8% C_4) in the Albert Ahrens glacial site (No-104, Fig. 6) suggest that C_4 grasses were absent or in low abundance during this cold interval, at about 0.602 Ma, although only two teeth were sampled. On the basis of isotopic studies, microwear, vegetation in mammoth feces, and gut contents of preserved *Mammuthus primigenius*, mammoths are considered hypergrazers with their diet consisting of >70% grasses and sedges (Koch et al. 1998, Cerling et al. 1999, van Geel et al. 2008, Rivals et al. 2010, van Geel et al. 2011), which means they consumed almost exclusively grasses. These animals are an excellent indicator of grassland composition.

Stable carbon isotope values from the Sheridan localities indicate that *Camelops* sp. was consuming a largely C_3 diet while horses at the same locality were incorporating more C_4 into their diet (Fig. 5). *Camelops* is usually considered a mixed feeder consuming both browse and grass based on premaxilla morphology and preserved vegetation in teeth (Akersten et al. 1988, Dompierre and Churcher 1996). Nevertheless, a mesowear study of *Camelops* from Hay Springs (Sh-1, Sh-2) suggests that it was grazing, whereas a microwear study indicates that it was a browser (Semperebon and Rivals 2010). Two camelid teeth from Sh-1 have high $\delta^{13}\text{C}$ values in the C_4 range (Fig. 5). These teeth, although, retaining hard and apparently non-decalcified enamel, differ markedly in color from other *Camelops* sp. teeth derived from the quarry, suggesting that they were collected from a lithologically different bed, deposited during different climatic conditions, or were diagenetically altered.

Body size change

Bergmann's Rule predicts that mammals will reduce their size under warm conditions and increase their size under cold conditions. Climate may affect body size through genetic change or ecophenotypic change (Barnosky et al. 2003, Millien et al. 2006, Caruso et al. 2014). Molar occlusal area is less prone to ecophenotypic changes because molars do not play a direct role in body support (Janis 1990). In contrast, limb measurements are often adapted to environmental conditions and record ecophenotypic changes (van Asperen 2010).

Red Willow bison show a trend that is expected based on previous studies, with respect to warming climate and C₄ expansion after the LGM (Hill et al. 2008, Lewis et al. 2010). First molar occlusal area decreased as C₄ consumption increased (Fig. 10). C₄ plants are less nutritious than C₃ plants, but the difference between nutrition does not adequately explain the observed magnitude of body size reduction (Barbehenn et al. 2004). Furthermore, since molar occlusal area is less prone to ecophenotypic changes, this body size proxy may not be susceptible to nutritional stress (Janis 1990). Nutritional differences between C₃ and C₄ plants occur seasonally. Most C₃ grasses will sprout twice a year in the spring and fall (Hill et al. 2008). In contrast, C₄ grasses only sprout during the summer. If an environment is dominated by C₄ grasses, there will be a great amount of forage during the summer, but a lack of proper forage during the spring and fall, so a pure C₄ grassland will provide less nutrition over the entire year than a mixed C₃/C₄ grassland, which has nutrient rich forage available during the spring, summer, and fall. The elevated $\delta^{13}\text{C}$ of bison from Red Willow suggest that this is a stressed environment.

The relationship between body size and $\delta^{13}\text{C}$ in bison at Red Willow is a much weaker one than in the late Irvingtonian equids. However, the significant relationship between $\delta^{13}\text{C}$ and first molar occlusal area suggests that climate played a role in bison body size in the Holocene. The stressed environment of the Holocene thermal maximum may have favored smaller body size explaining the trend between $\delta^{13}\text{C}$ and first molar occlusal area due to increased temperature and aridity. The median body size for bison was lowest at 6,000 yr BP around the thermal maximum; after this time median body size slowly increased to the modern median (Hill et al. 2008). Since the relationship between $\delta^{13}\text{C}$ and body size is weak, other factors are undoubtedly influencing the size in Holocene bison. In addition to elevated temperatures and aridity of the Holocene thermal maximum, human hunting may have contributed to selection of a small body size. Humans first immigrated into North America around 12,000 yr BP, and there is ample evidence of human predation on bison since their immigration (Guthrie 2006, Kenady et al. 2011, Driver and Maxwell 2013). By hunting the largest individuals, traits leading to large body size may not be inherited leading to an overall decrease in body size (Coltman et al. 2003, Crosmarby et al. 2013, Festa-Bianchet et al. 2014).

My results clearly indicate a northward expansion of grasslands during the Holocene climatic warming. Therefore, percent C_4 in the teeth of grazers serves as a proxy for warmer and/or drier climates at this latitude in the Great Plains. This strongly suggests that the significant correlation between $\delta^{13}\text{C}$ values and equid metacarpal length observed in the Sheridan County equids (Fig. 9) was the result of body size increase during warm intervals in the late Irvingtonian. However, the lack of significant correlations between first molar occlusal area, and $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in Sheridan

County equids suggests that equid body size change was not genetically fixed but rather was an ecophenotypic response. This change, however, is the opposite of that predicted from Bergmann's Rule. These equids increased in body size as climate warmed, precipitation increased, and C₄ grassland expanded northward. I hypothesize that the mixed C₃/C₄ grasslands provided a greater level of primary productivity for the equids. When faced with dietary stress, animals may reduce their body size, expressing a different phenotype based on environmental parameters as evidenced by modern populations of white tail deer (*Odocoileus virginiana*) (Metcalf and Monaghan 2001, Barr 2012). A single genotype may produce different phenotypes, and environmental pressures may favor the expression of one phenotype over another allowing for a plastic response to the environment over a genetic change (Metcalf and Monaghan 2001, Herfindal et al. 2014). An ecophenotypic decrease in body size may not affect molar occlusal area, but metacarpal length should decrease. The mixed C₃/C₄ grasslands of warm periods, coupled with increased precipitation, would have provided greater primary productivity and allowed equids to reach their maximum body size.

Allen's rule states that animals under cold climates reduce their extremities (e.g. limbs and ears) to reduce heat loss (Tilkens et al. 2007), as noted above. Animals can increase their body mass with decreased temperatures in accord with Bergmann's Rule as well as decrease the size of their limbs in accord with Allen's Rule. This scenario would result in stockier more robust limbs to support the increased body size (van Apseren 2010). To test this, I used metacarpal width as a proxy for robustness but width was not significantly correlated with either $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$. Thus, Sheridan equids do not seem to

be following Allen's Rule or Bergmann's Rule, suggesting that they were not altering their body size in direct response to temperature.

CONCLUSIONS

Results of this study strongly suggest that temperature change and C₄ grass distribution in Nebraska were closely linked during the Quaternary. As temperature increased, C₄ grasses extended their range northward. Carbon isotope values from the interglacial Fr-104, glacial Albert Ahrens, and Red Willow fauna support this finding. This implies that temperature exerted a stronger control on the distribution of C₄ vegetation during the Quaternary than did atmospheric CO₂ concentrations. Body size change in equids from Sheridan County suggests an ecophenotypic response to changing grassland composition and primary productivity. As a C₃ dominated biome in Nebraska during the Irvingtonian changed to a mixed C₃/C₄ biome, the biomass of available food resources increased allowing equids to increase in body size. These interpretations can be broadly applied to the entire Great Plains region.

Although mammoths and equids in the Red Willow fauna range from 33,000 to 10,000 radiocarbon yr BP, bison from this fauna appear to sample a younger time interval during the Holocene. Carbon isotopes of bison from the Red Willow fauna indicate an environment composed of ~70% C₄ grasses compared to modern Nebraskan prairie of ~50% C₄ grasses. This suggests warmer conditions that may correspond with the Holocene thermal maximum. Implied water stress to vegetation, and possible heat stress to bison, at this time may have contributed to the bison diminution. A weak correlation between $\delta^{13}\text{C}$ and body size indicates that a C₄ dominated habitat may have diminished

primary productivity leading to the diminution, but human hunting pressures or other factors may have also played significant roles, but the testing of such hypotheses is beyond the scope of the present study. Results of this study indicate that body size responses to climate in the Quaternary can be difficult to predict and that mammals may not follow the simple pattern suggested by Bergmann's Rule.

