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Stable Isotope Analysis of Bison latifrons and Paleoecological Inferences

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Stable Isotope Analysis of *Bison latifrons* and Paleoecological Inferences

By

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Bachelor of Science in Geology
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A thesis submitted in partial fulfillment of
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ABSTRACT

Stable Isotope Analysis of *Bison latifrons* and Paleoecological Inferences

by

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Bison latifrons was a large Pleistocene herbivore that is traditionally hypothesized to have been adapted to living in forest openings and woodlands. According to this view, the species was primarily a browser of high-growing, woody plants. Very little isotopic work has been conducted on this species, and there have been no prior studies of high altitude localities containing this species. This study aims to address both of these issues.

B. latifrons is known from sites in several states, including California, Idaho, Colorado, Nevada, and Florida, among others. These sites provide diverse examples of this species' habitat and the opportunity to collect a robust data set for the purpose of characterizing its paleoautecology.

I analyzed carbon and oxygen stable isotopes from tooth enamel to test hypotheses concerning the diet and possible migration patterns of these animals. Data for *B. latifrons* were collected from a variety of sites, including Diamond Valley Lake, CA, American Falls, ID, and Snowmass, CO.

Oxygen isotopic values of meteoric water vary seasonally, with low values occurring in cold months and higher values in warm months. *B. latifrons* teeth were serially sampled from occlusal surface to root, representing a period of about 18 months and multiple seasons. Seasonal climatic variation within individuals was exhibited in the bison teeth sampled, with the American Falls population subjected to a higher degree of seasonality. The Diamond Valley Lake population possessed a slightly dampened seasonal signal that may be the result of seasonal migration. The signal from Snowmastodon was intermediate between the two.

The average $\delta^{13}C$ value of *B. latifrons* in this study was -8.39‰, which is intermediate between a pure C_3 browser (approximately -14‰) and pure C_4 grazer (approximately 0‰). This indicates that the species was primarily a mixed feeder. This diet was maintained throughout changes in intra-annual climate, as shown by variation in $\delta^{18}O$ values. The data also suggest that *B. latifrons* adjusted its diet based on the different composition of vegetation communities in each site. This is primarily seen in data from the American Falls and Snowmastodon sites, where the populations consumed a higher proportion of C_4 plants especially during winter months. *B. latifrons* at all sites in this study were indiscriminate feeders, eating plant material based primarily on availability.

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1 - Introduction

The purpose of this study is to use carbon and oxygen isotopes to test the hypothesis that *Bison latifrons* was a C_3 browser. *Bison latifrons* was a North American species of Pleistocene long-horned bison. This species' temporal range was roughly 160 – 20 ka, which includes portions of the Illinoian and Wisconsin glacial periods and intervening Sangamon Interglacial (130 – 85 ka) (McDonald, 1981). *B. latifrons* went extinct well before the main megafaunal extinction event at the end of the Pleistocene (Green, 1962; McDonald, 1981).

B. latifrons is the largest known bison species to have ever lived. It stood up to 2.5 meters at the shoulder, with long and heavy limbs to support its mass (McDonald, 1981). Previous workers have inferred that the height of this species facilitated a diet of shrubs and small trees found in forests (McDonald, 1981, Widga, 2006). This large size, presumed specialized diet, and relatively small populations distinguish it as a K-selected species (McDonald, 1981). According to this inference, modern moose (*Alces alces*), which are reliant on ephemeral openings in forests, would be ecological analogues to *B. latifrons.*

The body morphology of *B. latifrons* (an extremely large and heavy head held high off the ground by long limbs) suggests that it preferred C_3 browse over C_4 grass-dominated vegetation, as a function of mechanical efficiency (McDonald, 1981). Partly for this reason, it is commonly assumed that *B. latifrons* was adapted to forest and woodland environments, which were prevalent in the Great Plains and Great Basin regions of North America when this species was present (McDonald, 1981). This hypothesis is testable using stable isotopic analysis of carbon recorded in tooth enamel (MacFadden and Cerling, 1996; Koch and Hoppe, 1998; Feranec and MacFadden, 2000).

Fossil remains of *B. latifrons* occur in "a crescent from the Pacific coast of California, across the northern Great Basin, onto the Great Plains, and south onto the coastal plain of Texas," (McDonald, 1981, p. 71). *B. latifrons* was a large animal, and it must have required significant forage to meet its energy requirements (McDonald, 1981). If its primary habitat was limited to forest openings, it may have lived in relatively small social groups which did not travel long distances.

To determine the dietary characteristics of this species, I sampled tooth enamel from sites across a wide range of altitudes and latitudes. These sites include a high-elevation site at Snowmass, Colorado, an intermediate-elevation site in Idaho, and a low-elevation site in southern California. $\delta^{13}C$ values of approximately -14‰ would have confirmed a C_3 dominated diet, while values in the range of 0 to -8‰ would indicate a mixed C_3-C_4 diet (Koch et al., 1998).

In addition to carbon, I measured oxygen isotopic variation, which can be used as a proxy for the values found in drinking water consumed by the animal (Baumann and Crowley, 2014). Oxygen isotopes, which are temperature sensitive, record variations in air temperature during the biomineralization of the tooth. Such variations may be used to track changes in diet during colder and warmer time periods (Baumann and Crowley, 2014). Each tooth represents about 18 months of growth, over multiple seasons. Serial sampling allowed me to measure climatic variation within the 18-month interval of tooth mineralization (Higgins, 2004). My goal was to use the data gathered to place temporally similar, but geographically disparate bison into a paleoenvironmental context.

2 - *Bison* Phylogeny and Paleoecology

Dispersal corridors between Eurasia and North America alternately formed and disappeared during the Pleistocene, allowing species to sporadically travel between these continents (Shapiro et al., 2004). *Bison* is an Old World genus that immigrated to North America across Beringia (Kurtén, 1980). The most important barrier to be removed, permitting the introduction of this genus into North America, was the Bering Strait (McDonald, 1981). Bison have a history of flexibility in response to environmental and evolutionary pressures, making them ideal candidates for such large scale range shifting (McDonald, 1981; Shapiro et al., 2004). The arrival of *Bison* into North America about 220 thousand years ago defines the beginning of the Rancholabrean North American Land Mammal Age (Savage, 1951). Figure 1 displays a proposed phylogeny of North American species and subspecies within this genus.

Availability of browse was in decline during the Middle Pleistocene due to dry climates and expansion of C_4 grasses. This in turn led to increased competition between megaherbivores (McDonald, 1981; Shapiro et al., 2004). Savanna and steppe habitats expanded throughout North America, and large body size became a prevalent adaptation among various taxa as a means to compete for resources and deter predators (Prothero, 2012). Niche partitioning became another important strategy among sympatric species as a means of avoiding competition and maximizing survivability (Feranec, 2000; Rivals and Semprebon, 2011). These two factors are likely mechanisms that led to habitat specialization and distribution seen among the North American taxa within genus *Bison*.

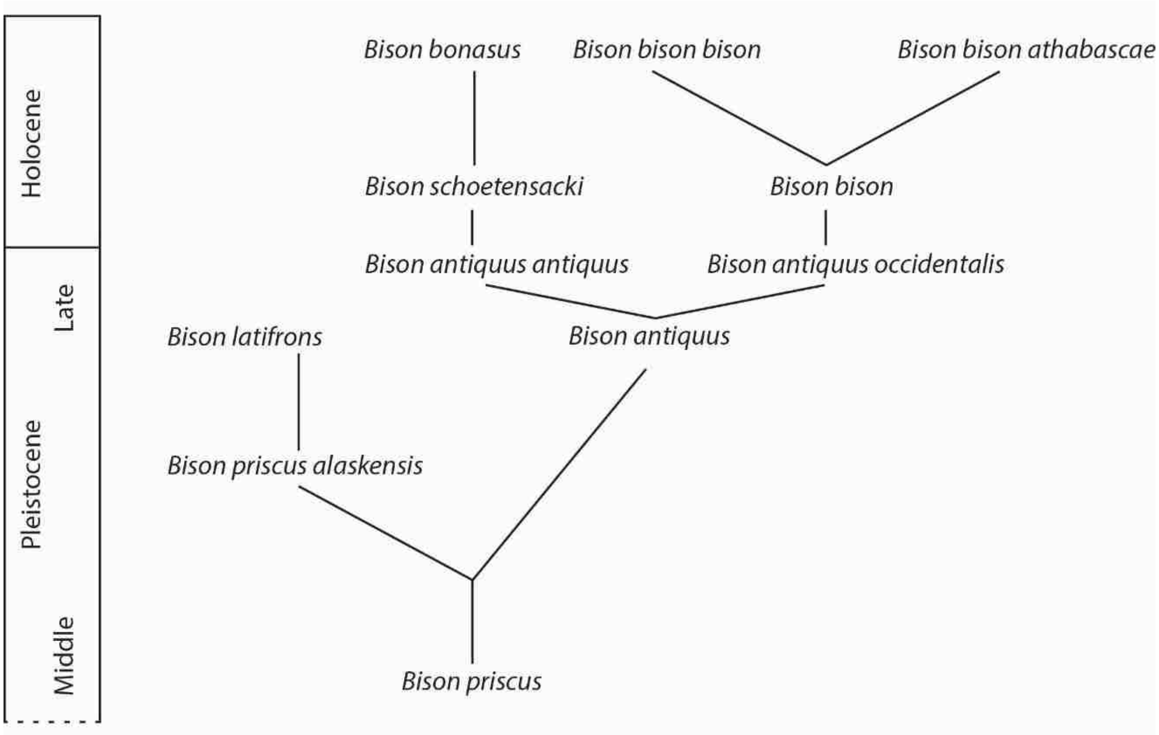


Figure 1: Simplified phylogeny of the genus *Bison*, with emphasis on North American lineages. (Adapted from McDonald, 1981, and Prusak, 2004). *Bison* phylogeny is highly debated; this chart represents a synthesis of current hypotheses.

Bison made their initial appearance in North America in the form of *Bison priscus* during the Middle Pleistocene (McDonald, 1981). *B. priscus* is most probably the ancestor of all subsequent North American *Bison* species, as well as the extant European *Bison bonasus*. This ancestry is supported by cytochrome b gene sequencing of the modern North American *Bison bison* and European *Bison bonasus* (Prusak, 2004). This method of genetic analysis was used by Prusak (2004) to help clarify the phylogenetic relationship between these two closely related extant species. The ancestry of *B. bison* was traced back to *B. antiquus*, itself a descendent of the earlier *B. priscus* (McDonald, 1981; Prusak, 2004).

B. priscus arrived via the Bering land bridge and radiated throughout Alaska and Canada (Prusak, 2004). The timing of maximum lowering of sea level at about 191 ka during the Illinoian glaciation roughly coincides with the arrival of *B. priscus* from Eurasia (Kurtén, 1980; McDonald, 1981; Scott, 2010). This species, which was roughly intermediate in size between *B. antiquus* and *B. latifrons*, is referred to as the "steppe bison" for its common distribution in mid-latitude Eurasia and North America's savanna-type environments (Kurtén, 1980; McDonald, 1981).

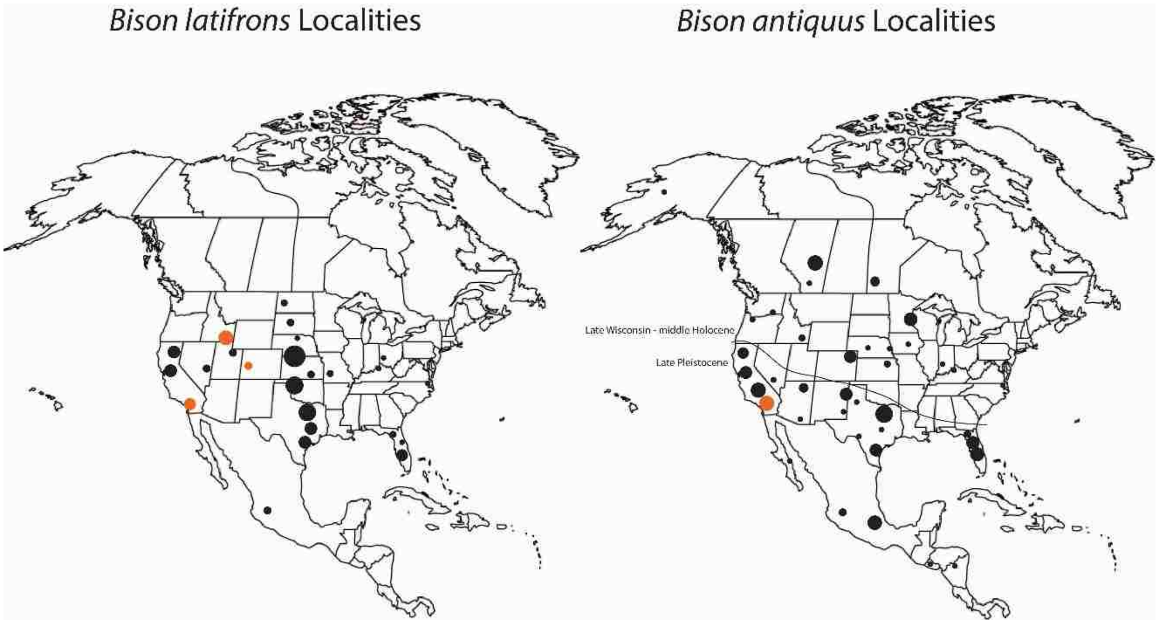
As the range of *B. priscus* shifted southward into mid-latitude North America, it diverged into two daughter species, *Bison latifrons* and *Bison antiquus*, between 22 and 15 ka (Fig. 1) (Skinner and Kaisen, 1947; Kurtén, 1980; McDonald, 1981; Prusak, 2004, Shapiro et al., 2004). The ancestor-descendant relationship between *B. priscus* and *B. antiquus* was strengthened by the recovery of an apparent *B. priscus*/*B. antiquus* hybrid at Cambridge, Massachusetts, dated to between 31 and 21 ka (McDonald and Anderson, 1975). The progenitor species became fully extinct toward the end of the late Wisconsin glaciation or in the early Holocene (Kurtén, 1980; McDonald, 1981).

A subspecies, *Bison priscus alaskensis*, appeared in mid-Pleistocene Eurasia and reached a wider range of localities throughout North America (McDonald, 1981). Its distribution pattern suggests that it was a browser that preferred woodland environments (McDonald, 1981). It was a large subspecies which has been hypothesized to be a transitional form between *B. priscus* and *B. latifons* (Kurtén, 1980; McDonald, 1981; Prusak, 2004).

B. latifrons is most commonly identified by its extremely large horn cores (55-109 cm in length) (McDonald, 1981). *B. latifrons* remains have been dated as far back as the late Illinoian glacial stage, at about 160 Ka. The species became extinct at about 20 Ka, with a possible relict population in Florida surviving into the latest Pleistocene (McDonald, 1981; MacFadden and Cerling, 1996; Koch et al., 1998). *B. latifrons* was the largest species of bison to have lived, and fossil assemblages suggest that it had less complex herd structure and interaction than its sister taxon *B. antiquus* (McDonald, 1981).

Bison antiquus evolved in North America between 83 and 64 Ka (Harrington and Clulow, 1973; Wilson et al., 2008; Scott, 2010). It was contemporaneous with *B. latifrons* for approximately 40 - 60 thousand years. *B. antiquus* is typically interpreted to have occurred farther south than *B. latifrons*, but an overlap in ranges is apparent throughout much of North America, including sites in California, Idaho, and Florida (McDonald, 1981; Scott, 2010) (Fig. 2). As a descendant of the steppe-dwelling *B. priscus*, *B. antiquus* is found in historically open environments. *B. antiquus* was slightly larger than its ancestor, but possessed shorter, less robust legs, suggesting an inclination toward grazing behavior (McDonald, 1981). Several prior carbon isotope studies have demonstrated that *B. antiquus* tooth enamel possesses relatively enriched δ^{13}C values, which indicates a diet dominated by C_4 plants (Fricke and O'Neil, 1996; Connin et al., 1998; Koch et al., 1998; Yann and DeSantis, 2014).

B. antiquus occidentalis and *B. antiquus antiquus* were a pair of contemporaneous subspecies which appeared during the latest Pleistocene or possibly early Holocene (McDonald, 1981; Scott, 2010). *B. a. occidentalis* is a controversial subspecies which may have arisen as a result of small populations becoming separated by geographic barriers, early human hunting, or interbreeding of isolated groups with relict *B. a. antiquus* populations (McDonald, 1981). This subspecies was smaller in stature than the parent taxon and is frequently associated with abnormalities in morphology, implying isolated inbreeding within small populations (McDonald, 1981).



Bison latifrons Localities

Bison antiquus Localities

Figure 2: Reported occurrences of *B. latifrons and B. antiquus.* Black dots indicate fossil sites; orange dots indicate sites sampled in this study. Dot size indicates the approximate population size of an assemblage, with larger dots representing a larger population. The line dividing the *B. antiquus* sites indicates the northern boundary of *B. antiquus* prior to the late Wisconsin glacial period; in the latest Wisconsin *B. antiquus* occurs north of this line. Adapted from McDonald, (1981).

Late in the Wisconsin glacial period, *B. a. antiquus* began to shift its range northward, likely interacting with *B. latifrons* in the boreal forests of North America. The larger size of *B. a. antiquus* relative to *B. a. occidentalis* presumably provided it with a means of competing with *B. latifrons* for habitat space. *B. a. antiquus* dispersed into Eurasia during the late Wisconsin glacial period (McDonald, 1981), eventually evolving into *Bison schoetensacki*, an early Holoene Eurasian species. *B. schoetensacki* in turn gave rise to *Bison bonasus*, the European analogue to the North American *Bison bison* (Prusak, 2004). Similarities in morphology between *B. bonasus* and *B. bison* are apparent, and a similar evolutionary history led to the success of *B. bonasus* in central Europe and the establishment of the European species whose common name is the wisent (Prusak, 2004).

A direct descendent of *B. a. occidentalis*, *Bison bison* first appeared at approximately 9.5 ka, when populations of bison had recovered from the general decline during the Wisconsin glaciation and expanded their range in the early Holocene (McDonald, 1981; Stuart, 1991). The species trended toward a smaller overall body size and a preference for C_4 grazing in a plains environment (McDonald, 1981; Tieszen, 1998; Widga, 2006).

Prior to the late 19th century and near-extinction of the species, *B. bison* diversified into two morphologically similar, but behaviorally distinct subspecies (McDonald, 1981, Hoppe, 2006b). *Bison bison bison* is the modern plains bison, which consumes a diet of almost exclusively C_4 grasses in open plains regions (Hoppe, 2006b). *Bison bison athabascae*, commonly called the wood bison, was traditionally found farther north, in Canada, in herds that did not range south of the Canadian/United States border (Feldhamer et al., 2003). *B. b. athabascae* persists today in regions dominated by woodlands, exhibiting the ecological flexibility of its parent species by incorporating a greater percentage of C_3 material into its diet (Feldhamer et al., 2003). This behavior has been confirmed by multiple dietary analyses where wood bison have been seen to prefer leafy C_3 plants to C_4 graze (Larter et al., 2000; Bergman et al., 2001). Some debate still lingers concerning the taxonomic position of *B. b. athabascae* as a subspecies. It is significantly larger than *B. b. bison*, with distinctive postcranial pelage, but genetic differences have not been identified (Geist, 1990). The possibility for variable phenotypic expression lies in the fundamentally disparate climates of the two major regions in which these subspecies are found (Geist, 1990; Feldhamer et al., 2003).

Unlike many other species of Pleistocene megaherbivores, *B. bison* may have avoided extinction by specializing in open grasslands more completely than did Native American humans (McDonald, 1981; Stuart, 1991). Bison were able to more fully utilize the resources of the North American plains than were Paleoindians, who required more shelter and greater variety in dietary intake than the grasslands provided (McDonald, 1981).

The fossil remains of Pleistocene bison are often found in conjunction with other megaherbivores, such as American mastodon (*Mammut americanum*), camelids, or closely related species of bison (Springer et al., 2009; Scott; 2010; Pigati et al., 2013). Intermittent overlap in range between them suggests that differences in feeding habits and adaptability were a necessity (Calandra et al., 2008).

The vast majority of dietary studies on modern bison have sampled living and recently expired *B. b. bison* from the lower 48 states region of North America (McDonald, 1981; Koch et al., 1998; Hoppe, 2006b; Widga, 2006). Tooth meso- and microwear analysis is the primary method by which the diets of modern and fossil animals have been assessed, but this method provides evidence for only the most recent vegetation consumed (Rivals and Semprebon, 2011). Stable isotope analysis provides a quantitative measurement that can be used independently, or in conjunction with tooth wear data to constrain the dietary preference of a fossil specimen (Widga, 2006; Rivals and Semprebon, 2011). Isotopic studies on bison have focused on the extant *B. bison*. These studies provide a clear picture of the species' preference for C_4 grazing with $\delta^{13}C$ (VPDB) averages of -0.7‰ (Koch et al., 1998), 2.4‰ (Larson, 2001), -3.9‰ (Widga 2010). These isotopic results match well with observable behavior. McDonald (1981) suggested that the smaller body size of *B. bison*, compared to the ancestral *B. antiquus*, is evidence for a change toward r-type selection, which is defined by relatively rapid and low-cost reproduction.

A shift toward quicker reproduction and a short maturation cycle was a potential difference in the biology of Holocene bison when compared with extinct congeners, and a probable response to multiple new ecologic factors such as the increasing prominence of the savanna biome and early human hunting (McDonald, 1981, Rivals et al., 2007).

Cannon (2004) reported a modern *Bison bison* skull radiometrically dated to 150 ± 40 yrs BP recovered in 2003 from a high altitude site (3,840 m) in the Uinta Mountains of northeastern Utah. The site is dominated by tundra vegetation, and the fossil was located in a marsh. The $\delta^{13}C$ values of the horn sheath averaged -22.51‰ VPDB. This implies that the animal primarily consumed C_3 browse, which correlates well with the low amount of available C_4 vegetation at the recovery site (Cannon, 2004). An increase in the relative abundance of C_3 browse material is correlated with increasing altitude and latitude (Cannon, 2004). Previous mesowear analyses have shown that all species of Pleistocene bison consumed a less abrasive diet than do modern bison, indicating a greater percentage of C_3 material than is consumed by their modern counterparts (Rivals et al., 2007). The isolated bison skull from an atpyical modern locality provides an example of the adaptability of bison to their environment, a trait that was almost certainly shared by their ancestors. Dietary plasticity may have been present throughout the genus and is further examined in this study.

3 - Carbon and Oxygen Isotope Paleoecology

3.1 - Carbon Reservoirs in Plants

Reduced organic carbon is formed by the reduction of CO_2 during photosynthesis (Sharp, 2007). Terrestrial plants utilize atmospheric CO_2 to obtain their carbon, removing ~10% from the atmosphere each year (Sharp, 2007). This percentage is balanced by the later decomposition of plant material (Sharp, 2007). C_3 plants have $\delta^{13}C$ values that typically range from -20 to -34‰, with an average of -27‰. C_4 plants have $\delta^{13}C$ values ranging from -6 to -23‰, averaging -13‰ (Ehleringer, Cerling, and Helliker, 1997). Seasonal variations in plant $\delta^{13}C$ values can be up to 0.5‰ (Hoppe, 2006b).

Most woody plants, including trees, shrubs, and aquatic plants utilize the C_3 photosynthetic pathway (Connin et al., 1998). These plants thrive in cool climates and high latitudes. Forest floor plants may have a $\delta^{13}C$ signal that is up to 5‰ lower than the signal found in the canopy, because the decaying biomass surrounding them continuously releases ^{13}C-depleted CO_2 (Cerling, 2004, Sharp, 2007).

Hatch and Slack (1966) showed that the C_4 photosynthetic pathway minimizes water loss and is therefore utilized by many arid-adapted plant species. There is a strong correlation between the percentage of C_4 plants in a community and minimum growing-season temperature (Terri and Stowe, 1976). C_4 plants are more sensitive to temperature, and their growth may be inhibited in cooler regions (Poorter and Navas, 2003). C_4 photosynthesis is more water efficient than C_3, while being less energy efficient, promoting the expansion of C_4 plants in arid regions (Ehleringer, Cerling, and Helliker, 1997).

McDonald (1981) suggested that the *B. latifrons* diet consisted mainly of C_3 plants, but this inference has not previously been tested using stable isotopes.

3.2 - Oxygen Isotopic Signatures in Precipitation

Atmospheric moisture is mainly derived from evaporation from the oceans in warm areas (Sharp, 2007). The $\delta^{18}O$ value of water is subject to both equilibrium and kinetic fractionation as phase change from liquid to vapor occurs. The various effects on the isotopic value of meteoric water are collectively named Rayleigh fractionation (Dansgaard, 1964).

As an air mass travels, it undergoes depletion in ^{18}O, especially when travelling over raised topography. Due in part to cold temperatures at high elevations, air masses lose significant amounts of vapor as they travel upward over topographic relief. The general signal for the altitude effect is -0.26‰ per 100 meters (Dansgaard, 1964).

There is a strong correlation between surface temperature and the isotopic composition of meteoric water. Lower temperature equates to lower $\delta^{18}O$ values of precipitation. Cold air is less capable of retaining moisture, so, as a general rule, $\delta^{18}O$ values of meteoric water are ~0.2‰ to 0.9‰ higher with each degree C of increase in air temperature (Sharp, 2007).

As an air mass moves inland away from its source, it moves through cycles of precipitation, which in turn cause more fractionation. This continentality effect is seen more strongly in cold conditions and is more pronounced when there is a large difference between the current location of the air mass and its source. The general effect in modern conditions is -1.5‰ to -3‰ per 1000 kilometers (Dansgaard, 1964).

The latitude of a site also influences the $\delta^{18}O$ value of meteoric water due to increasing rainout, with a drop of about 0.5‰ per degree of latitude (Dansgaard, 1964). At higher latitudes, the isotopic signal of meteoric water is mainly influenced by temperature variations, as there is less evaporation of rainfall (Dansgaard, 1964; Higgins and MacFadden, 2004). Higher latitudes are also subject to greater seasonality, as a result of increased variation in annual solar insolation (Dutton et al., 2005). Oxygen isotope values at high latitude sites are thus expected to have a greater absolute range over the course of a year (Dansgaard, 1964; Sharp, 2007).

Each fossil site investigated in this study should have a distinctive range of oxygen isotopic values that were present when the bison were living there. Snowmass, Colorado, for example, is a Sangamonian Interglacial site located at high elevation (2,087 m), in a mid-continental setting. The cold temperatures at that site will determine the range of possible $\delta^{18}O$ values. In comparison, the low-latitude, and low-elevation (451 - 481 m) population from the Diamond Valley Lake site is expected to display more positive $\delta^{18}O$ values. The isotopic values of fossil material should reflect those expected at the site, based on the sum of the myriad fractionation effects. These values provide insight into the temperatures experienced by each of the studied populations.

The sum of these effects on the fractionation of oxygen isotopes in meteoric water can be seen in a simple comparison of absolute values. Enriched $\delta^{18}O$ values indicate warm weather, while depleted $\delta^{18}O$ values indicate cooler weather (Higgins and MacFadden, 2004).

3.3 - Properties of Enamel and Use in Isotopic Studies

Enamel from bison teeth can be used to obtain $\delta^{13}C$ and $\delta^{18}O$ values, which reflect the isotopic fractionation between the animal and its environment. Stable isotopic analysis is a more reliable means of tracking long-term dietary trends than other techniques, such as tooth microwear analysis or morphology alone (Grine, 1986; Lambert et al., 2004). The mineral in tooth enamel is hydroxylapatite, which has the chemical formula $Ca_{10}[PO_4]_6[OH]_2$. Carbonate is found as a replacement within both the phosphate and hydroxyl sites (LeGeros, 1981; Crowley, 2012). This material is almost entirely inorganic (<2%), non-porous, and highly crystalline, with relatively large crystals (130 x 30 nm) that are resistant to defects and substitutions (LeGeros, 1981). The carbonate found within tooth enamel hydroxylapatite is more retentive of primary isotopic signatures than that of bone or dentin (Wang and Cerling, 1994).

Consumed water is the dominant factor in determining the $\delta^{18}O$ value of an animal's body water, and mammalian teeth mineralize at a constant temperature of about 37 ^{o}C, in equilibrium with body water (Luz, 1984). The $\delta^{18}O$ value preserved in the tooth enamel of a water-dependent animal is closely correlated with the value in local precipitation (Ayliffe, 1992). As an animal grows, the mineralization of the enamel in its teeth record the succession of changes in the isotopic composition of water it ingested (Fricke and O'Neil, 1996). In living bison, individuals within a population may have enamel $\delta^{18}O$ values that vary from one another 1-3‰, averaging 1.4‰, and it is expected that fossil bison would have had similar variability within a single population (Hoppe, 2006a). These variations may be caused by changes in $\delta^{18}O$ of environmental water on an inter-annual time scale. Hoppe (2006a) recommended that a minimum of eight individuals be sampled whenever possible in a living population. Access to this number of samples is unrealistic in most fossil assemblages, as fragmentary and unidentifiable specimens tend to dominate collections. The level of uncertainty within fossil assemblages is therefore expected to be greater than 1.4‰ if the number of samples is fewer than eight.

Hoppe (2006b) showed that modern bison tooth enamel exhibits a $\delta^{13}C$ fractionation of +14.6 ± 0.3‰ from the plants in their diet, leading to expected mean values of -14‰ for a C_3 browsing animal and 0‰ for a C_4 grazing diet. Koch (1994) found that in a different community, the fractionation was closer to +11‰ (Fig. 3), but this difference may be due to variation within individuals in either population of up to ±3‰. By combining the known biogenic $\delta^{13}C$

fractionation ranges of bison tooth mineralization (+14.6 to +11‰ VPDB) with known $\delta^{13}C$ ranges in plant communities, I was able to estimate reasonable values for C_3 and C_4 specialists. An animal that consumed primarily C_3 vegetation should display a $\delta^{13}C$ range of -10 to -19‰, while a C_4 graze-dominated diet should lead to a $\delta^{13}C$ range of +3 to -1‰. By observing modern bison, McDonald (1981) concluded that, in mixed C_3/C_4 environments, the bison preferentially feed on C_3 plants. Feranec (2007) showed that isotopic values confirm this conclusion. *B. latifrons* may also have preferred a C_3 diet, but they may have been forced to consume some amount of C_4 plants due to resource availability (Tieszen, 1998).

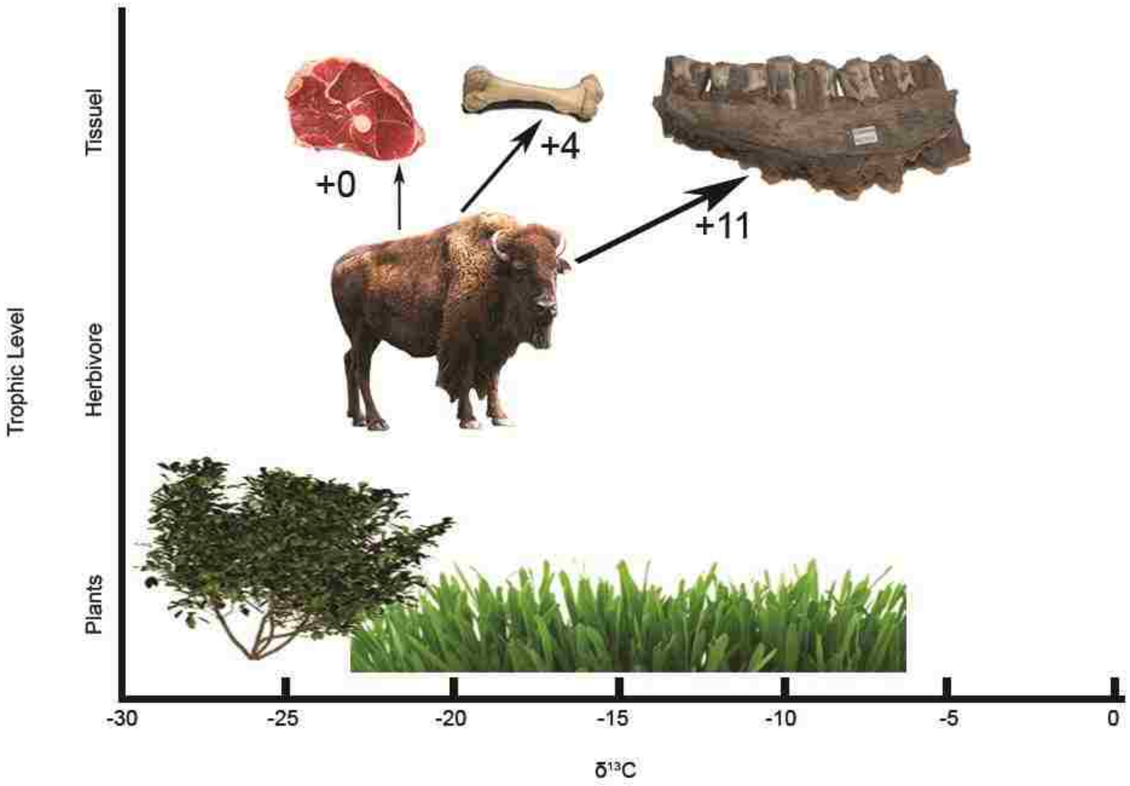


Figure 3: Carbon isotopic fractionation from dietary source to mammalian body tissue. Muscle exhibits low fractionation, bone collagen has a mean fractionation of +4‰, and tooth enamel hydroxylapatite exhibits fractionation of roughly +11 to +14.6‰. C_3 browse plants (such as trees and shrubs) fall to the more negative range of the chart (-30 to -20‰), while C_4 plants (arid adapted grasses) are found with values that are closer to -23 to -6‰ (Adapted from Koch, 1994).