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FIGURES AND TABLES

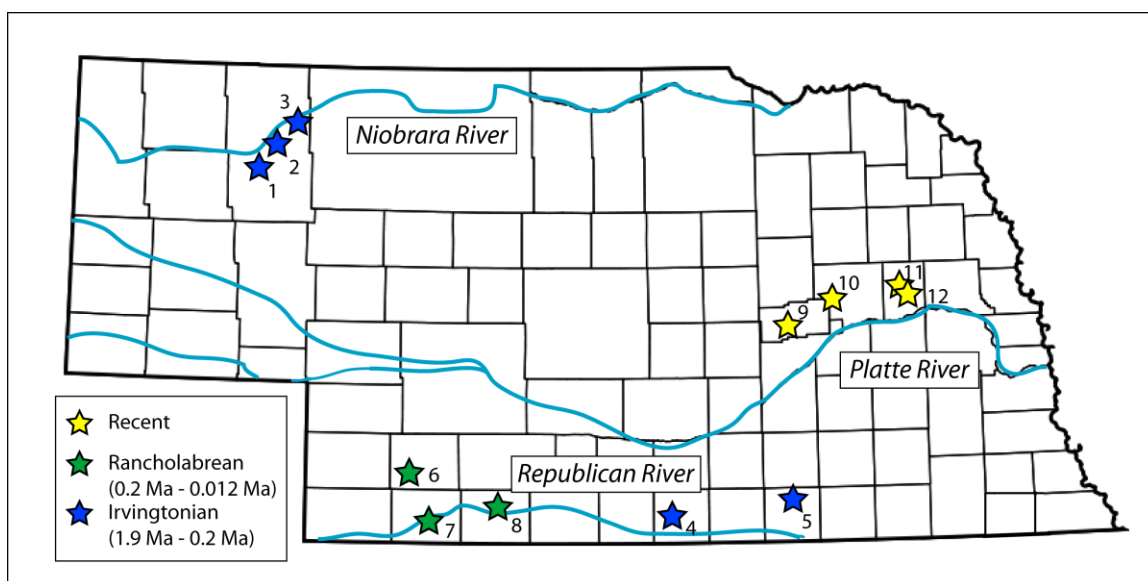


Figure 1. Map of Nebraska showing twenty localities used in this study (eight are too close to others to distinguish on map). 1, 2, and 3, Sheridan Co.; 4, Franklin Co.; 5, Nuckolls Co.; 6, Hayes Co.; 7, Hitchcock Co.; 8, Red Willow Co.; 9, Nance Co.; 10, Platte Co.; 11 and 12, Colfax Co.

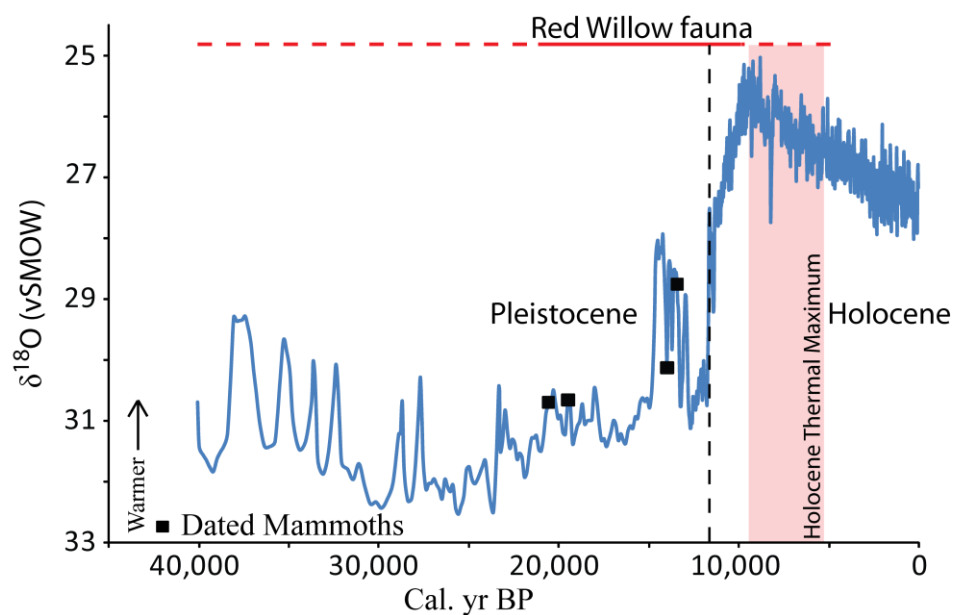


Figure 2. Oxygen isotope record from Renland Ice Core, Greenland (Vinther et al. 2008), showing inferred, relative temperature changes over last 40,000 cal. yr BP. Black squares correspond to radioisotopic dates (Enk, 2014) for mammoth teeth from the Red Willow

fauna (left to right, UNSM: 49826, 2022, 49736, 49414) that were sampled for stable isotopes in this study. Dashed horizontal line for Red Willow fauna represents hypothesized extent of *Bison* spp. into the Holocene and an older dated mammoth (UNSM 1811) with large error associated with it.

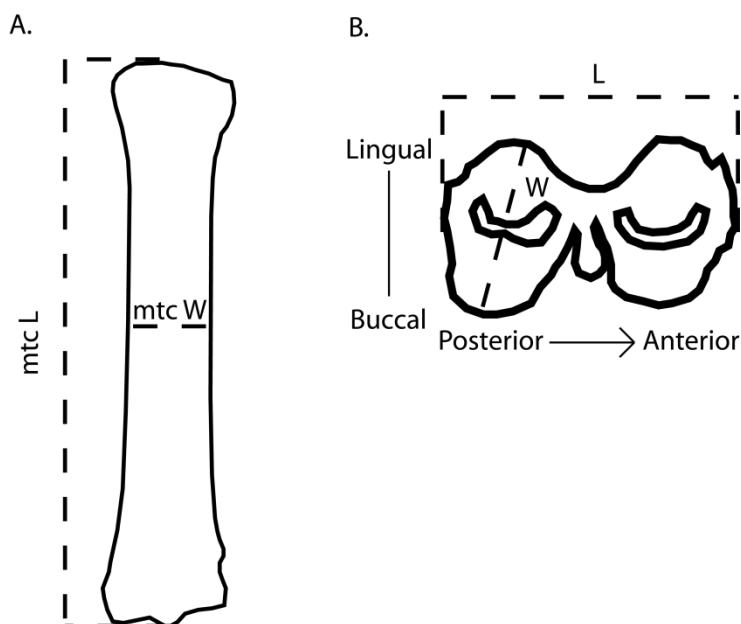


Figure 3. Landmarks used for metacarpal (A) and lower first molar (B) measurements. mtcL, length of the metacarpal; mtcW, width of the metacarpal; L, molar length; W, greatest molar width of the talonid basin.

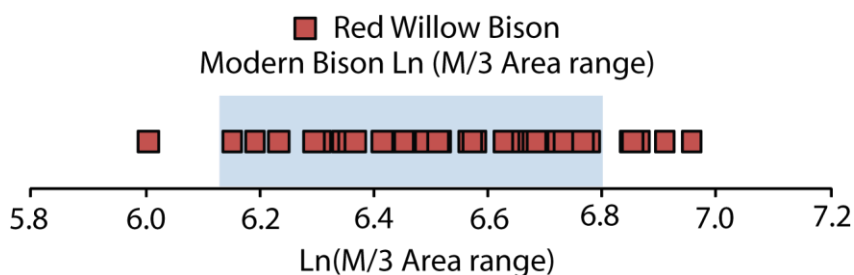


Figure 4. Ln (M/3 Area) of Red Willow bison. The blue box represents 3 standard deviations on either side of the mean for modern *Bison bison* Ln(M/3 Area). Five bison fall out of the modern range expected for *Bison bison*.

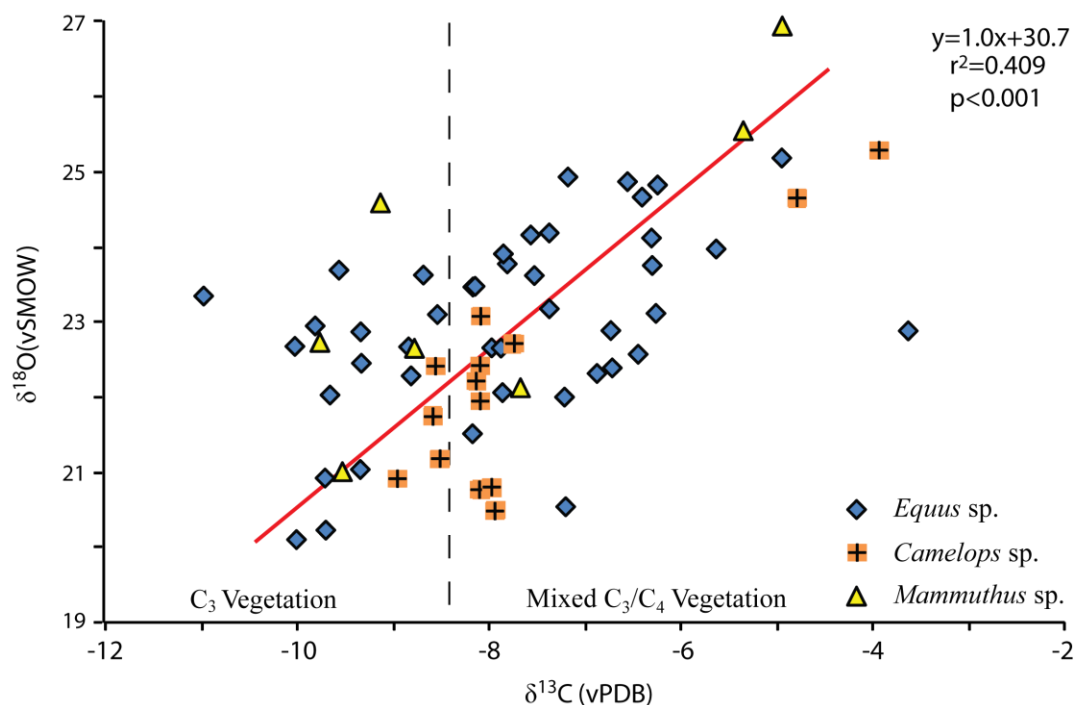


Figure 5. Carbon and oxygen stable isotope values from tooth enamel for various Irvingtonian taxa from all localities (No-104, Fr-104, and Sh-1 through Sh-6). Vertical dashed line (-8.4‰) shows approximate boundary between maximum water-stressed C_3 diet and mixed C_3/C_4 diet. Reduced major axis regression line is for Sheridan County (Sh-1 through Sh-6) equids only (Fig. 1).

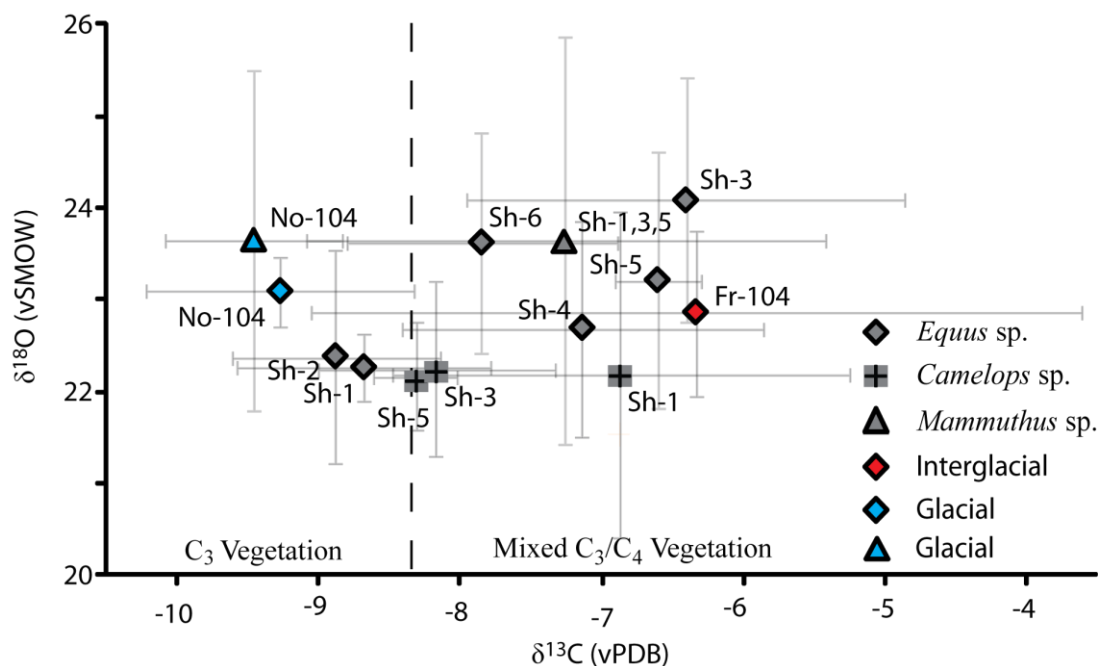


Figure 6. Mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for tooth enamel from Irvingtonian localities in Franklin (Fr), Nuckolls (No), and Sheridan (Sh) counties (see Fig. 1). Error bars show ± 2 standard error of mean. Sheridan County mammoth mean value is composite of mammoths from Sh-1, Sh-3, and Sh-5 due to low sample size.

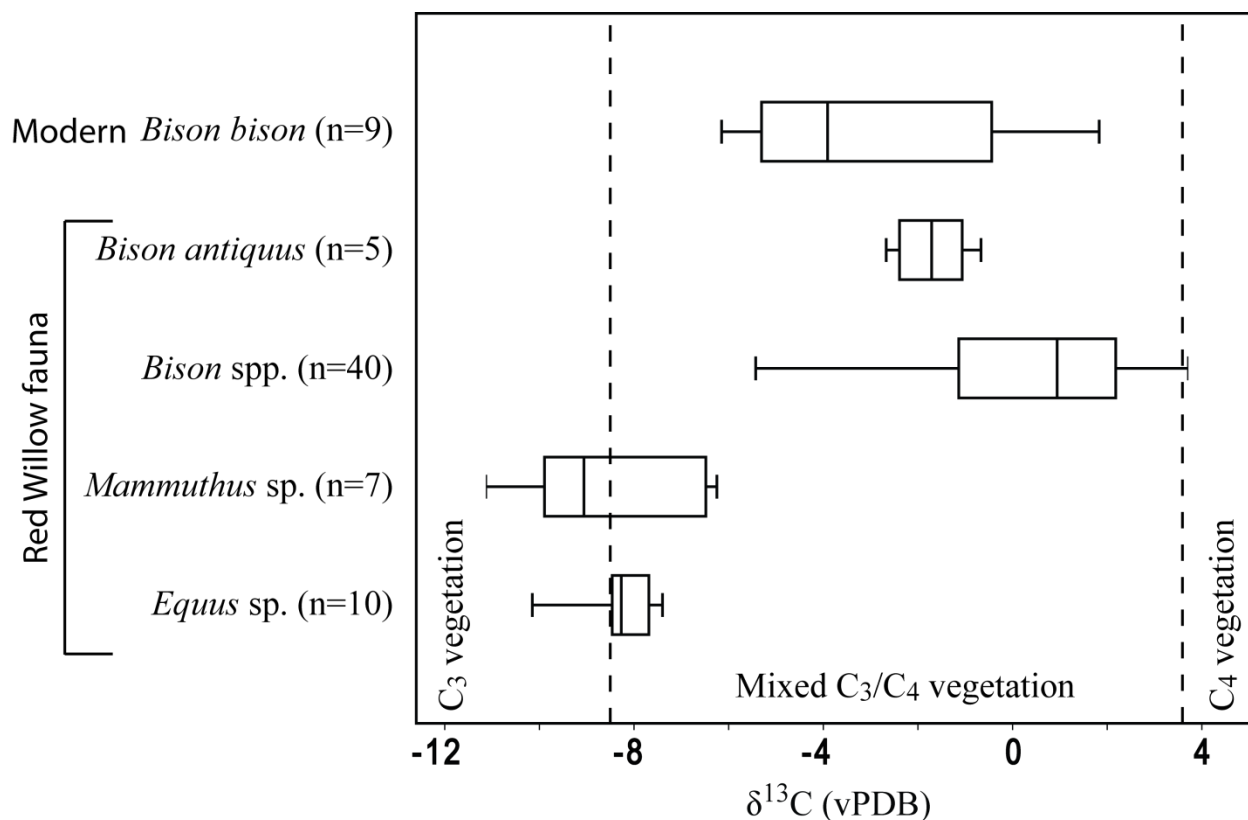


Figure 7. Box and Whisker plot of $\delta^{13}\text{C}$ values for Rancholabrean mammals from the Red Willow fauna and modern *Bison bison* from Platte River valley, Nebraska (see Fig. 1). Maximum and minimum values are represented by whiskers. Box contains 50% of data, and ends of box are 25th and 75th percentiles. Line inside box represents median.