3.4 - Isotopic Signals of Seasonality

Extant bison populations have predictable reproductive patterns, with their birthing season universally occurring during spring (Berger and Cunningham, 1994). The M_3 tooth mineralizes beginning at 9 months of age and is fully developed by 24 months (Berger and Cunningham, 1994). These patterns have been observed in multiple modern herds, and it is reasonable to assume that extinct bison exhibited similar synchronicity (Hoppe, 2006a). Due to the orderliness of these processes, seasonal isotopic values found in teeth can be predicted (Hoppe, 2006a). An animal that did not migrate would be exposed to the variation of weather and temperature patterns of the site, and record the changes in plant communities at its habitat.

Holroyd et al. (2014) demonstrated that serial sampling of mammalian enamel does not capture a precise seasonal signal because of the low resolution of the sampling method. For that reason, I interpret intra-tooth variation observed in this study to be a blurred seasonal signal. Pleistocene bison were very likely migratory, and they were certainly exposed to seasonal variations of weather regardless of movement. This may help to explain the variable $\delta^{18}O$ signal seen in nearly all teeth sampled in this study.

Bovid tooth formation is overall sequential, beginning at the cusp and progressing to the root, but the details of two-phase matrix deposition and maturation lead to potential overlap in isotopic values (Towers et al., 2014). The majority of mineralization occurs during the maturation phase, which takes several months and produces a degree of intra-tooth isotopic variability among layers (Towers et al., 2014). Bovid teeth do maintain a relatively constant rate of matrix progression as they develop, and an overall signal can be gleaned from sampling the surface enamel (Towers et al., 2014).

A graph of isotopic values in a hypothetical idealized M_3 tooth of a non-migratory bison is presented in Figure 4. This graph assumes a minimum loss of the occlusal end of the tooth, as would be the case in a relatively young animal. A slight lag time is estimated to allow for a period of mineralization after ingestion of meteoric precipitation. The M_3 begins to form during late winter (9 months after birth), and low temperatures result in depleted $\delta^{18}O$ values near the occlusal surface. These values become more enriched as temperatures increase, peaking roughly halfway through the tooth (16 months) during the transition between summer and autumn. The values become more depleted toward the lower 1/3 of the tooth during winter, reaching a low point near 21 months, during the animal's second winter. A final predicted enrichment should become evident as the root tapers at 24 months (Fig. 4).

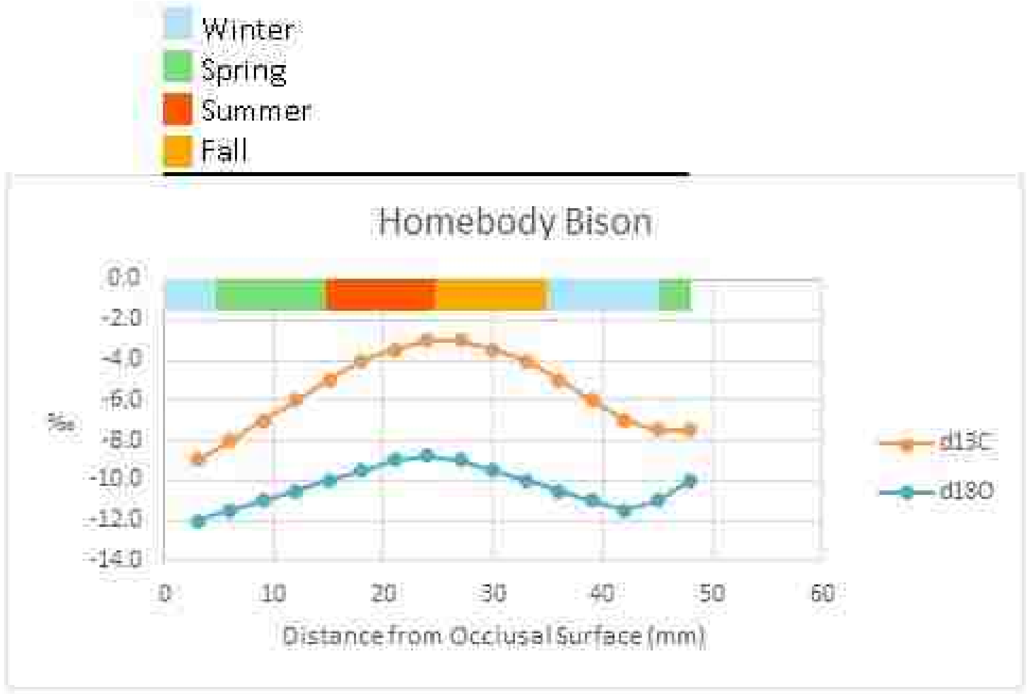


Figure 4: Idealized patterns of isotopic variation in a hypothetical, non-migratory individual. The two isotopic systems exhibit positive covariance, in response to seasonality. In old animals the left side of the graph will be truncated by wear on the tooth.

Carbon values in the idealized tooth follow a similar pattern. C_3 browse material thrives in cooler environments, and its greater availability during the cool season leads to higher consumption by a population. In the idealized tooth, this is reflected by depleted $\delta^{13}C$ values during these months. C_4 vegetation expands during warm and dry seasons, and the $\delta^{13}C$ values are accordingly expected to become more enriched (Figure 4). An exception to this pattern would occur in deciduous forests, where C_3 vegetation would be scarce during the fall and winter months, but abundant in the spring and summer. I will use this idealized isotopic pattern to assist in the interpretation of data obtained in this study.

4 - Geologic Setting of Localities

4.1 - American Falls Reservoir Mid-elevation (1,330 m) Fossil Site, American Falls, Idaho

The American Falls Reservoir (AF) fauna was collected over a period of 70 years between 1920 to 1990, beginning with the construction of a dam in the 1920s (Pinsof, 1992). The strata are primarily alluvial to lacustrine in origin, and units contain clasts that range from gravel to clay/silt in size (Pinsof, 1992). Two prominent fossiliferous horizons are present in the local reservoir deposits, referred to as the B and E layers. The faunal assemblage from the upper B horizon was described by McDonald and Anderson (1975), while Pinsof (1992) focused on the recovered specimens from the E layer. This unit is a 15- to 16-meter-thick fluvial deposit of sand and gravel, at an elevation of about 1,330 m (Pinsof, 1992). Radiometric dating of sedimentary and volcanic units that bracket the fossiliferous horizons show that the unit was deposited sometime between 210 and 72 ka (Pinsof, 1992). The site was placed into the Sangamon Interglacial due to the presence of *Panthera leo atrox* (American lion), which does not appear south of Alaska prior to this interval. This further constrains the site to 125 to 72 ka (Pinsof, 1992).

Five thousand specimens, representing a minimum of 51 taxa, have been recovered from the lower member of the American Falls Fm. The most abundant taxon is *Bison* spp., and the locality also contains *Equus scotti* (horse), *Camelops hesternus* (camel), *Megalonyx jeffersonii* and *Paramylodon harlani* (ground sloths), *Mammuthus columbi* (Columbian mammoth), and *Mammut americanum* (mastodon) (Pinsof, 1992). Some of the *Bison* spp. specimens in this assemblage were later identified as *Bison latifrons* based primarily on horn cores (Pinsof, 1992), so it is generally assumed that all of the bison from this site belong to this species. The Sangamon Interglacial temporal setting of the site further supports this interpretation, as *B. antiquus* had not yet reached the region (Fig. 2).

Based upon this diverse assemblage of megafaunal herbivores, Pinsof (1992) interpreted the site to contain a minimum of four communities within the depositional basin of the ancestral Snake River. He reviewed nine Sangamon local faunas from North America to support his position and concluded that a predominance of large herbivores and mild climate indicated the dominant habitat of the locality to be grassland/steppe.

4.2 - Ziegler Reservoir High-elevation (2,087 m) Fossil Site, Snowmass, Colorado

Snowmass, CO is home to the high altitude fossil site known as Snowmastodon. Around 140 kyr ago, the Snowmass Creek valley was occupied by a glacier during the Illinoian Bull Lake glaciation. The glacier extended above the ridge where Snowmass Village is currently located (Johnson and Miller, 2012). This glacier carved a 30-acre basin at the top of the ridge, and the basin was filled by melt-water as the Sangamon interglacial arrived (~120 ka) (Pigati et al., 2014). The result was Glacial Lake Ziegler (Johnson and Miller, 2012). The lake was filled with sediment between 130 and 40 ka, primarily by airborne dust and landslides from the moraine around its edges (Johnson and Miller, 2012). The lake became shallower and eventually transitioned to a marsh environment, which possibly catered to the dietary needs of *Mammut americanum* (mastodon) and *B. latifrons* (Johnson and Miller, 2012).

The glacial moraine forms the basement layer of the site, comprised of large boulders and poorly sorted clasts (Johnson and Miller, 2012). This unit is overlain by a thick layer of smooth, dark gray silt, up to 4.5 meters thick (Johnson and Miller, 2012). The silt interfingers with several coarse clastic lobes interpreted to be debris flows, each of which is ~0.6 m thick. These coarse intervals contain boulders, mixed clasts, tree branches, and fossils within a mixed matrix of clay, silt, and sand (Knell, 2009). Several specimens of *B. latifrons* were found in the silty layer (Johnson and Miller, 2012). A layer of brown, organic peat lies above the debris flows. This peat layer contains moss, leaves, and other fossil plant material (Johnson and Miller, 2012). The site is capped by a ~0.6 m thick layer of clay, which contained a young Columbian mammoth (Johnson and Miller, 2012).

The Snowmass fossil assemblage was spared from destruction by the later Wisconsin Pinedale glaciation (~21 ka), which created a glacier in the same valley. The younger glacier was not large enough to reach the top of the ridge, so it did not destroy the Ziegler fossil site (Pigati et al., 2014).

The 2011 excavation at the Ziegler Reservoir site in Snowmass Village, Colorado, revealed over 5,000 fossil bone specimens, including a minimum of four *B. latifrons*, eight to ten American mastodons (*Mammut americanum*), and four Columbian mammoths (*Mammuthus columbi*). It is the highest elevation *B. latifrons* site known, and provides an opportunity to examine high-altitude fossil bison paleoecology.

4.3 - Diamond Valley Lake Reservoir Low-elevation (451 - 481 m) Fossil Site, Hemet, California

The Diamond Valley Lake Reservoir (DVL) assemblage is notable in that it is the largest open-environment, non-asphaltic late Pleistocene assemblage known from the North American southwest (Springer et al., 2009). The DVL site is rimmed by granitic and metamorphic basement rocks, and the basin itself is filled with alluvial sediments with paleosols (Morton, 2004). More recent alluvial fans and recent soils overlie the slopes of the surrounding hills, and older alluvial sediments contain alternating beds of silt, clay, and coarse-grained stream sediments (Springer et al., 2009). This sequence implies a braided stream environment; it is unconformably overlain by an extensive lacustrine unit (Springer et al., 2009). The fossils occurred in the lacustrine unit, and preservation is excellent (Springer et al., 2009).

Approximately 100,000 identifiable fossils, representing 105 distinct taxa were recovered during the 1993-2000 excavation period. Numerous *B. latifrons* and *B. antiquus* specimens are included in the assemblage (Springer et al., 2009). *Bison* sp. is the most abundant large mammal taxon within the assemblage (24%), with some elements identified to species level. This abundance, together with the presence of both *B. latifrons* and *B. antiquus*, makes this site ideal for a study of the relationship between populations of these two species of Pleistocene bison. Other large herbivores present include *Mammuthus* (mammoth), *Mammut* americanum (American mastodon), *Paramylodon harlani, Megalonyx jeffersoni*, and *Nothrotheriops shastensis* (three species of giant ground sloth), *Camelops* (camel), and numerous *Equus* sp. (horse). The presence of *Bison* indicates that the assemblage is Rancholabrean, and sediments from DVL contained wood that was radiocarbon dated to between 48 – 34 ka (Springer et al., 2009).

5 - Methodology

In this study, I sampled as many individuals as possible at each locality, but material was typically limited to only a few individuals of each species. While there is a greater variability of $\delta^{13}C$ and $\delta^{18}O$ values within terrestrial environments than in aquatic ecosystems, Clementz and Koch (2001) determined that a standard error on both $\delta^{13}C$ and $\delta^{18}O$ values within terrestrial populations is 0.01‰ when n=5, and they concluded that five samples is sufficient for the purpose of comparing mean variations between different populations. In fossil collections, it is often impossible to sample this number of individuals from a single site. The methods presented here therefore are less precise than a similar study of modern populations; a slightly greater range of values still provides significant insights into the paleoecology of an extinct species.

I photographed each tooth prior to sampling (Figs. 5-26). Where possible, I sampled M3/m3 molars, as these teeth are biomineralized after the animal is weaned (Gadbury, 2000). This prevents isotopic influence of the mother's milk, thereby achieving a primary signal of the animal being studied (Bryant, 1994). Initially, I used a Dremel rotary tool with a 0.5 mm diamond bit to drill out enamel powder in a serial sequence from the occlusal surface to the root of the tooth, as recommended by Bernard et al. (2009). However, complications in collection and potential cross-contamination from previously sampled surfaces resulted from an air vent directly adjacent to the rotary head of the tool. In subsequent sampling I solved this problem by using a snake attachment on the Dremel tool. This allowed for greater control on the amount of enamel powder collected, and it eliminated the problem of air vented from the Dremel motor blowing powder away. Prior to sampling a tooth, I scoured the surface of the tooth with the Dremel tool, to remove any cementum or secondary calcification from the surface of each sample site. I collected approximately 3 mg of enamel powder from each point on the tooth, and I placed each sample in a plastic centrifuge vial. After I drilled a groove and collected a sample of powder, I cleaned the surface with a combination of brushes and air-blasting in order to remove any excess powder before I began to drill another sample pit.

Back in the lab, I weighed each powder sample and then placed the sample in a 1 mL plastic centrifuge vial. In order to eliminate as much organic material and diagenetic carbonate minerals as possible, I followed the procedure recommended by Koch (1997). I treated each sample with 0.1 volume to sample weight of 30% H_2O_2 and refrigerated it for 24 hours. I agitated the samples three times within this resting period. I then centrifuged each sample for 9 minutes, and removed the H_2O_2. I rinsed the samples with distilled, deionized water four times, and pipetted 0.05 volume to sample weight of 0.1M Ca-buffered acetic acid into each vial. This treatment preserves hydroxylapatite while removing organic matter and secondary adsorbed carbonate (Koch, 1997). I again refrigerated the new solution for 24 hours, and agitated each sample three times prior to the next step. I then aspirated out the acetic acid and washed the samples with 1mL of distilled, deionized water four times. I froze the samples for storage, and finally lyophilized them prior to final processing to remove any excess water.