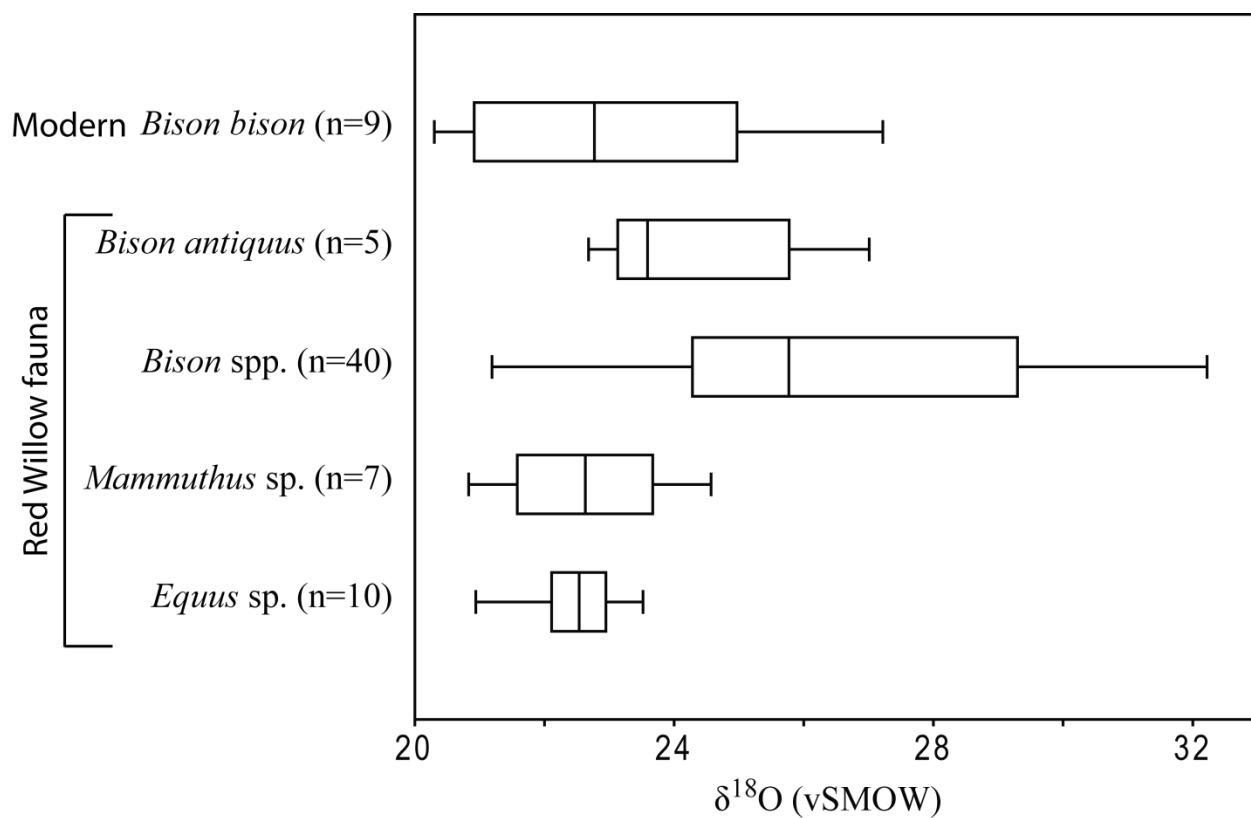


Figure 8. Box and Whisker plot for $\delta^{18}\text{O}$ values for Rancholabrean animals. Box symbols as in Fig. 7.

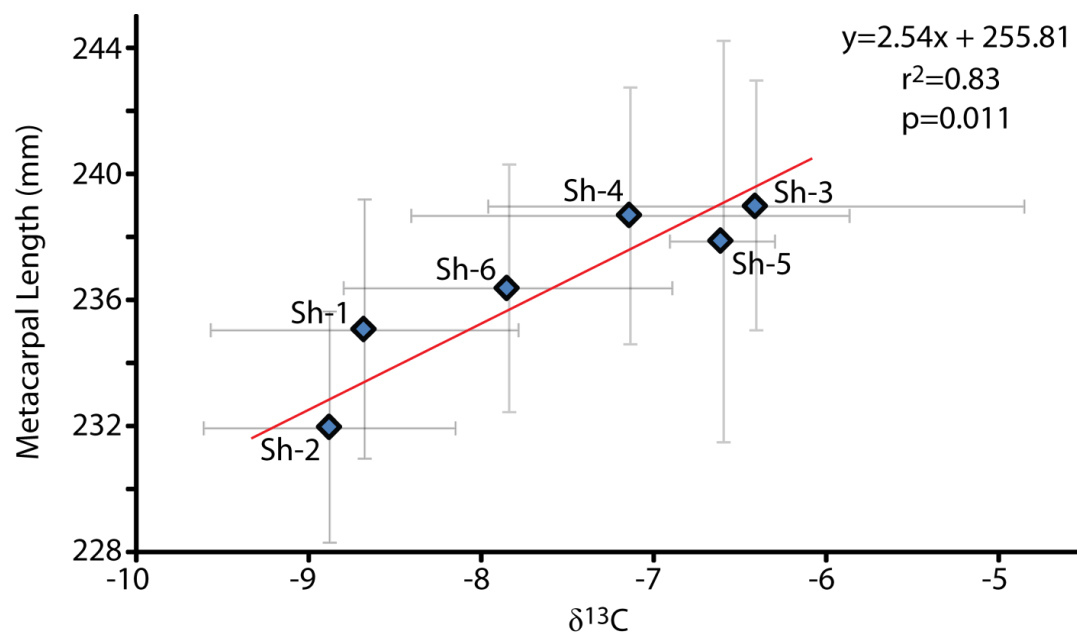


Figure 9. Relationship between mean metacarpal length and mean $\delta^{13}\text{C}$ values for equids from Sheridan County localities of late Irvingtonian age. The trend line was fit using a reduced major axis linear regression. Error bars are ± 2 SE.

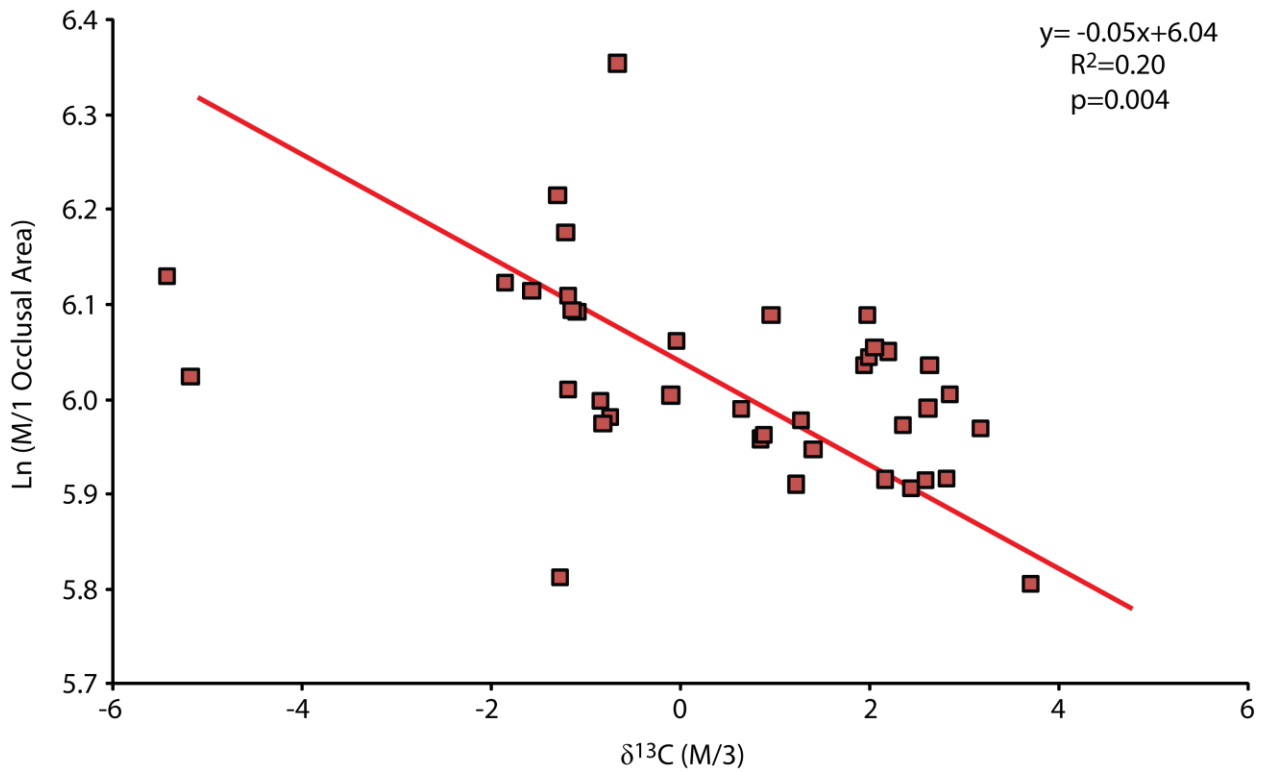


Figure 10. Comparison of *Bison* spp. body size, using M/1 occlusal crown area as proxy, and $\delta^{13}\text{C}$ values from third molars, based on jaws containing both teeth from the Red Willow fauna. Trend line was fit using reduced major axis linear regression.

Table 1. UNSM localities used in this study. Number after locality name corresponds to map numbers in Fig. 1. Asterisks indicate localities that are commercial gravel pits

UNSM Locality	County	NALMA	Age
Sh-1, Sh-2 [1]	Sheridan	Irvingtonian	Ir-3
Sh-3, Sh-4 [2]	Sheridan	Irvingtonian	Ir-3
Sh-5, Sh-6 [3]	Sheridan	Irvingtonian	Ir-3
Fr-104 [4]	Franklin	Irvingtonian	Ir-1
No-104 [5]	Nuckolls	Irvingtonian	Ir-2
Hy-101 [6]	Hayes	Rancholabrean	37-5 kyr BP
Hk-102* [7]	Hitchcock	Rancholabrean	37-5 kyr BP
Rw-101* [8]	Red Willow	Rancholabrean	37-5 kyr BP
Rw-102 [8]	Red Willow	Rancholabrean	37-5 kyr BP
Rw-104 [8]	Red Willow	Rancholabrean	37-5 kyr BP
Rw-108 [8]	Red Willow	Rancholabrean	37-5 kyr BP
Rw-109 [8]	Red Willow	Rancholabrean	37-5 kyr BP
Rw-110 [8]	Red Willow	Rancholabrean	37-5 kyr BP
25NC2 [9]	Nance	Recent	200 yr BP
25PT1 [10]	Platte	Recent	200 yr BP
25BU2 [11]	Colfax	Recent	200 yr BP
25CX1 [12]	Colfax	Recent	200 yr BP

Table 2. Ln(M/3 Area) of modern *Bison bison* from Montana and *Bison* spp. from the Red Willow fauna.

	N	Mean	Median	Range	SD	SE
Modern <i>Bison</i>						
<i>bison</i>	20	6.46	6.46	6.30 to 6.68	0.11	0.03
Red Willow bison	45	6.54	6.51	6.01 to 6.96	0.21	0.03

Table 3. Descriptive statistics for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. The Red Willow fauna is abbreviated as RWF in above table.

Taxon	Locality	Age	N	Mean	Median	$\delta^{13}\text{C}$			Mean	Median	$\delta^{18}\text{O}$		
						(vPDB)	(‰)				(vSMOW)	(‰)	
						Range	SD	SE			Range	SD	SE
<i>Bison bison</i>		Modern	9	-3.1	-3.9	-6.2 to 1.8	2.88	0.96	23.1	22.8	20.3 to 27.2	2.40	0.80
<i>Bison</i> sp.	RWF	Holocene	40	0.5	0.9	-5.4 to 3.7	2.09	0.33	26.4	25.8	21.2 to 32.2	2.99	0.47
<i>Bison antiquus</i>	RWF	Holocene	5	-1.7	-1.7	-2.7 to -0.7	0.75	0.33	24.3	23.6	22.7 to 27.0	1.66	0.74
<i>Mammuthus columbi</i>	RWF	Rancholabrean	7	-8.5	-9.1	-11.1 to -6.3	1.93	0.73	22.7	22.6	20.8 to 24.6	1.26	0.48
<i>Equus</i> sp.	RWF	Rancholabrean	10	-8.3	-8.3	-10.2 to -7.4	0.79	0.25	22.5	22.5	20.9 to 23.5	0.76	0.24
<i>Mammuthus columbi</i>	No-104	Irvingtonian	2	-9.5	-9.5	-9.8 to -9.1	0.45	0.32	23.7	23.7	22.7 to 24.6	1.32	0.93
<i>Equus</i> sp.	No-104	Irvingtonian	6	-9.3	-9.2	-11.0 to -8.0	1.16	0.47	23.1	23.0	22.7 to 23.7	0.47	0.19
<i>Equus</i> sp.	Fr-104	Early Irvingtonian	3	-6.3	-7.5	-7.9 to -3.6	2.36	1.36	22.9	22.9	22.1 to 23.6	0.78	0.45
<i>Equus</i> sp.	Sh-1	Late Irvingtonian	6	-8.7	-9.1	-9.7 to -6.7	1.09	0.45	22.3	22.3	21.5 to 22.9	0.45	0.19
<i>Mammuthus columbi</i>	Sh-1	Late Irvingtonian	1	-	-	-4.9	-	-	-	-	26.9	-	-
<i>Equus</i> sp.	Sh-2	Late Irvingtonian	6	-8.9	-9.0	-9.8 to -7.8	0.89	0.36	22.4	22.8	20.2 to 23.8	1.44	0.59
<i>Equus</i> sp.	Sh-3	Late Irvingtonian	3	-6.4	-6.7	-7.6 to -4.9	1.34	0.78	24.1	24.2	22.9 to 25.2	1.15	0.07
<i>Mammuthus columbi</i>	Sh-3	Late Irvingtonian	1	-	-	-8.8	-	-	-	-	22.6	-	-
<i>Equus</i> sp.	Sh-4	Late Irvingtonian	6	-7.1	-6.8	-10.0 to -5.6	1.56	0.64	22.7	23.2	20.1 to 24.0	1.44	0.59
<i>Equus</i> sp.	Sh-5	Late Irvingtonian	6	-6.6	-6.5	-7.2 to -6.2	0.37	0.15	23.2	23.4	20.6 to 24.9	1.70	0.69
<i>Mammuthus columbi</i>	Sh-5	Late Irvingtonian	3	-7.5	-7.7	-9.5 to -5.4	2.10	1.21	22.9	22.1	21.0 to 25.5	2.36	1.36
<i>Equus</i> sp.	Sh-6	Late Irvingtonian	6	-7.9	-7.6	-9.7 to -6.4	1.16	0.47	23.6	24.1	20.9 to 24.9	1.46	0.60
<i>Camelops</i> sp.	Sh-1	Late Irvingtonian	6	-6.9	-8.0	-8.5 to -3.9	1.97	0.81	22.2	21.0	20.5 to 25.3	2.17	0.88
<i>Camelops</i> sp.	Sh-3	Late Irvingtonian	2	-8.2	-8.2	-8.6 to -7.8	0.59	0.42	22.2	22.2	21.8 to 22.7	0.67	0.48
<i>Camelops</i> sp.	Sh-5	Late Irvingtonian	6	-9.0	-8.1	-9.0 to -8.1	0.36	0.15	22.2	22.3	20.9 to 23.1	0.72	0.30

APPENDIX A

Bulk $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$

Bulk $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. Asterisk numbers are from modern bison from the Nebraska

Historical Society.

UNSM no.	Taxon	Locality	Age	$\delta^{13}\text{C}$ (vPDB)	$\delta^{18}\text{O}$ (vSMOW)
29552*	<i>Bison bison</i>	25CX1	Recent	-3.68	22.41
27530*	<i>Bison bison</i>	25CX1	Recent	-2.10	23.57
29551*	<i>Bison bison</i>	25CX1	Recent	-4.08	20.85
30114*	<i>Bison bison</i>	25CX1	Recent	-4.47	22.77
27847*	<i>Bison bison</i>	25CX1	Recent	1.83	27.22
30709*	<i>Bison bison</i>	25CX1	Recent	-3.91	20.98
812*	<i>Bison bison</i>	25PT1	Recent	1.22	26.37
C50*	<i>Bison bison</i>	25NC2	Recent	-6.14	23.31
BU2-286-SF*	<i>Bison bison</i>		Recent	-6.15	20.30
49238	<i>Bison antiquus</i>	Rw-102	Holocene	-2.11	22.68
49806	<i>Bison antiquus</i>	Rw-102	Holocene	-2.67	24.54
49236	<i>Bison antiquus</i>	Rw-101	Holocene	-1.46	27.01
49237	<i>Bison antiquus</i>	Rw-102	Holocene	-1.71	23.59
132521	<i>Bison antiquus</i>	Rw-109	Holocene	-0.67	23.58
49965	<i>Bison sp.</i>	Rw-109	Holocene	1.47	26.04
132543	<i>Bison sp.</i>	Hk-102	Holocene	-0.05	22.25
132547	<i>Bison sp.</i>	Hk-102	Holocene	-5.43	21.54
132546	<i>Bison sp.</i>	Hk-102	Holocene	-0.11	22.92
132551	<i>Bison sp.</i>	Hk-102	Holocene	2.63	29.30
132550	<i>Bison sp.</i>	Hy-101	Holocene	-1.30	29.57
132553	<i>Bison sp.</i>	Hy-101	Holocene	-1.19	29.68
132548	<i>Bison sp.</i>	Hy-101	Holocene	0.64	23.51
132549	<i>Bison sp.</i>	Hy-101	Holocene	1.27	32.22
132552	<i>Bison sp.</i>	Rw-101	Holocene	2.05	26.64
132542	<i>Bison sp.</i>	Rw-101	Holocene	2.81	28.65
132544	<i>Bison sp.</i>	Rw-101	Holocene	3.70	25.53
132541	<i>Bison sp.</i>	Rw-102	Holocene	-1.15	29.73
132540	<i>Bison sp.</i>	Rw-102	Holocene	-1.10	29.78
132533	<i>Bison sp.</i>	Rw-102	Holocene	-0.83	25.32
132528	<i>Bison sp.</i>	Rw-102	Holocene	-0.75	22.72
132516	<i>Bison sp.</i>	Rw-102	Holocene	0.84	22.91
132545	<i>Bison sp.</i>	Rw-102	Holocene	0.93	31.86
132514	<i>Bison sp.</i>	Rw-102	Holocene	0.95	25.38
132536	<i>Bison sp.</i>	Rw-102	Holocene	1.22	32.17
132517	<i>Bison sp.</i>	Rw-102	Holocene	1.93	22.79
132515	<i>Bison sp.</i>	Rw-102	Holocene	2.15	25.57