During processing, each powder sample was transferred from the plastic centrifuge vials into glass vials compatible with the Kiel IV carbonate device, and stored at 60 ^{o}C in the Las Vegas Isotope Science (LVIS) Lab at the University of Nevada Las Vegas. To ensure analytical accuracy, two USC-1 standards were loaded before each run of experimental samples, and one standard at the end of each run. Each sample was processed in the following manner: five drops of phosphoric acid were added to the samples and given 10 minutes to react. Gas was then collected in a trap cooled by liquid nitrogen. The temperature in the trap was lowered to -170^{o}C to freeze excess water, and it was then heated to -90 °C to allow CO_2 gas to escape into a Thermo Electron Delta V Plus Mass Spectrometer, where the ratio of heavy to light isotopes was measured and reported to the control station.

Mechanical issues led to downtime in the LVIS Lab, and subsequent samples were run at the University of Utah Stable Isotope Ratio Facility for Environmental Research (SIRFER) to maintain a reasonable timetable for the project.

Percentage of C_4 plants consumed was calculated following the methodology of Koch et al. (1998). Atmospheric CO_2 is assigned an average value of 0.5‰ based on a range for glacial to interglacial times. The $\delta^{13}C$ value for a pure C_4 feeder is assigned to be 1.6‰ and a pure C_3 browser has a $\delta^{13}C$ value of about -12.4‰. X represents the percent of C_4 plants consumed in the following equations:

$$\delta^{13}C_{\text{apatite}} = (\delta^{13}C \text{ pure } C_4 \text{ feeder})(X) + (\delta^{13}C \text{ pure } C_3 \text{ feeder})(1 - X)$$

or

$$X = (\delta^{13}C + 12.4)/14$$

6 - Results and Interpretation

Data from all three sites are presented here, and summarized in Table 1. Each site is given its own section, with photos of individual teeth displayed next to their respective graphs. Interpretations for each site follow the graphs, and raw data may be found in Appendices (2-6).

Table 1: Isotopic mean values for each individual sampled in this study, with percent C_4 plants consumed. Percentage is calculated following the methodology of Koch et al. (1998).

Specimen ID	Locality	Species	$\delta^{13}C$	$\delta^{18}O$	Percent C4
IMNH 17906	American Falls	*Bison latifrons*	-7.33	-5.61	36.18
IMNH 17909	American Falls	*Bison latifrons*	-7.91	-6.70	32.08
IMNH 17922	American Falls	*Bison latifrons*	-7.79	-10.71	32.90
IMNH 17931	American Falls	*Bison latifrons*	-6.69	-12.20	40.77
IMNH 17930	American Falls	*Bison latifrons*	-8.35	-9.25	28.96
IMNH 17917	American Falls	*Bison latifrons*	-7.34	-9.56	36.15
IMNH 17915	American Falls	*Bison latifrons*	-8.61	-10.51	27.06
Site Average	**American Falls**	***Bison latifrons***	**-7.72**	**-9.22**	**33.43**
L2726-16708	Diamond Valley Lake	*Bison latifrons*	-11.07	-10.35	9.50
L2726-10492	Diamond Valley Lake	*Bison latifrons*	-11.43	-8.56	6.93
L2726-22118	Diamond Valley Lake	*Bison latifrons*	-8.56	-8.48	27.43
L2726-22135	Diamond Valley Lake	*Bison latifrons*	-9.50	-8.40	20.71
Site Average	**Diamond Valley Lake**	***Bison latifrons***	**-10.13**	**-8.94**	**16.21**
L2726-775	Diamond Valley Lake	*Bison antiquus*	-10.23	-9.48	15.50
L2726-4039A	Diamond Valley Lake	*Bison antiquus*	-9.38	-8.26	21.57
L2726-4039B	Diamond Valley Lake	*Bison antiquus*	-10.46	-7.92	13.86
L2726-21338C	Diamond Valley Lake	*Bison antiquus*	-6.82	-6.66	39.86
Site Average	**Diamond Valley Lake**	***Bison antiquus***	**-9.22**	**-8.08**	**22.71**
Site Average	**Diamond Valley Lake**	**Combined**	**-9.68**	**-8.51**	**19.43**
DMNH 60.703	Snowmastodon	*Bison latifrons*	-7.72	-13.63	33.43
DMNH 58.446	Snowmastodon	*Bison latifrons*	-7.24	-12.44	36.86
DMNH 59.005	Snowmastodon	*Bison latifrons*	-7.30	-15.22	36.43
DMNH 56.322	Snowmastodon	*Bison latifrons*	-7.06	-12.48	38.14
DMNH 67.512	Snowmastodon	*Bison latifrons*	-7.98	-12.14	31.57
DMNH 67.517	Snowmastodon	*Bison latifrons*	-5.75	-16.28	47.50
DMNH 67.505	Snowmastodon	*Bison latifrons*	-7.82	-12.92	32.71
DMNH 67.503	Snowmastodon	*Bison latifrons*	-7.37	-11.51	35.93
Site Average	**Snowmastodon**	***Bison latifrons***	**-7.32**	**-13.11**	**36.29**
Taxon Average	**Combined**	***Bison latifrons***	**-8.39**	**-10.42**	**28.64**
Taxon Average	**Combined**	**Combined**	**-8.60**	**-9.84**	**27.16**

6.1 - American Falls Formation Results

Measured isotopic values of teeth from the American Falls Formation (AF) yielded mean δ^{13}C values between -8.61 to -6.69‰ VPDB, while mean δ^{18}O values range from -12.20 to -5.61‰ VPDB. The mean values for the site are -7.72‰ δ^{13}C VPDB and -9.22‰ δ^{18}O VPDB. Specimen IMNH 17906 exhibits a spike in δ^{18}O at +7.0‰. This anomalously high value has been omitted from calculations as it was likely an error that occurred during processing. The magnitude of intra-population variation caps at ± 6.59‰ VPDB. The most depleted δ^{13}C value within the population is -10.6 ‰ VPDB. The maximum variation between bulk δ^{13}C values among the population is ± 1.92‰ VPDB. Several teeth (IMNH 17922, 17930, 17931, 17915) do not have values plotted near the occlusal surface due to lack of pristine enamel, complications during preparation, or analysis that produced unreliable results.

Several teeth sampled at this location exhibited intervals of positive covariation. IMNH 17906 displays positive covariation near the occlusal surface of the tooth, and also toward the root, but negative covariation near the midpoint of the tooth from 12 to 27 mm (Fig. 5). A δ^{18}O value is not plotted at 7.5 mm; the value reported by the lab was +7.0‰, which (compared to a δ^{13}C value of -7.5‰) is clearly a spurious value. Positive covariation between both isotopic systems is seen throughout IMNH 17909 (Fig. 6). The greatest change in values is seen approaching 17 mm, with a maximum δ^{18}O shift of ± 6.1‰. IMNH 17922 displays positive covariation between both isotopic systems near the root of tooth (Fig. 7). δ^{18}O is more variable than oxygen within this tooth. δ^{13}C is relatively consistent, with a range of ± 0.9‰. The majority of samples were taken near the root, as pristine enamel powder was unobtainable closer to the occlusal surface

IMNH specimens 17931, 17930, 17917, and 17915 present a more complex pattern of negative covariation between isotopic systems, particularly specimens IMNH 17915 and 17917, while maintaining a mean deviation of ± 5.4‰.

IMNH 17931 displays negative covariance of the two isotopic systems throughout the midsection of the tooth. $\delta^{18}O$ is more variable than carbon, with a maximum difference of ± 2.65‰, while $\delta^{13}C$ varies roughly ± 1.0‰. Enamel closer to the occlusal surface did not yield pristine powder from this tooth.

IMNH 17930 displayed the highest variability in $\delta^{18}O$ values seen at this location (Fig. 9). Value vary up to ± 7.1‰, and ± 1.2‰ in $\delta^{13}C$. Values closer to the occlusal surface were unreliable due to small sample size.

IMNH 17917 displays relatively constant $\delta^{13}C$ values, only varying ±1.9‰, while $\delta^{18}O$ exhibits much greater variability. $\delta^{18}O$ ranges from -12.7‰ to -5.1‰ Negative covariance is seen at various sections of the tooth, notably from 5 – 14 mm and from 23 – 32 mm.

A correlation is seen between both isotopic systems in IMNH 17915 from 29 – 47 mm, where oxygen becomes more negative, while carbon values increase in the positive direction (Fig. 11). This trend continues until 41 mm, where the values of both systems begin to converge.

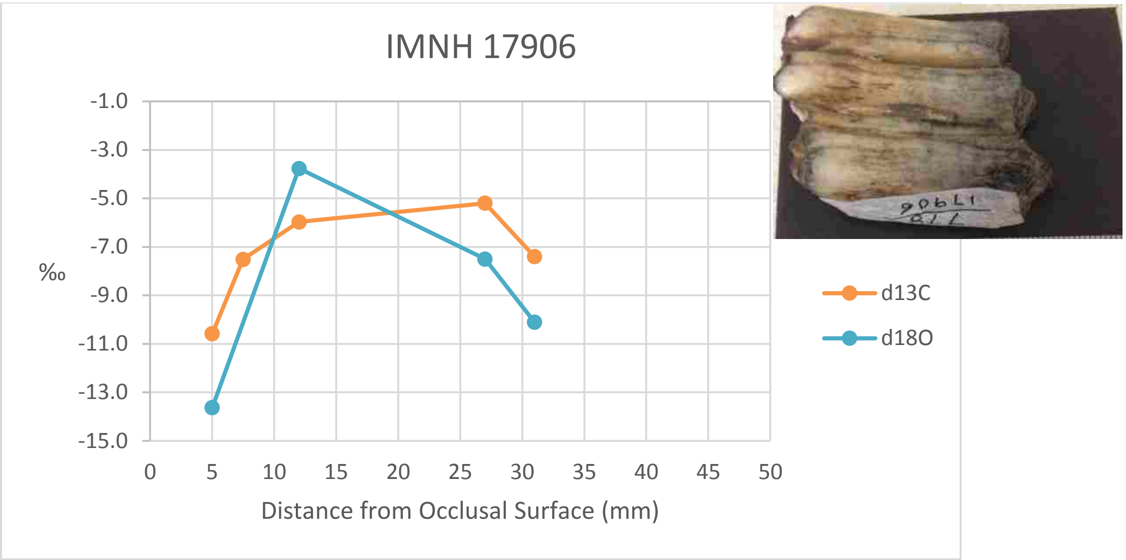


Figure 5: IMNH 17906. Note positive covariation near occlusal surface and also toward root. Negative covariation from 12-27 mm (near midpoint).

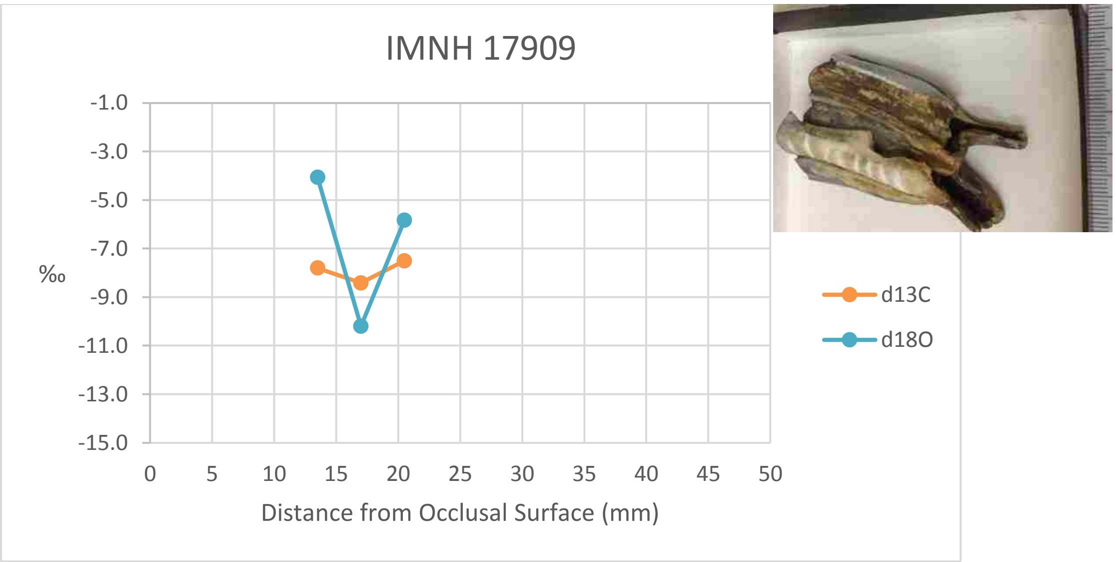


Figure 6: IMNH 17909. Positive covariation near midpoint of tooth. Values from other locations in this tooth are not due to loss during preparation or contamination during analysis.

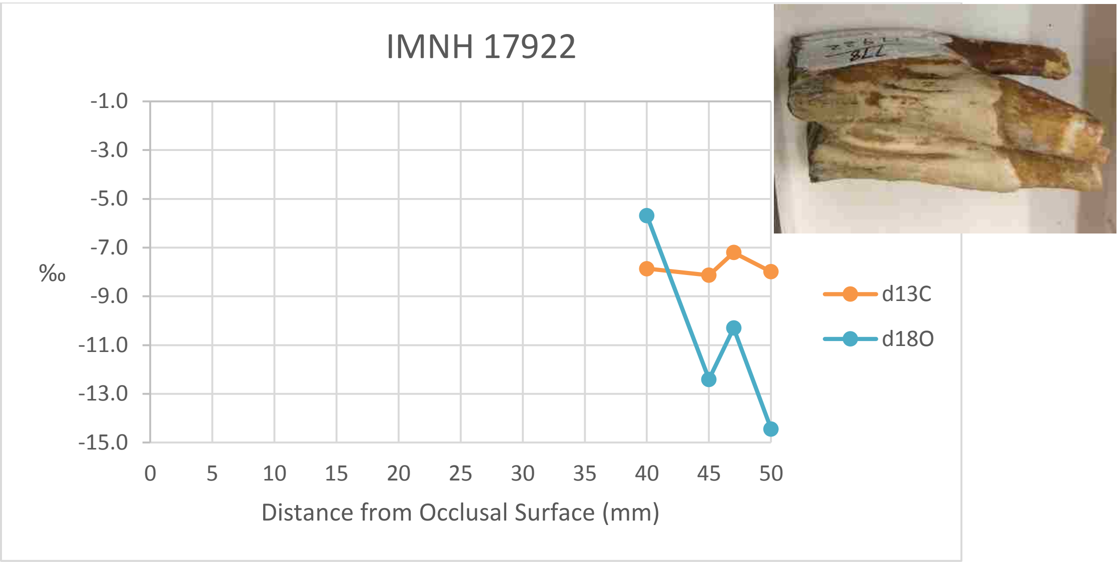


Figure 7: IMNH 17922. Samples taken near root, showing pattern of positive covariation between isotopic systems. Values from closer to the occlusal surface were unreliable based on known isotopic ranges in a biogenic system, or due to errors during preparation or analysis.

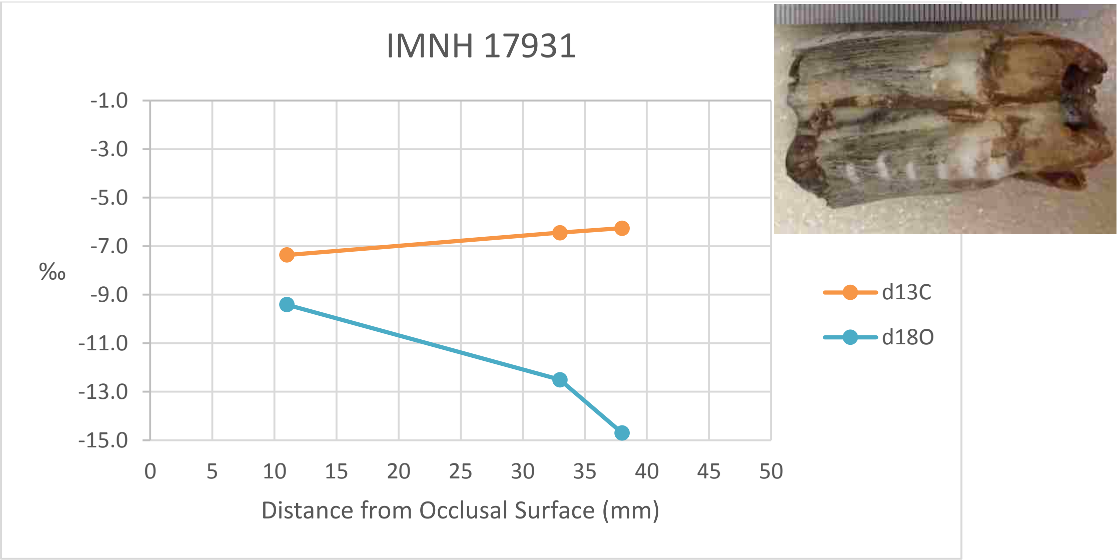


Figure 8: IMNH 17931. Note negative covariance throughout tooth. Enamel near occlusal surface provided brown/tan powder, as opposed to the pristine white seen in samples that yielded reliable results.