132522	<i>Bison</i> sp.	Rw-102	Holocene	2.35	28.37
132529	<i>Bison</i> sp.	Rw-102	Holocene	2.59	26.85
132523	<i>Bison</i> sp.	Rw-102	Holocene	2.61	30.11
132534	<i>Bison</i> sp.	Rw-102	Holocene	3.17	26.01
132537	<i>Bison</i> sp.	Rw-108	Holocene	0.87	25.52
132535	<i>Bison</i> sp.	Rw-108	Holocene	1.97	24.35
132525	<i>Bison</i> sp.	Rw-109	Holocene	-5.19	21.19
132518	<i>Bison</i> sp.	Rw-109	Holocene	-1.58	29.28
132519	<i>Bison</i> sp.	Rw-109	Holocene	-1.22	24.05
132526	<i>Bison</i> sp.	Rw-109	Holocene	-1.19	24.26
132527	<i>Bison</i> sp.	Rw-109	Holocene	1.40	25.32
132538	<i>Bison</i> sp.	Rw-109	Holocene	1.99	28.01
132520	<i>Bison</i> sp.	Rw-109	Holocene	2.43	25.97
132539	<i>Bison</i> sp.	Rw-109	Holocene	2.84	29.56
132532	<i>Bison</i> sp.	Rw-110	Holocene	-1.86	24.59
132531	<i>Bison</i> sp.	Rw-110	Holocene	-1.27	27.13
132530	<i>Bison</i> sp.	Rw-110	Holocene	-0.85	24.99
132524	<i>Bison</i> sp.	Rw-110	Holocene	2.19	25.13
2022	<i>Mammuthus</i> sp.	Rw-0	Rancholabrean	-9.06	22.63
50535	<i>Mammuthus</i> sp.	Rw-101	Rancholabrean	-6.25	20.83
50909	<i>Mammuthus</i> sp.	Rw-101	Rancholabrean	-9.89	23.67
49736	<i>Mammuthus</i> sp.	Rw-102	Rancholabrean	-11.12	21.58
49826	<i>Mammuthus</i> sp.	Rw-102	Rancholabrean	-9.84	22.29
49359	<i>Mammuthus</i> sp.	Rw-109	Rancholabrean	-6.48	23.09
49414	<i>Mammuthus</i> sp.	Rw-110	Rancholabrean	-7.01	24.57
45931	<i>Mammuthus</i> sp.	Sh-1	Rancholabrean	-4.94	26.93
1938	<i>Mammuthus</i> sp.	Sh-3	Rancholabrean	-8.79	22.64
2483	<i>Mammuthus</i> sp.	Sh-5	Rancholabrean	-7.68	22.12
1284	<i>Mammuthus</i> sp.	Sh-5	Rancholabrean	-9.54	21.00
2484	<i>Mammuthus</i> sp.	Sh-5	Rancholabrean	-5.35	25.53
132574	<i>Equus</i> sp.	Rw-101	Rancholabrean	-8.08	22.30
132555	<i>Equus</i> sp.	Rw-101	Rancholabrean	-8.36	21.54
132556	<i>Equus</i> sp.	Rw-102	Rancholabrean	-10.15	20.94
46455	<i>Equus</i> sp.	Rw-102	Rancholabrean	-8.35	22.51
46444	<i>Equus</i> sp.	Rw-102	Rancholabrean	-8.36	22.60
46456	<i>Equus</i> sp.	Rw-102	Rancholabrean	-8.76	22.40
132557	<i>Equus</i> sp.	Rw-104	Rancholabrean	-8.19	23.33
50225	<i>Equus</i> sp.	Rw-104	Rancholabrean	-7.41	23.52
132573	<i>Equus</i> sp.	Rw-104	Rancholabrean	-7.78	22.56
132575	<i>Equus</i> sp.	Rw-108	Rancholabrean	-7.40	22.82
113009	<i>Equus</i> sp.	No-104	Irvingtonian	-10.04	22.68
113007	<i>Equus</i> sp.	No-104	Irvingtonian	-7.98	22.66
113027	<i>Equus</i> sp.	No-104	Irvingtonian	-8.18	23.47

132501	<i>Equus</i> sp.	No-104	Irvingtonian	-8.85	22.67
113025	<i>Equus</i> sp.	No-104	Irvingtonian	-9.58	23.69
113029	<i>Equus</i> sp.	No-104	Irvingtonian	-10.99	23.35
132502	<i>Equus</i> sp.	Fr-104	Irvingtonian	-7.53	23.62
132500	<i>Equus</i> sp.	Fr-104	Irvingtonian	-3.62	22.89
132554	<i>Equus</i> sp.	Fr-104	Irvingtonian	-7.87	22.06
132512	<i>Equus</i> sp.	Sh-1	Irvingtonian	-8.82	22.29
132508	<i>Equus</i> sp.	Sh-1	Irvingtonian	-9.67	22.03
132509	<i>Equus</i> sp.	Sh-1	Irvingtonian	-9.35	22.87
132559	<i>Equus</i> sp.	Sh-1	Irvingtonian	-9.34	22.46
132558	<i>Equus</i> sp.	Sh-1	Irvingtonian	-8.18	21.52
132560	<i>Equus</i> sp.	Sh-1	Irvingtonian	-6.72	22.39
132505	<i>Equus</i> sp.	Sh-2	Irvingtonian	-7.82	23.78
132513	<i>Equus</i> sp.	Sh-2	Irvingtonian	-8.69	23.63
128149	<i>Equus</i> sp.	Sh-2	Irvingtonian	-7.88	22.66
6035	<i>Equus</i> sp.	Sh-2	Irvingtonian	-9.71	20.24
132566	<i>Equus</i> sp.	Sh-2	Irvingtonian	-9.83	22.95
132567	<i>Equus</i> sp.	Sh-2	Irvingtonian	-9.35	21.04
132571	<i>Equus</i> sp.	Sh-3	Irvingtonian	-7.57	24.16
132568	<i>Equus</i> sp.	Sh-3	Irvingtonian	-6.73	22.89
132569	<i>Equus</i> sp.	Sh-3	Irvingtonian	-4.94	25.19
132510	<i>Equus</i> sp.	Sh-4	Irvingtonian	-7.22	22.01
132506	<i>Equus</i> sp.	Sh-4	Irvingtonian	-10.02	20.11
132507	<i>Equus</i> sp.	Sh-4	Irvingtonian	-7.38	23.18
132570	<i>Equus</i> sp.	Sh-4	Irvingtonian	-6.30	23.76
132562	<i>Equus</i> sp.	Sh-4	Irvingtonian	-6.26	23.12
132561	<i>Equus</i> sp.	Sh-4	Irvingtonian	-5.63	23.98
87539	<i>Equus</i> sp.	Sh-5	Irvingtonian	-7.21	20.55
87506	<i>Equus</i> sp.	Sh-5	Irvingtonian	-6.88	22.32
87528	<i>Equus</i> sp.	Sh-5	Irvingtonian	-6.56	24.87
132563	<i>Equus</i> sp.	Sh-5	Irvingtonian	-6.45	22.58
87533	<i>Equus</i> sp.	Sh-5	Irvingtonian	-6.31	24.12
87515	<i>Equus</i> sp.	Sh-5	Irvingtonian	-6.24	24.83
132511	<i>Equus</i> sp.	Sh-6	Irvingtonian	-7.18	24.93
87512	<i>Equus</i> sp.	Sh-6	Irvingtonian	-7.38	24.19
87519	<i>Equus</i> sp.	Sh-6	Irvingtonian	-6.41	24.66
132565	<i>Equus</i> sp.	Sh-6	Irvingtonian	-9.72	20.93
132564	<i>Equus</i> sp.	Sh-6	Irvingtonian	-8.55	23.10
123644	<i>Equus</i> sp.	Sh-6	Irvingtonian	-7.86	23.91
45723	<i>Camelops</i> sp.	Sh-1	Irvingtonian	-7.97	20.78
45727	<i>Camelops</i> sp.	Sh-1	Irvingtonian	-7.93	20.51
45719	<i>Camelops</i> sp.	Sh-1	Irvingtonian	-3.93	25.28
45726	<i>Camelops</i> sp.	Sh-1	Irvingtonian	-8.52	21.18

45717	<i>Camelops</i> sp.	Sh-1	Irvingtonian	-4.80	24.65
45705	<i>Camelops</i> sp.	Sh-1	Irvingtonian	-8.09	20.77
132503	<i>Camelops</i> sp.	Sh-3	Irvingtonian	-7.76	22.71
21482	<i>Camelops</i> sp.	Sh-3	Irvingtonian	-8.59	21.76
45806	<i>Camelops</i> sp.	Sh-5	Irvingtonian	-8.08	23.08
132504	<i>Camelops</i> sp.	Sh-5	Irvingtonian	-8.95	20.91
45804	<i>Camelops</i> sp.	Sh-5	Irvingtonian	-8.10	22.42
45832	<i>Camelops</i> sp.	Sh-5	Irvingtonian	-8.55	22.42
45801	<i>Camelops</i> sp.	Sh-5	Irvingtonian	-8.13	22.21
45802	<i>Camelops</i> sp.	Sh-5	Irvingtonian	-8.09	21.95

APPENDIX B

Bison Identification

Lower third molar measurements of modern bison and Red Willow bison.

UNSM No.	Taxon	Locality	Tooth Position	Length (mm)	Width (mm)	Area (mm ²)	Ln (Area)
1/12/2012	<i>Bison bison</i>	Montana	M/3	44.16	16.75	739.68	6.61
55250	<i>Bison bison</i>	Montana	M/3	41.84	17.07	714.21	6.57
55241	<i>Bison bison</i>	Montana	M/3	43.11	15.13	652.25	6.48
55249	<i>Bison bison</i>	Montana	M/3	41.00	13.32	546.12	6.30
55238	<i>Bison bison</i>	Montana	M/3	43.57	15.83	689.71	6.54
55246	<i>Bison bison</i>	Montana	M/3	41.68	14.43	601.44	6.40
55244	<i>Bison bison</i>	Montana	M/3	39.58	14.37	568.76	6.34
55243	<i>Bison bison</i>	Montana	M/3	40.28	14.17	570.77	6.35
55223	<i>Bison bison</i>	Montana	M/3	42.07	14.96	629.37	6.44
55214	<i>Bison bison</i>	Montana	M/3	42.81	16.79	718.78	6.58
55244	<i>Bison bison</i>	Montana	M/3	43.26	14.54	629.00	6.44
55215	<i>Bison bison</i>	Montana	M/3	43.82	17.27	756.77	6.63
55226	<i>Bison bison</i>	Montana	M/3	42.31	15.76	666.81	6.50
55216	<i>Bison bison</i>	Montana	M/3	40.92	14.08	576.15	6.36
55232	<i>Bison bison</i>	Montana	M/3	42.89	15.32	657.07	6.49
55229	<i>Bison bison</i>	Montana	M/3	39.54	14.04	555.14	6.32
55217	<i>Bison bison</i>	Montana	M/3	40.66	13.46	547.28	6.30
55230	<i>Bison bison</i>	Montana	M/3	48.68	16.28	792.51	6.68
55222	<i>Bison bison</i>	Montana	M/3	40.28	15.38	619.51	6.43
55231	<i>Bison bison</i>	Montana	M/3	41.93	15.72	659.14	6.49
49236	<i>Bison antiquus</i>	Rw-101	M/3	52.07	20.17	1050.25	6.96
49237	<i>Bison antiquus</i>	Rw-102	M/3	50.74	18.86	956.96	6.86
49238	<i>Bison antiquus</i>	Rw-102	M/3	51.44	18.32	942.38	6.85
49806	<i>Bison antiquus</i>	Rw-102	M/3	48.21	19.64	946.84	6.85
132521	<i>Bison antiquus</i>	Rw-109	M/3	51.63	19.42	1002.65	6.91
49965	<i>Bison</i> sp.	Rw-109	M/3	48.41	18.18	880.09	6.78
132514	<i>Bison</i> sp.	Rw-102	M/3	47.98	16.20	777.28	6.66
132515	<i>Bison</i> sp.	Rw-102	M/3	42.44	15.72	667.16	6.50
132516	<i>Bison</i> sp.	Rw-102	M/3	41.09	15.12	621.28	6.43
132517	<i>Bison</i> sp.	Rw-102	M/3	41.94	15.21	637.91	6.46
132518	<i>Bison</i> sp.	Rw-109	M/3	45.53	14.75	671.57	6.51
132519	<i>Bison</i> sp.	Rw-109	M/3	41.38	14.82	613.25	6.42
132520	<i>Bison</i> sp.	Rw-109	M/3	42.02	14.86	624.42	6.44
132522	<i>Bison</i> sp.	Rw-102	M/3	44.95	18.85	847.31	6.74
132523	<i>Bison</i> sp.	Rw-102	M/3	42.17	18.70	788.58	6.67
132524	<i>Bison</i> sp.	Rw-110	M/3	39.00	15.72	613.08	6.42
132525	<i>Bison</i> sp.	Rw-109	M/3	40.98	13.90	569.62	6.34
132526	<i>Bison</i> sp.	Rw-109	M/3	37.71	13.51	509.46	6.23

132527	<i>Bison</i> sp.	Rw-109	M/3	41.17	13.33	548.80	6.31
132528	<i>Bison</i> sp.	Rw-102	M/3	41.71	14.65	611.05	6.42
132529	<i>Bison</i> sp.	Rw-102	M/3	40.37	13.42	541.77	6.29
132530	<i>Bison</i> sp.	Rw-110	M/3	44.02	19.08	839.90	6.73
132531	<i>Bison</i> sp.	Rw-110	M/3	32.25	12.58	405.71	6.01
132532	<i>Bison</i> sp.	Rw-110	M/3	44.88	19.33	867.53	6.77
132533	<i>Bison</i> sp.	Rw-102	M/3	42.37	19.17	812.23	6.70
132534	<i>Bison</i> sp.	Rw-102	M/3	40.84	14.08	575.03	6.35
132535	<i>Bison</i> sp.	Rw-108	M/3	45.24	14.63	661.86	6.50
132536	<i>Bison</i> sp.	Rw-102	M/3	40.76	16.58	675.80	6.52
132537	<i>Bison</i> sp.	Rw-108	M/3	40.80	15.77	643.42	6.47
132538	<i>Bison</i> sp.	Rw-109	M/3	44.81	14.59	653.78	6.48
132539	<i>Bison</i> sp.	Rw-109	M/3	44.33	18.10	802.37	6.69
132540	<i>Bison</i> sp.	Rw-102	M/3	43.78	16.25	711.43	6.57
132541	<i>Bison</i> sp.	Rw-102	M/3	42.81	15.80	676.40	6.52
132542	<i>Bison</i> sp.	Hy-101	M/3	40.29	16.33	657.94	6.49
132543	<i>Bison</i> sp.	Rw-101	M/3	41.93	15.12	633.98	6.45
132544	<i>Bison</i> sp.	Rw-102	M/3	36.66	13.33	488.68	6.19
132545	<i>Bison</i> sp.	Hk-102	M/3	45.82	15.69	718.92	6.58
132546	<i>Bison</i> sp.	Hk-102	M/3	46.14	16.35	754.39	6.63
132547	<i>Bison</i> sp.	Hy-101	M/3	44.28	16.14	714.68	6.57
132548	<i>Bison</i> sp.	Hy-101	M/3	41.98	13.88	582.68	6.37
132549	<i>Bison</i> sp.	Hy-101	M/3	42.40	18.72	793.73	6.68
132550	<i>Bison</i> sp.	Hk-102	M/3	46.52	17.21	800.61	6.69
132551	<i>Bison</i> sp.	Rw-101	M/3	39.43	11.90	469.22	6.15
132552	<i>Bison</i> sp.	Rw-101	M/3	42.08	17.01	715.78	6.57
132553	<i>Bison</i> sp.	Hy-101	M/3	43.77	15.39	673.62	6.51

APPENDIX C

Bison first molar occlusal area

Bison first molar occlusal area. Asterisk numbers are from modern bison from the Nebraska Historical Society.