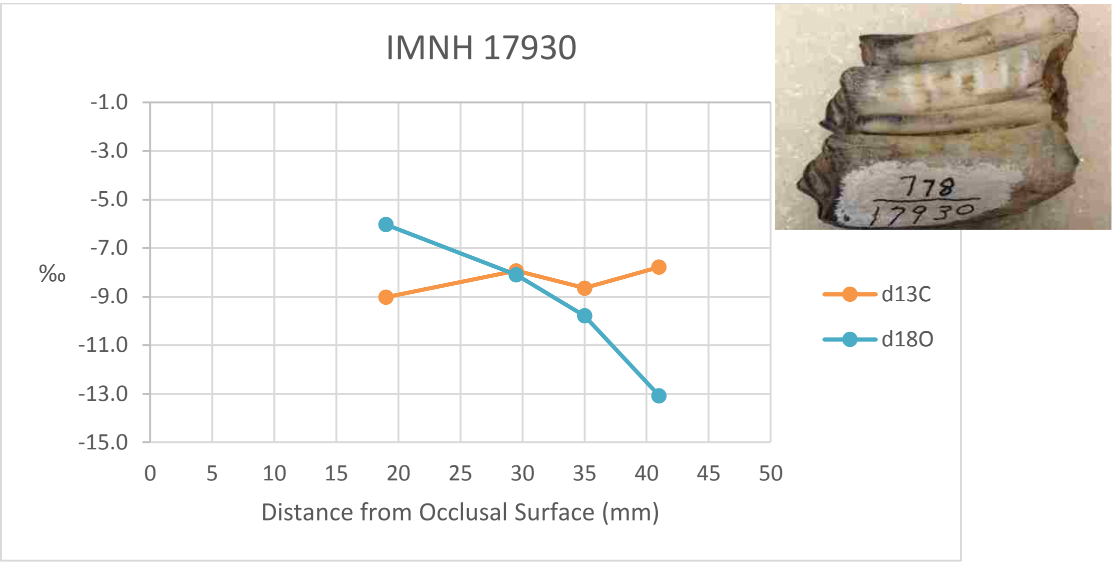


Figure 9: The maximum difference in δ ^{18}O values in IMNH 17930 is 7.1‰, and 1.2‰ in δ ^{13}C. Values closer to the occlusal surface were unreliable due to small sample size.

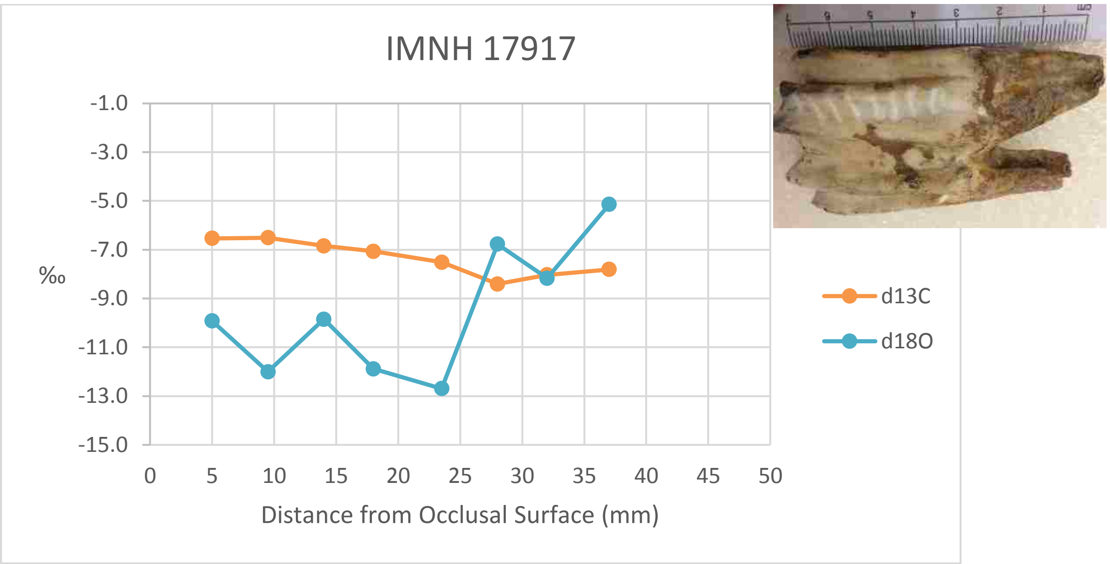


Figure 10: IMNH 17917. Negative covariance is seen at various sections of the tooth, particularly from 5 – 14 mm and from 23 – 32 mm.

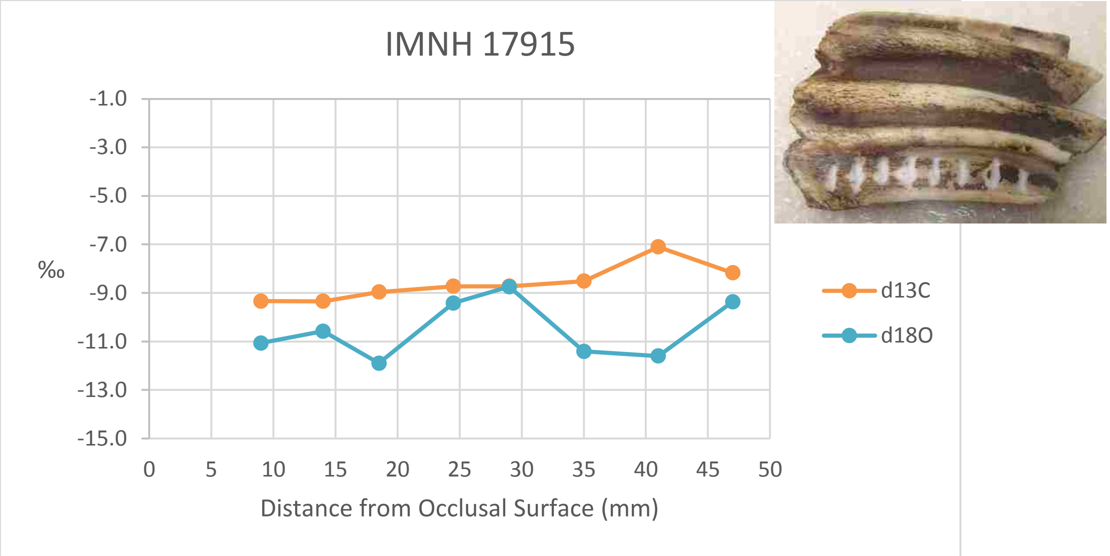


Figure 11: IMNH 17915. Negative covariation occurs between systems throughout tooth. Values converge toward midpoint and again near root.

6.2 - American Falls Formation Interpretation

The American Falls (AF) population of *B. latifrons* all consumed greater than 25% C_4 plants. A majority was measured to have consumed greater than 32%, implying that a full third of their diets consisted of C_4 plants at this location. A diet consisting of such a large percentage implies that C_4 plants were readily available during the interval in which the AF fauna was preserved (125 – 72 ka). *B. latifrons* in this habitat presumably incorporated a significant amount of C_4 material into its diet due to the abundance of warm-weather grasses.

A positive rootward shift in $\delta^{13}C$ fractionation implies that the relative abundance of C_4 plant material in the animal's diet increased during the interval of time that the sampled tooth was mineralizing. This is a trend seen in the majority of individuals sampled from this population (Figs. 8, 9, 10, 11).

Changes in $\delta^{18}O$ values imply a change in temperature, with more negative values as a signal of cooler climate. The variation in $\delta^{18}O$ may also indicate a change in feeding location, especially when it occurs in conjunction with variation in $\delta^{13}C$ values. A positive rootward shift in $\delta^{18}O$ indicates that the animal experienced an increase in ambient temperature, which could be the result of seasonality, movement to a lower elevation or lower latitude, or some combination of these factors. When coupled with a positive shift in $\delta^{13}C$, I interpret the animal to have moved to a warmer location, and possibly a lower elevation, with a higher percentage of C_4 grasses occurring where the weather is warmer (Fig. 4). Similar behavior has been documented in historic American and European bison, which undergo home range contraction of up to 32 km and migrate to lower elevations (downslope 1300 - 1700 m) during winter (van Vuren, 1983, Kowalczyk et al., 2013). Modern populations exhibit such patterns despite artificial barriers; prehistoric bison would have had greater freedom to migrate during cold periods.

AF teeth 17906 and 17909 (Figs. 5, 6) show slight positive correlation trends, as carbon isotopes indicate that the animals consumed a modestly higher amount of C_4 plants during warm intervals, but their diets remained constant otherwise. Teeth 17931 and 17930 (Figs. 8, 9) exhibit sharp declines in $\delta^{18}O$ values, while $\delta^{13}C$ values remain fairly constant; this suggests that the animals' diets were not linked to changing temperature. AF teeth 17922, 17917 and 17915 (Figs. 7, 10, 11) are notable in that the individuals sampled were subject to a much wider range of temperatures, but maintained a relatively constant $\delta^{13}C$ level between -9 and -7‰; this indicates that these animals consumed roughly 30% C_4 plants regardless of climate. AF teeth 17917 and 17915 in particular experienced multiple cold intervals, probably within the span of a single year.

The areas inhabited by this population were open, with high insolation and a high minimum growing-season temperature (Terri and Stowe, 1976). The warm climate of the Sangamon Interglacial compared to modern conditions was conducive to the expansion of C_4 plants, especially in a mid-elevation (1,330 m) site such as the AF locality. The isotopic data thus support Pinsof's (1992) interpretation of a grassland/steppe-dominated environment. The data also demonstrate that *B. latifrons* exhibited dietary plasticity in this environment. Evidence for indiscriminate grazing and browsing is apparent in the mean $\delta^{13}C$ value of -7.72‰ of the population at this site, which is notably more enriched than values expected of a C_3 specialist, yet not as extreme as a C_4 exclusive feeder.

Only one individual at the AF site, 17906 (Fig. 5), conforms to the seasonal signal displayed in the hypothetical nonmigratory tooth. The rest of the teeth with enough data to address this question diverge from this pattern, indicating a different behavioral pattern.

6.3 - Snowmastodon Results

Initial results from the Snowmastodon site in Snowmass, CO were inconclusive. The majority of samples were determined to be inaccurate representations of the isotopic values of the sites. Measured $\delta^{13}C$ values have a range between -5.34 to +8.93‰ VPDB, with a mean value of +0.93‰. The range in $\delta^{18}O$ values is -8.99 to -5.20‰ VPDB, with a site average of -7.49‰. DMNH 60.703 and DMNH 56.322 in particular display extreme variation in carbon values, on the order of ± 13‰, while oxygen values stay relatively consistent. These samples were determined to be problematic due to losing too much mass during preparation, or contaminated by water while in transition from carbonate device to mass spectrometer. My original sampling method did not include a snake attachment on the Dremel tool, which may have contributed to cross-contamination of sample points. Additionally, the surface of each tooth contains secondary material, which must be scoured using physical or chemical means from the surface. In most cases, the drilling depth was not sufficient to penetrate this layer, and enamel powder collected was typically light tan to brown in color.

Due to these problematic results, I resampled teeth from the Snowmastodon site, using a revised sampling technique. Enamel powders collected during this process were uniformly white in color, which is characteristic of successful samples from other sites in this study. Some previously sampled portions of the teeth were excluded from sampling, mainly near the midsection to root. This was due to the inability to separate enamel from dentin in these locations. Results from the second round of sampling appear to be primary signals, and reflect a range of values that are reasonable for a site such as Snowmass.

Second round $\delta^{13}C$ values at Snowmastodon have a range from -9.1 to -4.7‰ (Appendix 5). The mean $\delta^{13}C$ value for the population is -7.32‰ (Table 1). The magnitude of intrapopulation $\delta^{13}C$ variance is ±4.4‰, and the maximum variation among bulk values for individuals is ±2.23‰. The mean $\delta^{18}O$ value is -13.11‰, with a range from -16.28 to -11.51‰ (Table 1). The range of oxygen values is greater than that of AF.

DMNH 60.703, 58.446, and 67.505 display positive covariation between isotopic systems from occlusal surface to roughly halfway down the tooth (Figs. 12, 13, 18). DMNH 67.512 and 67.503 display negative covariation between systems, trending toward convergence of values (Figs. 16, 19). In DMNH 67.512, the values diverge once again at 21 mm (Figs. 16). DMNH 59.005 and 67.517 display relatively enriched carbon values in the presence of significantly depleted oxygen values (Figs. 14, 17). DMNH 56.322 primarily displays positive covariance between both systems, with the exception of a short interval of convergence from 3 to 15.5 mm (Fig. 15).

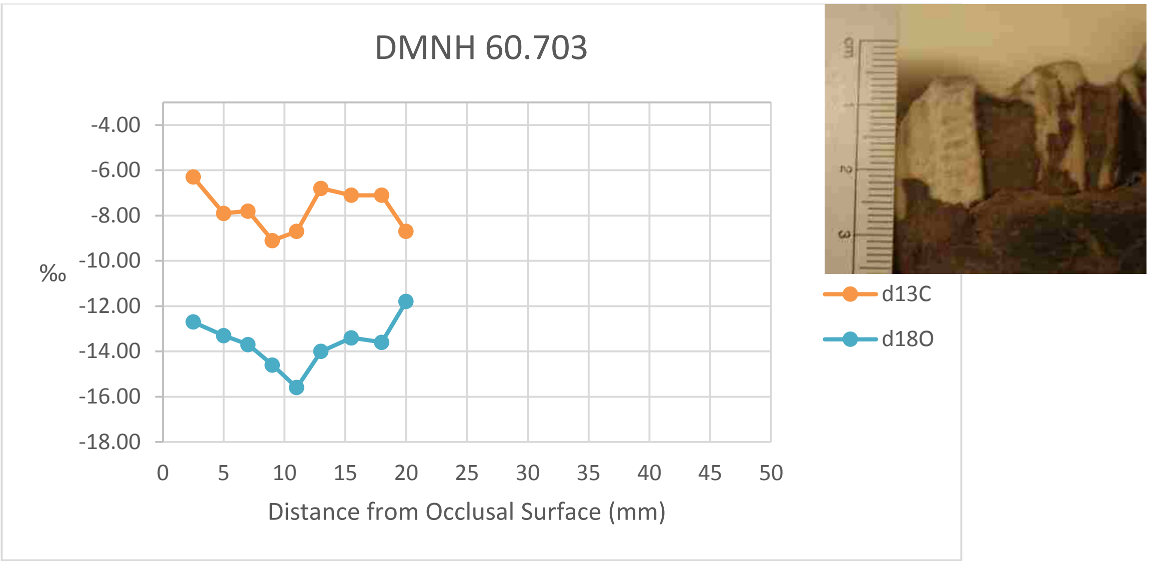


Figure 12: DMNH 60.703. Note positive covariance from 2.5 to 13 mm, followed by convergence toward midpoint of tooth. Further sampling was prevented by presence of the alveolus.

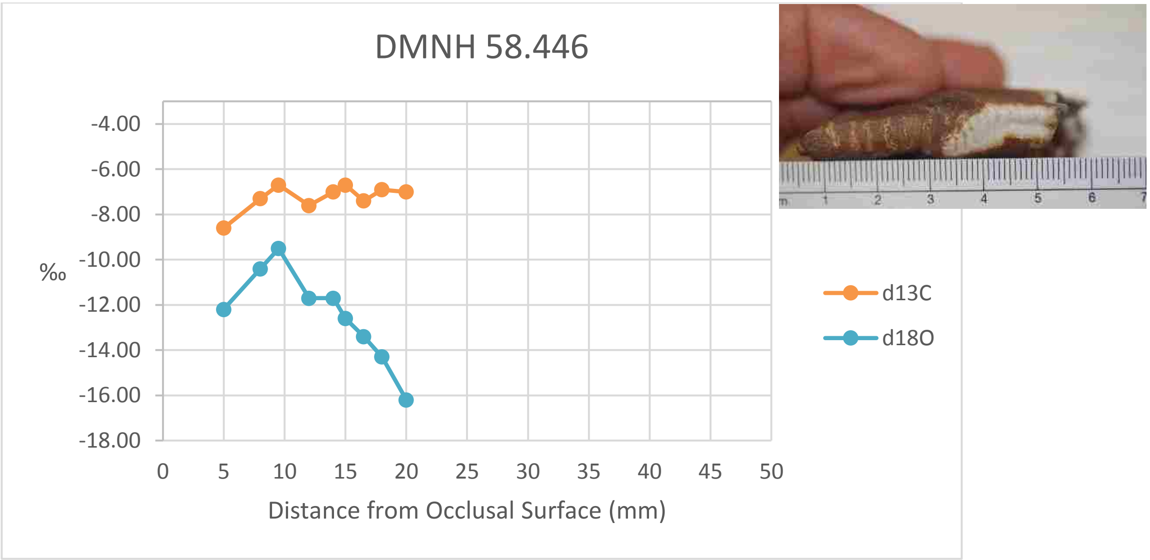


Figure 13: DMNH 58.446. Note extreme depletion of δ^{18}O toward midpoint. Samples from past midpoint provided unreliable values, as enamel was not pristine past this point.

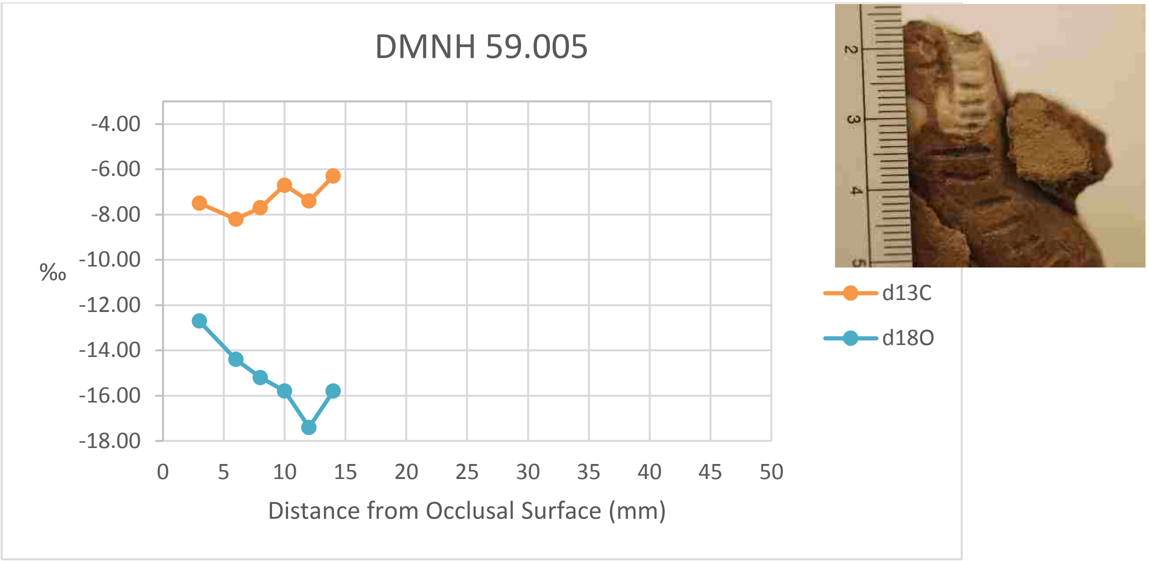


Figure 14: DMNH 59.005. Negative covariance appears between both isotopic systems near occlusal surface until 12 mm. Samples past 14 mm were not pristine

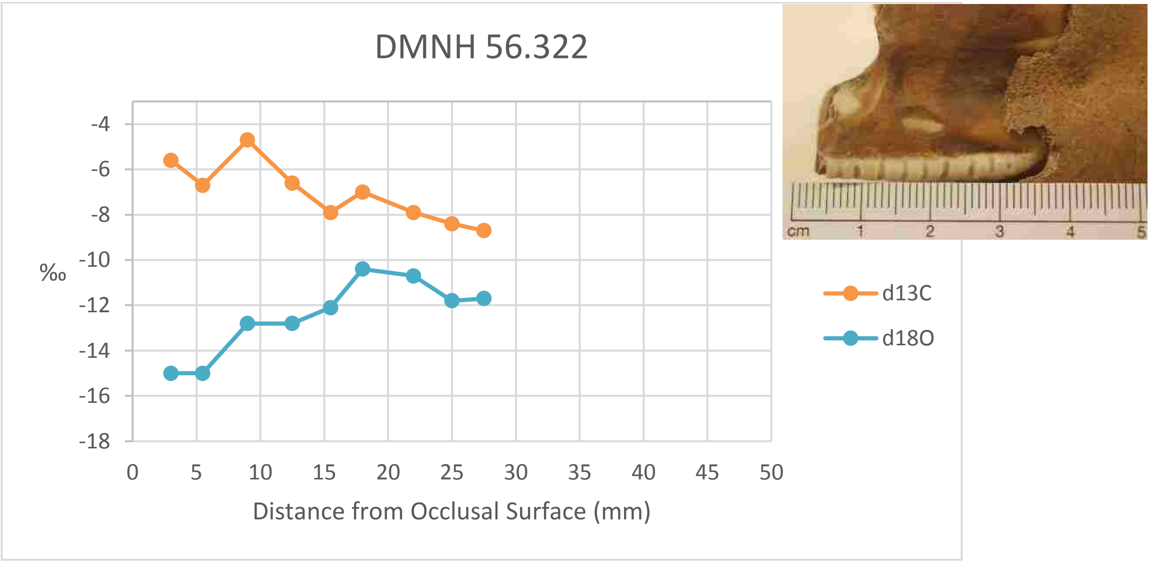


Figure 15: DMNH 56.322. Note predominantly declining δ^{13}C values from 9 to 27.5 mm, despite enriched δ^{18}O values.

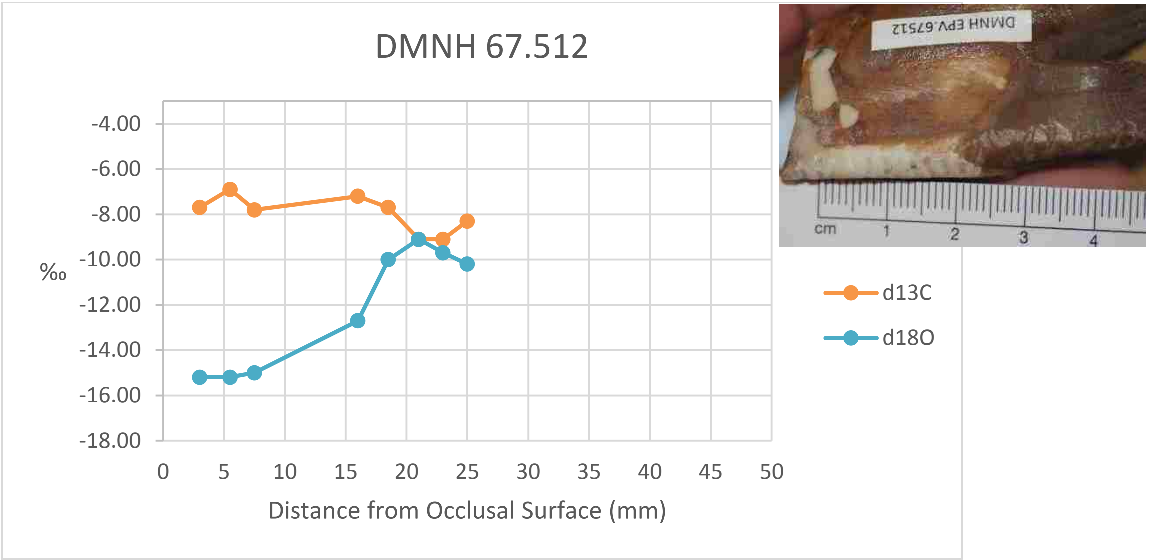


Figure 16: DMNH 67.512. Original sampling was under specimen ID: DMNH 58.394. Note peak δ^{18}O value near midpoint of tooth (21 mm), followed by negative covariation of isotopic systems afterwards.

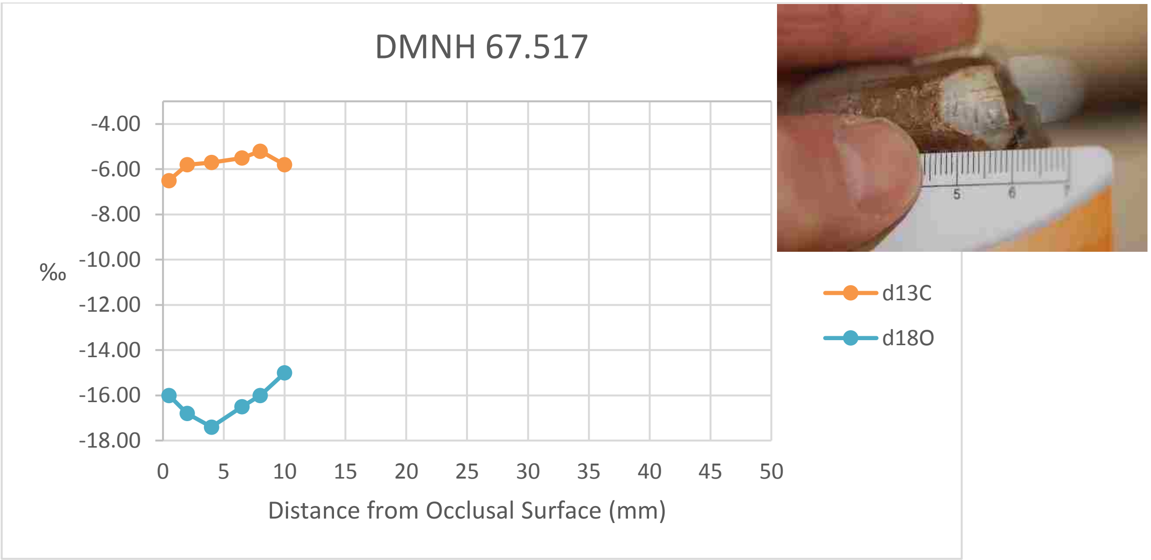


Figure 17: DMNH 67.517. Original sampling under specimen ID: DMNH 60.022. δ^{18}O is more variable than δ^{13}C in this tooth. Positive covariation runs from 4 to 8 mm. Further samples were unreliable based on first-round sampling, as enamel powder was no longer pristine.

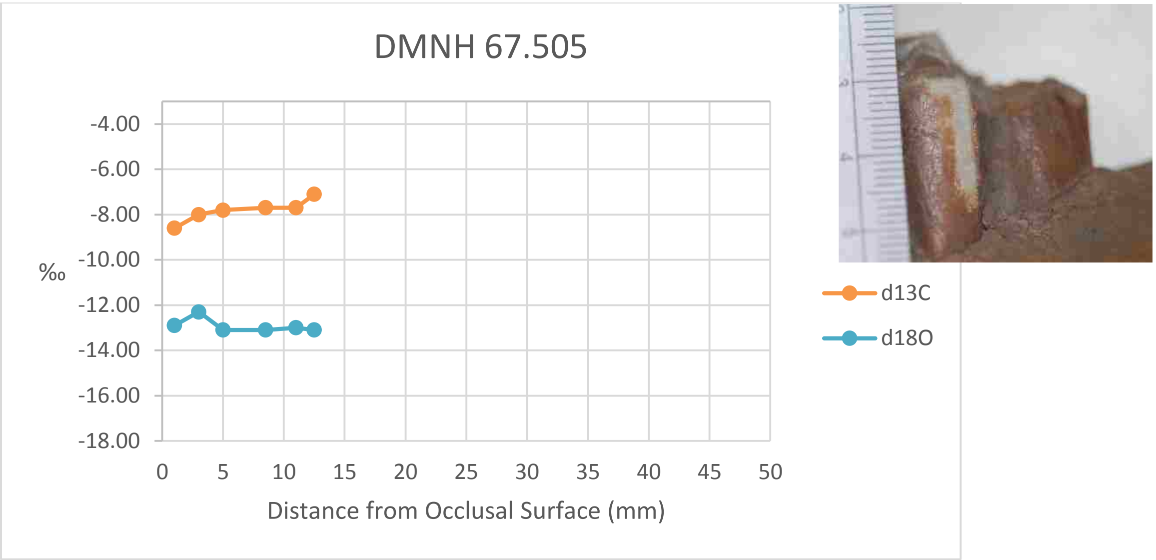


Figure 18: DMNH 67.505. Positive covariation is dominant throughout the tooth, until 11mm. Note consistent values in both isotopic systems from 5 to 11 mm. Further sampling was prevented by the presence of the alveolus.

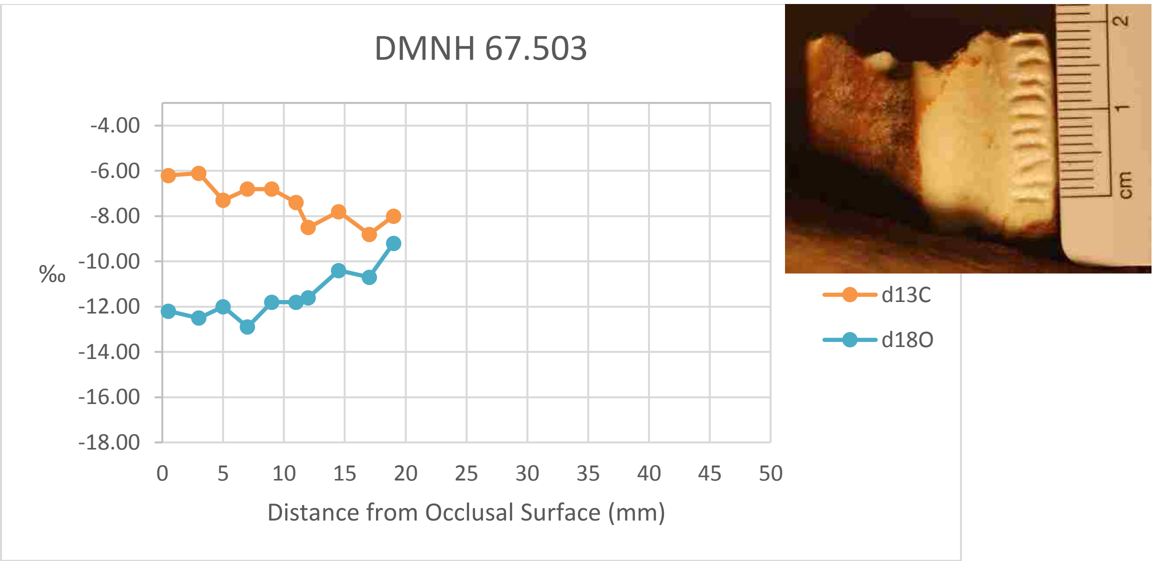


Figure 19: DMNH 67.503. Negative covariation begins near occlusal surface until 12 mm, where positive correlation becomes the dominant trend. Further sampling was blocked by the presence of the alveolus.

6.4 - Snowmastodon Interpretation

Snowmastodon is a unique site in that it is the highest elevation (2,087 m) assemblage known to contain *B. latifrons*. The animals here were exposed to a colder climate than those at the other sites in this study. The plant material at this site was expected to have been comprised of a higher percentage of C_3 vegetation, due to its high altitude and low temperatures. On average, *B. latifrons* at this site consumed 36.29% C_4 vegetation (Table 1), indicating a greater availability of C_4 plants at the site than expected. The majority of individuals exhibited a relatively stable $\delta^{13}C$ signal, similar to the patterns seen at AF.