UNSM No.	Taxon	Locality	Tooth Position	Length (mm)	Width (mm)	Area	Ln (Area)
29552*	<i>Bison bison</i>	25CX1	M/1	23.69	14.15	335.21	5.81
27530*	<i>Bison bison</i>	25CX1	M/1	23.09	15.10	348.66	5.85
29551*	<i>Bison bison</i>	25CX1	M/1	23.26	14.46	336.34	5.82
30114*	<i>Bison bison</i>	25CX1	M/1	23.19	17.12	397.01	5.98
27847*	<i>Bison bison</i>	25CX1	M/1	26.49	18.34	485.83	6.19
30709*	<i>Bison bison</i>	25CX1	M/1	25.70	15.87	407.86	6.01
812*	<i>Bison bison</i>	25PT1	M/1	24.99	15.23	380.60	5.94
C50*	<i>Bison bison</i>	25NC2				0.00	
BU2-286-SF*	<i>Bison bison</i>		M/1	28.13	14.75	414.92	6.03
132514	<i>Bison</i> sp.	Rw-102	M/1	23.59	18.69	440.90	6.09
132515	<i>Bison</i> sp.	Rw-102	M/1	22.19	16.71	370.79	5.92
132516	<i>Bison</i> sp.	Rw-102	M/1	24.10	16.05	386.81	5.96
132517	<i>Bison</i> sp.	Rw-102	M/1	24.16	17.30	417.97	6.04
132518	<i>Bison</i> sp.	Rw-109	M/1	27.04	16.73	452.38	6.11
132519	<i>Bison</i> sp.	Rw-109	M/1	28.29	17.00	480.93	6.18
132520	<i>Bison</i> sp.	Rw-109	M/1	22.28	16.48	367.17	5.91
132521	<i>Bison</i> sp.	Rw-109	M/1	27.50	20.91	575.03	6.35
132522	<i>Bison</i> sp.	Rw-102	M/1	21.50	18.25	392.38	5.97
132523	<i>Bison</i> sp.	Rw-102	M/1	21.72	18.40	399.65	5.99
132524	<i>Bison</i> sp.	Rw-110	M/1	24.85	17.07	424.19	6.05
132525	<i>Bison</i> sp.	Rw-109	M/1	25.03	16.50	413.00	6.02
132526	<i>Bison</i> sp.	Rw-109	M/1	28.46	14.32	407.55	6.01
132527	<i>Bison</i> sp.	Rw-109	M/1	25.50	15.00	382.50	5.95
132528	<i>Bison</i> sp.	Rw-102	M/1	24.94	15.88	396.05	5.98
132529	<i>Bison</i> sp.	Rw-102	M/1	25.04	14.79	370.34	5.91
132530	<i>Bison</i> sp.	Rw-110	M/1	21.01	19.16	402.55	6.00
132531	<i>Bison</i> sp.	Rw-110	M/1	24.76	13.51	334.51	5.81
132532	<i>Bison</i> sp.	Rw-110	M/1	24.53	18.60	456.26	6.12
132533	<i>Bison</i> sp.	Rw-102	M/1	22.85	17.20	393.02	5.97
132534	<i>Bison</i> sp.	Rw-102	M/1	23.41	16.72	391.42	5.97
132535	<i>Bison</i> sp.	Rw-108	M/1	25.84	17.06	440.83	6.09
132536	<i>Bison</i> sp.	Rw-102	M/1	22.57	16.34	368.79	5.91
132537	<i>Bison</i> sp.	Rw-108	M/1	21.67	17.94	388.76	5.96
132538	<i>Bison</i> sp.	Rw-109	M/1	24.70	17.08	421.88	6.04
132539	<i>Bison</i> sp.	Rw-109	M/1	22.73	17.85	405.73	6.01
132540	<i>Bison</i> sp.	Rw-102	M/1	25.28	17.51	442.65	6.09

132541	<i>Bison</i> sp.	Rw-102	M/1	23.81	18.62	443.34	6.09
132542	<i>Bison</i> sp.	Rw-101	M/1	22.04	16.84	371.15	5.92
132543	<i>Bison</i> sp.	Hk-102	M/1	24.78	17.32	429.19	6.06
132544	<i>Bison</i> sp.	Rw-101	M/1	23.49	14.13	331.91	5.80
132545	<i>Bison</i> sp.	Rw-102				0.00	
132546	<i>Bison</i> sp.	Hk-102	M/1	24.33	16.65	405.09	6.00
132547	<i>Bison</i> sp.	Hk-102	M/1	25.66	17.90	459.31	6.13
132548	<i>Bison</i> sp.	Hy-101	M/1	23.09	17.30	399.46	5.99
132549	<i>Bison</i> sp.	Hy-101	M/1	22.18	17.79	394.58	5.98
132550	<i>Bison</i> sp.	Hy-101	M/1	25.39	19.71	500.44	6.22
132551	<i>Bison</i> sp.	Hk-102	M/1	28.76	14.54	418.17	6.04
132552	<i>Bison</i> sp.	Rw-101	M/1	23.40	18.20	425.88	6.05
132553	<i>Bison</i> sp.	Hy-101	M/1	24.12	18.65	449.84	6.11

APPENDIX D

Horse Metacarpal Length

Length and width measurement of Pleistocene horse metacarpals.

UNSM No.	Taxon	Locality	Length (mm)	Width (mm)
6244	<i>Equus</i> sp.	Sh-1	229	30.75
6252	<i>Equus</i> sp.	Sh-1	238	35.68
6253	<i>Equus</i> sp.	Sh-1	225	32.41
6267	<i>Equus</i> sp.	Sh-1	238	37.96
6268	<i>Equus</i> sp.	Sh-1	233	35.25
6269	<i>Equus</i> sp.	Sh-1	237	31.44
6270	<i>Equus</i> sp.	Sh-1	249	36.92
6271	<i>Equus</i> sp.	Sh-1	237	36.09
6272	<i>Equus</i> sp.	Sh-1	231	35.69
6339	<i>Equus</i> sp.	Sh-1	234	40.18
6327	<i>Equus</i> sp.	Sh-2	235	35.2
6328	<i>Equus</i> sp.	Sh-2	230	33.57
6337	<i>Equus</i> sp.	Sh-2	239	37.16
6339	<i>Equus</i> sp.	Sh-2	232	35.73
6363	<i>Equus</i> sp.	Sh-2	226	32.6
6367	<i>Equus</i> sp.	Sh-2	230	32.58
6332	<i>Equus</i> sp.	Sh-3	247	42.48
6333	<i>Equus</i> sp.	Sh-3	233	35.52
6334	<i>Equus</i> sp.	Sh-3	242	36.25
6357	<i>Equus</i> sp.	Sh-3	231	32.45
93208	<i>Equus</i> sp.	Sh-3	245	38.65
6331	<i>Equus</i> sp.	Sh-3	240	37.14
6329	<i>Equus</i> sp.	Sh-3	238	33.47
6330	<i>Equus</i> sp.	Sh-3	236	37.03
132572	<i>Equus</i> sp.	Sh-4	245	35.64
6255	<i>Equus</i> sp.	Sh-4	241	32.63
6257	<i>Equus</i> sp.	Sh-4	238	36.47
6284	<i>Equus</i> sp.	Sh-4	242	37.57
6283	<i>Equus</i> sp.	Sh-4	240	35.5
6285	<i>Equus</i> sp.	Sh-4	228	35.46
6326	<i>Equus</i> sp.	Sh-4	237	34.12
6254	<i>Equus</i> sp.	Sh-5	230	31.8
6247	<i>Equus</i> sp.	Sh-5	230	33.68
6243	<i>Equus</i> sp.	Sh-5	223	30.35
6340	<i>Equus</i> sp.	Sh-5	246	36.71
6325	<i>Equus</i> sp.	Sh-5	238	38.13
6323	<i>Equus</i> sp.	Sh-5	231	34.48
6319	<i>Equus</i> sp.	Sh-5	250	34.87

6314	<i>Equus</i> sp.	Sh-5	236	37.48
3275	<i>Equus</i> sp.	Sh-5	255	38.15
3113	<i>Equus</i> sp.	Sh-5	240	34.71
6256	<i>Equus</i> sp.	Sh-6	233	35.58
6258	<i>Equus</i> sp.	Sh-6	247	33.11
6277	<i>Equus</i> sp.	Sh-6	241	36.24
6349	<i>Equus</i> sp.	Sh-6	221	34.68
6365	<i>Equus</i> sp.	Sh-6	240	37.06
6366	<i>Equus</i> sp.	Sh-6	229	32.3
6369	<i>Equus</i> sp.	Sh-6	237	39.9
6370	<i>Equus</i> sp.	Sh-6	242	35.66
6372	<i>Equus</i> sp.	Sh-6	240	36.23
6374	<i>Equus</i> sp.	Sh-6	230	36.43
6373	<i>Equus</i> sp.	Sh-6	232	36.04
93212	<i>Equus</i> sp.	Sh-6	229	32.74
93206	<i>Equus</i> sp.	Sh-6	238	33.21