The population at Snowmastodon displays an intermediate degree of seasonality. The isotopic spread of $\delta^{18}O$ is ± 4.77‰, which lies between the isotopic width of AF and DVL. Oxygen values shift roughly with the onset of each season, but overall the data are significantly more depleted and confirm a much colder environment at Snowmastodon than the other sites in this study. These shifts are sometimes correlated with significant shifts in $\delta^{13}C$ (Figs. 15, 16), but the majority of $\delta^{13}C$ values remain relatively constant (Figs. 13, 14, 17, 18). This is evidence for a decoupled relationship between season and diet in the Snowmastodon population.

B. latifrons values at the Snowmastodon site display a similar $\delta^{13}C$ signal regardless of season, which corresponds with the primary pattern seen at AF. They apparently consumed whatever vegetation was available, and maintained this diet during seasonal changes. Bison recovered from this site may have been migratory, and the presence of this pattern at two independent sites is an indicator of similar behavior in the absence of the closely related *B. antiquus*.

Of the teeth sampled, DMNH 56.322, 60.703 and 59.005 share similarities to the hypothetical “homebody bison” in that positive covariation is seen between both isotopic systems during expected seasonal intervals (Fig. 4). However, teeth 60.703 and 59.005 have evidently lost several mm due to wear (Figs. 12, 14).

6.5 - Diamond Valley Lake Results

The Diamond Valley Lake Reservoir (DVL) fauna contains a mix of *B. latifrons* and *B. antiquus*, which provided the opportunity to directly compare the diets of these closely related taxa. *B. latifrons* recovered from the DVL site displayed an average $\delta^{13}C$ value of -10.13‰, and $\delta^{18}O$ of -8.94‰ VPDB (Table 1). On average, the population at this site consumed about 16% C_4 vegetation, but the values are highly variable, ranging from about 7% in one animal to about 27% in another (Table 1).

Positive covariance of the two isotopic systems is seen in all teeth with the exception of specimen WSC 22135, in which they diverge roughly halfway down the tooth. In contrast to *B. latifrons*, *B. antiquus* at the DVL site consumed an average of 22.71% C_4 plants (Table 1). The mean $\delta^{13}C$ value of the population was -9.22‰ VPDB, with a maximum of -6.82‰ and minimum of -10.46‰. Average $\delta^{18}O$ was measured to be -8.08‰ VPDB, with an absolute variation of 2.82‰ (Table 1).

B. latifrons teeth at this location show a trend of positive covariance until the midpoint of each tooth, where the values begin to diverge. This is seen in teeth WSC 16708, 10492, and 22135. It is unknown whether tooth 22118 exhibits this behavior, as samples near and proximal to the midpoint were contaminated or lost during preparation and analysis.

In *B. latifrons* tooth WSC 16708, the sample taken at 2 mm contains an unusually negative, and potentially spurious $\delta^{13}C$ value of -21.8. The remainder of carbon values range between -11.5‰ and -8.3‰ VPDB, with an absolute variation of 3.2‰ (Fig. 20). Oxygen values exhibit positive covariance with oxygen values until the midpoint of the tooth at H1E (11 mm) and again at H1K (23 mm). Tooth WSC 10492 exhibits a $\delta^{13}C$ range of ± 3.5‰ VPDB and a relatively narrow $\delta^{18}O$ range of ± 2.1‰ VPDB (Fig. 21). Tooth WSC 22135 exhibits slight negative covariance between sample sites H8C (12 mm) and H8J (36 mm), followed by convergence toward the root (Fig. 23). $\delta^{13}C$ varies ± 2.6‰ VPDB, while $\delta^{18}O$ is more variable, with an absolute difference of ± 3.5‰.

The three DVL *B. antiquus* teeth display generally positive covariance of carbon and oxygen values (Figs. 24, 25, 26), although WSC 775 displays negative covariance in the middle of the tooth (Fig. 24). This tooth has a maximum $\delta^{13}C$ value of -7.2‰ VPDB, with a minimum value of -14.2‰ (Fig. 24). $\delta^{18}O$ values range from a maximum value -7.9‰ to a minimum of -10.8‰.

B. antiquus specimens WSC 4039A & 4039B are from the same individual (Fig. 25). Both specimens were m3 molars from opposite sides of the mandible, providing the opportunity to roughly confirm the accuracy of serial sampling of an individual's tooth. A $\delta^{13}C$ range of only ± 0.5‰ VPDB and a $\delta^{18}O$ range of ± 1.1‰ was seen between the two sides of the mandible. Positive covariance is seen throughout the tooth. $\delta^{13}C$ values have a maximum difference of ±5.3‰ and $\delta^{18}O$ values display a maximum difference of ± 5.4‰.

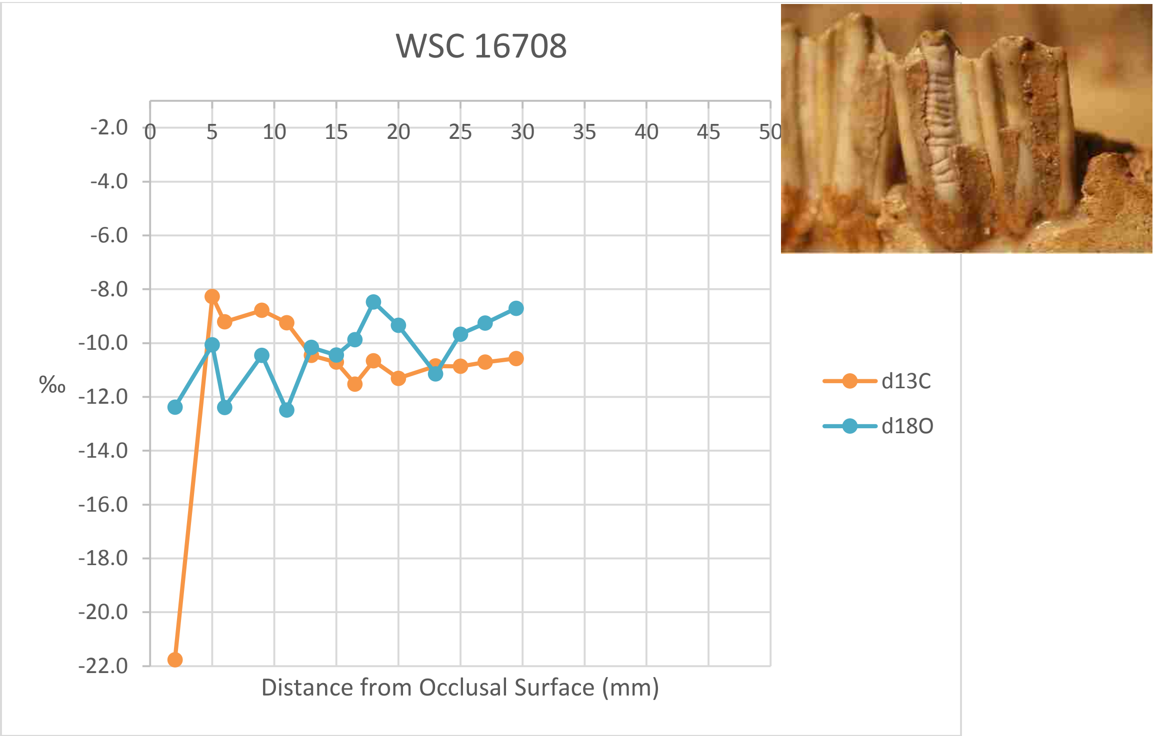


Figure 20: WSC 16708, *B. latifrons*. Note positive covariance near occlusal surface, divergence near midpoint, and reconvergence near root. Sample at 2 mm contains a potentially spurious δ^{13}C value of -21.8‰.

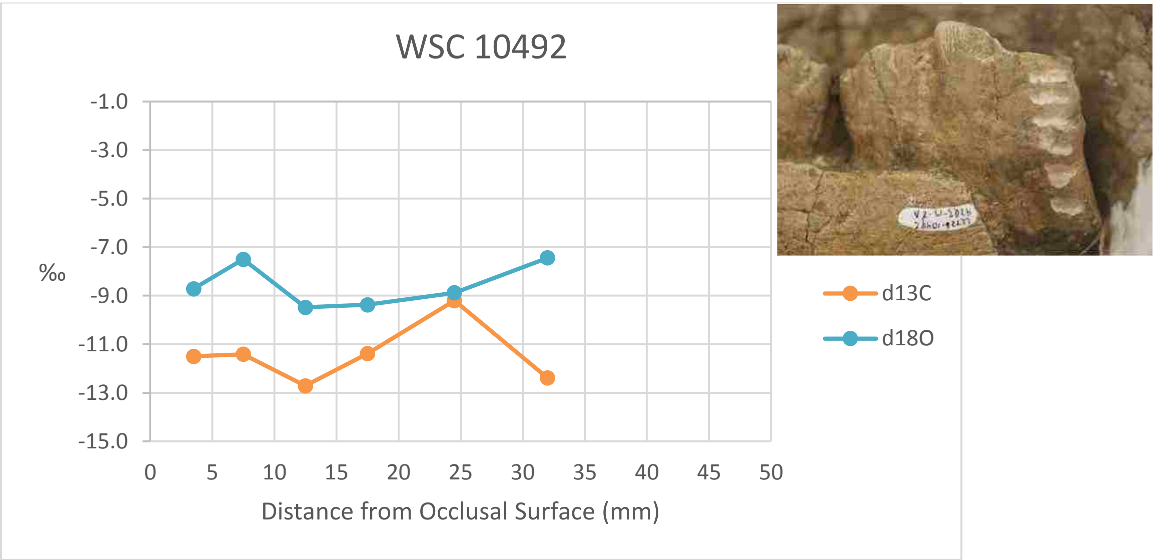


Figure 21: WSC 10492, *B. latifrons.* Note negative covariance in most proximal segment (24.5 to 32 mm).

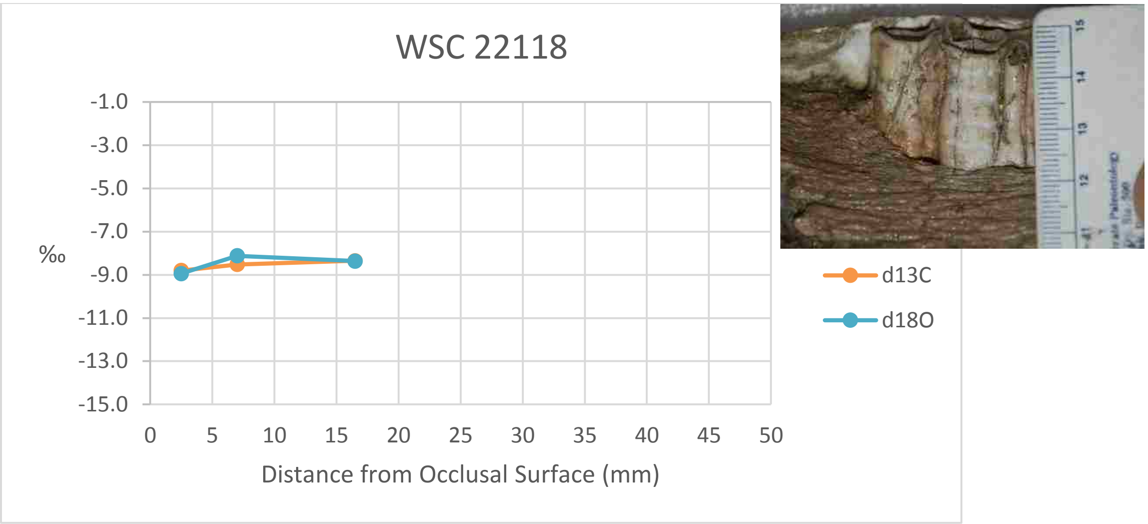


Figure 22: WSC 22118, *B. latifrons.* Enamel from distal portion was lost during preparation and analysis.

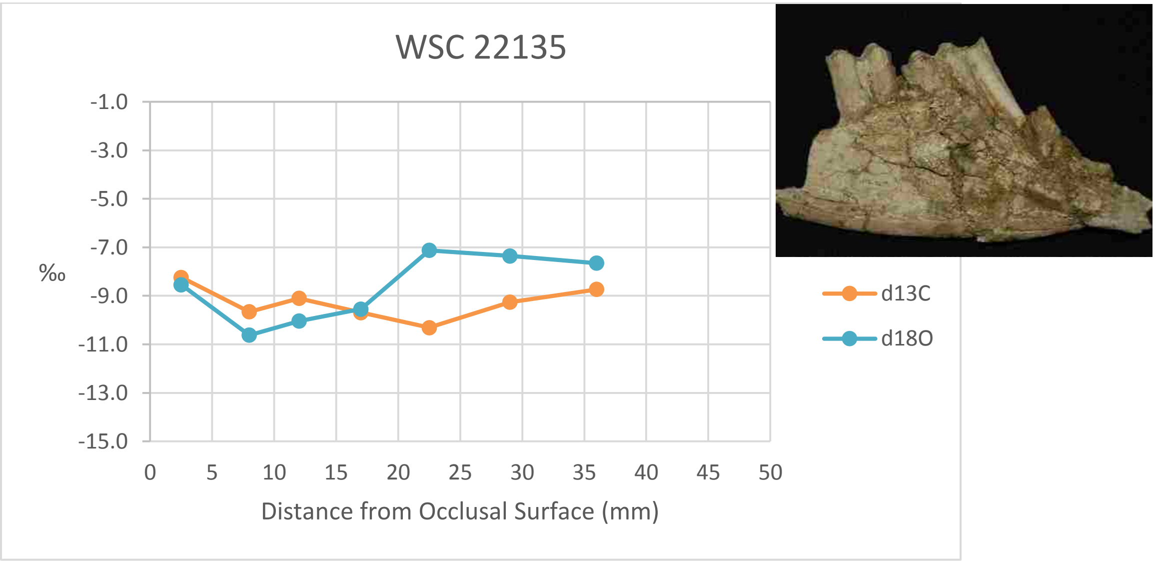


Figure 23: WSC 22135, *B. latifrons*. Note negative covariance between sample sites H8C (12 mm) and H8J (36 mm).

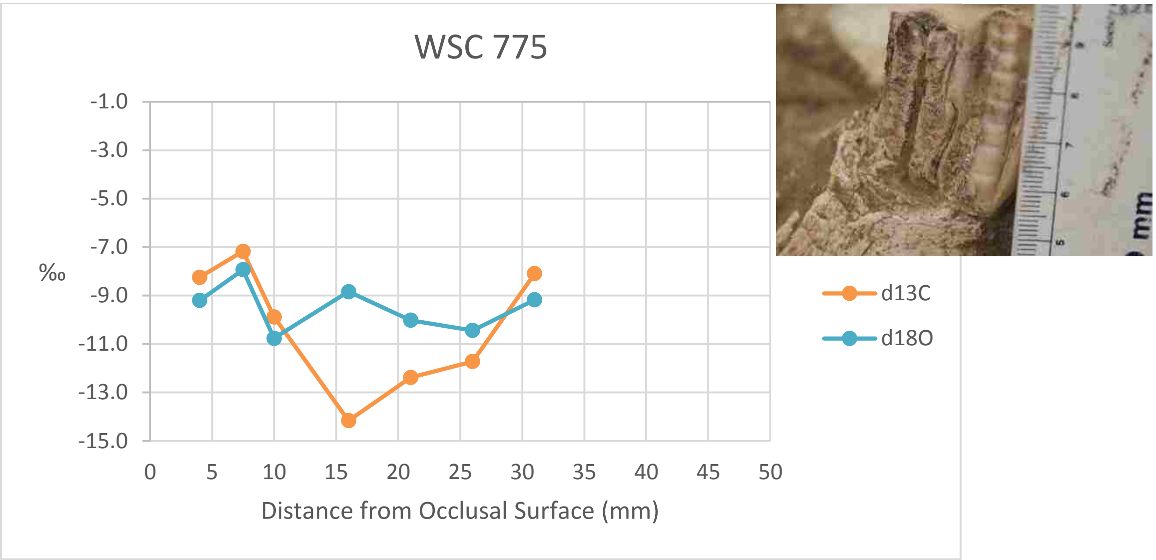


Figure 24: WSC 775, *B. antiquus.* Negative covariance near midsection of tooth, from 11 mm to 26 mm.

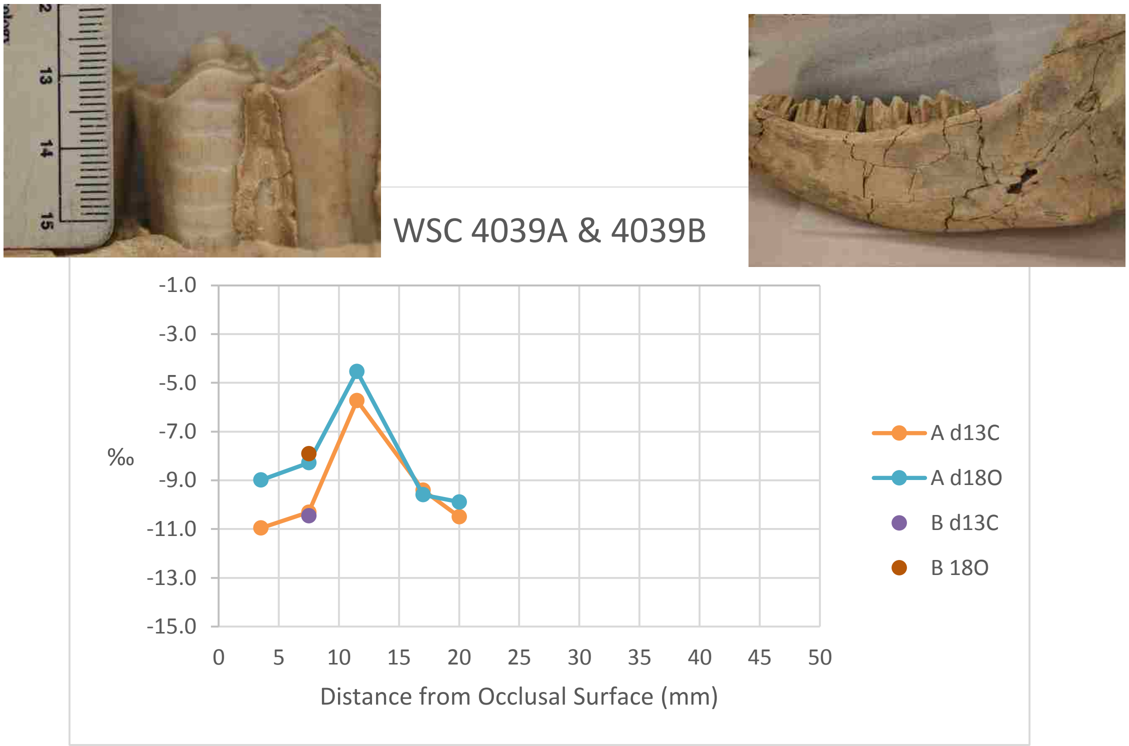


Figure 25: WSC 4039A & 4039B, *B. antiquus.* Both samples from same individual, opposite sides of the mandible. Note positive covariance throughout sampled locations, and close proximity between A and B teeth.

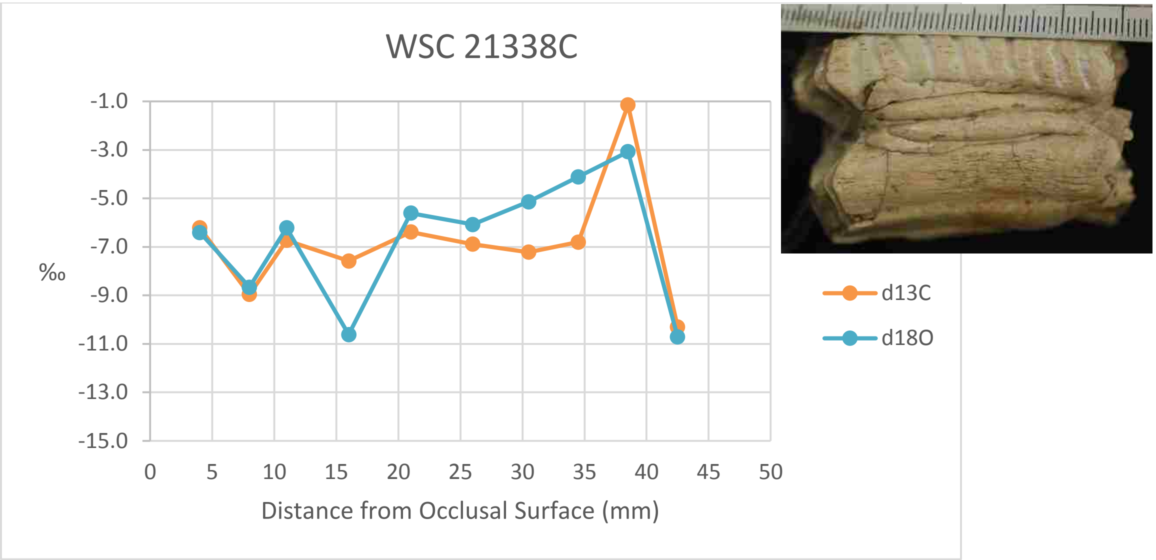


Figure 26: WSC 21338C, *B. antiquus.* Note increased variability of oxygen values with respect to carbon.

6.6 - Diamond Valley Lake Site Interpretation

The Diamond Valley Lake (DVL) assemblage provided the opportunity to directly compare individuals of both *Bison latifrons* and *Bison antiquus*. The two species of bison presumably occurred contemporaneously at this location, which also supported other megafaunal species such as mastodons (*Mammut americanum*) and three species of giant ground sloths (Springer et al., 2009). Of the sites examined in this study, DVL has the lowest elevation (451 - 481 m) and continentality, leading to a milder climate.

DVL B. latifrons

The *B. latifrons* population within the DVL assemblage consumed an average of 16.21% C_4 plants (Table 1). This percentage supports McDonald's (1981) hypothesis that this species was primarily a browser more closely than the other sites in this study. However, the percentages at this site are highly variable, ranging from 6.9% in specimen WSC 10492 to 27.4% in specimen 22118 (Table 1). This variation may be a result of individuals occupying the area at different times when the plant communities were different. A $\delta^{13}C$ change as little as 1‰ can be the result of as much as a 7% increase in consumed C_4 vegetation. This reflects the amount of C_4 plants necessary to shift the value in a biogenic system.

DVL tooth WSC 16708 exhibits variable carbon values, with a preference for enriched $\delta^{13}C$ plants during the earlier interval of tooth mineralization as indicated by the proximal portion of the tooth (Fig. 20). Following this interval, it consumed a lower proportion of C_4 plants than during its early development. This may be a signal of seasonal migration within a single individual, especially due to the distinct shift at approximately 15 mm.

DVL tooth 10492 exhibits more constant $\delta^{13}C$ values through time, with a positive spike near the root at 24.5 mm (Fig. 21). This point correlates with warming temperatures as shown by the oxygen value of the sample. Although the animal's $\delta^{13}C$ values are predominantly those of a browser, C_4 plants were more heavily consumed as the temperature rose. The animal transitioned back to a higher percentage of C_3 browse between points H2E and H2F (24.5 to 32 mm).

Teeth 22118 and 22135 record less variation in diet than the other teeth from this site, but the animals consumed a higher percentage of C_4 plants than the other *B. latifrons* sampled at DVL (Figs. 22, 23). Tooth 22135 displays a preference for more browse as the weather warmed. The animal may have travelled to a new source of C_3 material as the temperature increased.

Half of the *B. latifrons* sampled at DVL had diets that fluctuated with temperature and seasonal changes, while the others maintained a more constant percentage of C_4 throughout

M3 tooth mineralization. This split may be evidence of multiple herds occupying the area during different time intervals.

DVL B. antiquus

On average, the population of *B. antiquus* recovered from DVL consumed 22.71% C_4 plants (Table 1), a higher proportion than *B. latifrons*.

DVL teeth 4039A and 4039B and their corresponding samples (Fig. 25) were collected from the same individual, represented by a complete dentary. The jaw was split at the mandibular symphysis, and I opted to serially sample one tooth while collecting a bulk sample from its opposite. The comparison samples were collected from approximately the same location in each tooth. The $\delta^{13}C$ values between right and left sides of the jaw were off by 0.5‰, while $\delta^{18}O$ had an absolute difference of 1.1‰; these variations are well within the expected variability range of an individual (MacFadden and Cerling, 1996; Koch et al., 1998; Hoppe, 2006b).

DVL tooth 775 (Fig. 24) exhibits the greatest variability at the site, with one sample yielding a depleted $\delta^{13}C$ value of -14.2‰. This value is surprising for an animal that is expected to have spent the majority of its time in a mid-elevation environment with access to abundant C_4 plants to graze upon. The relatively constant temperature indicated by the $\delta^{18}O$ values of the tooth do not seem to have heavily influenced the feeding habits of the animal.

DVL 21338C (Fig. 26) contains a highly enriched $\delta^{13}C$ signal, and I calculated its diet to average 39.86% C_4. Throughout the tooth, oxygen values fluctuate with a range of ± 7.6‰. Carbon maintains a relatively constant value, with the exception of a positive spike of -1.1‰ at point H6I (38.5 mm), followed by a rapid drop to -10.3‰ at point H6J (42.5 mm). This rapid variation occurs near the root of the tooth, implying a mobile individual following its preferred food source. Alternatively, the rapid drop in both carbon and oxygen values could be recording the arrival of cold winter temperatures in the second winter of this animal's life, along with a drop in the abundance of C_4 grasses.

In both species, half of the individuals sampled consumed a significantly higher proportion of C_4 plants, on the order of 8-20% more than the remainder of the population. This increase in C_4 grass consumed correlates directly with a positive increase in $\delta^{18}O$ values. Slight niche partitioning is seen between the taxa, as *B. latifrons* consumed 6.5% less C_4 plant material than *B. antiquus*. This suggests that there was overlap between the habitats of both taxa, but the degree of competition is unclear. *B. latifrons* samples from this site display a preference for C_3 browse plants, but they were apparently opportunistic grazers, consuming a mixed diet of both plant types. $\delta^{13}C$ values at this site are more variable than at the AF locality, especially in *B. antiquus*, exemplifying the adaptability of the genus. Plant communities change over time, and bison inhabiting the site may have occurred during these multiple time intervals. The presence of both species during these intervals may be accounted for as evidenced by the similar patterns of isotopic fractionation seen in half of the individuals from each species.

The presumed contemporaneous presence of both species of bison at DVL implies that there was a mechanism through which they partitioned resources. Kleynhans et al. (2011) established that seasonal migration, habitat segregation, and differing food resources are all strategies employed by African savanna grazers to avoid competition. There is certainly overlap in habitat and diet consumed, both of which are criteria for interspecific competition between *B. latifrons* and *B. antiquus* (Mysterud, 2000). The third strategy, partitioning food resources, is difficult to critically evaluate in a fossil assemblage. Both species consumed C_4 grass as roughly a quarter of their diets, implying that the more nutritious C_3 browse material must have been present in considerable abundance.

7 - Cross-site Comparison

Across all sites, while excluding the first run of Snowmastodon data, *B. latifrons* data display mean values of -8.39‰ δ ^{13}C VPDB, and -10.42‰ δ ^{18}O VPDB. The overall average percentage of C_4 plants consumed by the species is 28.64% (Table 1).

I plotted the data from all sites in a pair of bivariate scatter graphs (Figs. 27, 28). I selected oxygen values as the y-axis in part to illustrate the effect of a decrease in temperature; δ^{18}O values tend to become more negative as temperature lowers and altitude decreases. Carbon serves as the x-axis, and trends toward the positive direction as more C_4 plant material is consumed. These graphing conventions help to illustrate the trends between carbon and oxygen isotopes in a biogenic system.

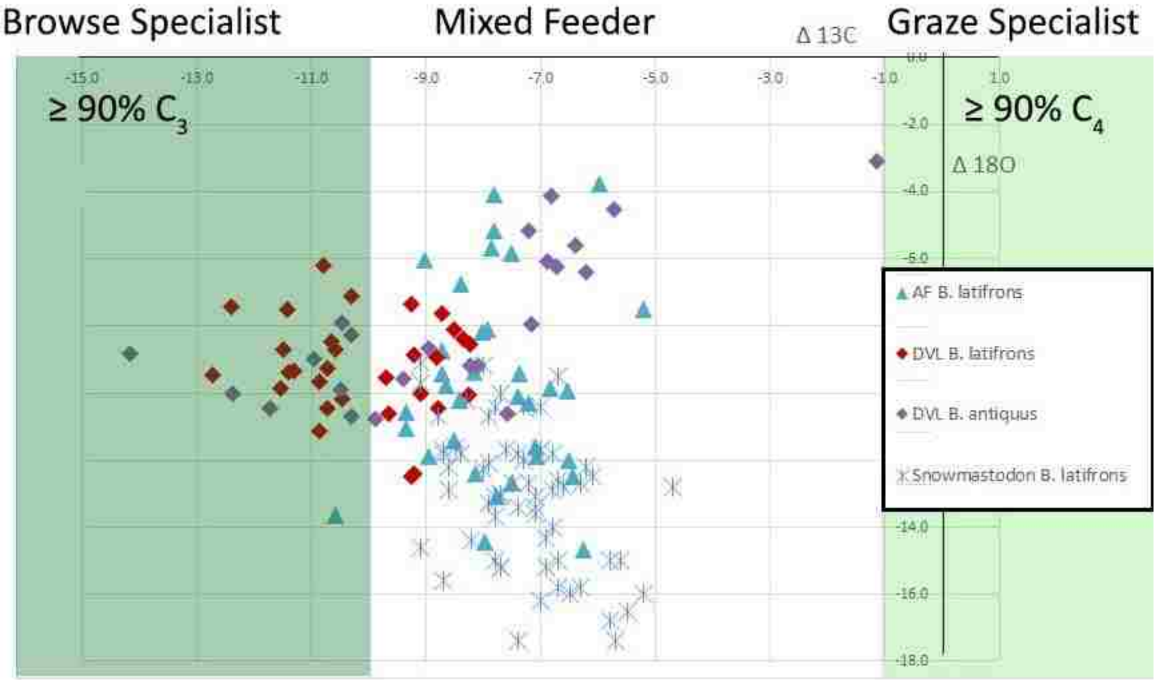


Figure 27: Scatterplot of all localities studied, including multiple samples from individual teeth. All points are *B. latifrons*, with the exception of purple “diamond” symbols, which represent *B. antiquus*. American Falls, Snowmastodon, and Diamond Valley Lake assemblages lump together in Quadrant IV.

Data from all three sites are distributed exclusively in Quadrant IV. Several outlier points are excluded (Appendices 1-3), as I consider them to be spurious data points. Oxygen values from these sites have a maximum range of ± 14.3‰ among the populations (ignoring an outlier in Quadrant I). Carbon values display a maximum range of ± 13.1‰.

The majority of DVL $\delta^{13}C$ *B. latifrons* values group between -6‰ to -13‰ VPDB, while $\delta^{18}O$ values fall between -7‰ and -11‰. The seasonality of the DVL site is dampened in comparison to the AF and Snowmastodon localities, and the $\delta^{13}C$ values are much more depleted than at the other two sites. Coupled with the relatively close grouping of $\delta^{13}C$ values, this suggests that *B. latifrons* consumed C_3 browse when it was available in a relatively mild, constant climate, but supplemented this intake with abundant C_4 graze. *B. latifrons* exhibited a consistent mixed feeder diet in all sites (Figs. 27, 28). *B. antiquus* had a more variable diet which incorporated a greater percentage of C_4 plants.

B. latifrons at the AF and Snowmastodon sites consumed a narrower range of plant types (27 to 40% and 31 to 47%, respectively) than those at DVL (7 to 27%). These ranges may have been influenced by the availability of plant material, high seasonality of the site, or successful migration in pursuit of a preferred diet.

The AF site oxygen values (-4.5 to -14.7‰) display greater variability than those at other sites. I interpret this high variability to be the result of a high degree of seasonality, due to the site's continentality and relatively flat topography. The Snowmastodon oxygen data (values from -9.1 to -17.4‰) reveal a moderate degree of seasonality, but the site remained cool throughout all seasons, consistent with its high elevation.

I combined data points from each tooth into average values for each individual sampled. Figure 28 is a representation of the individuals from each population placed into context.

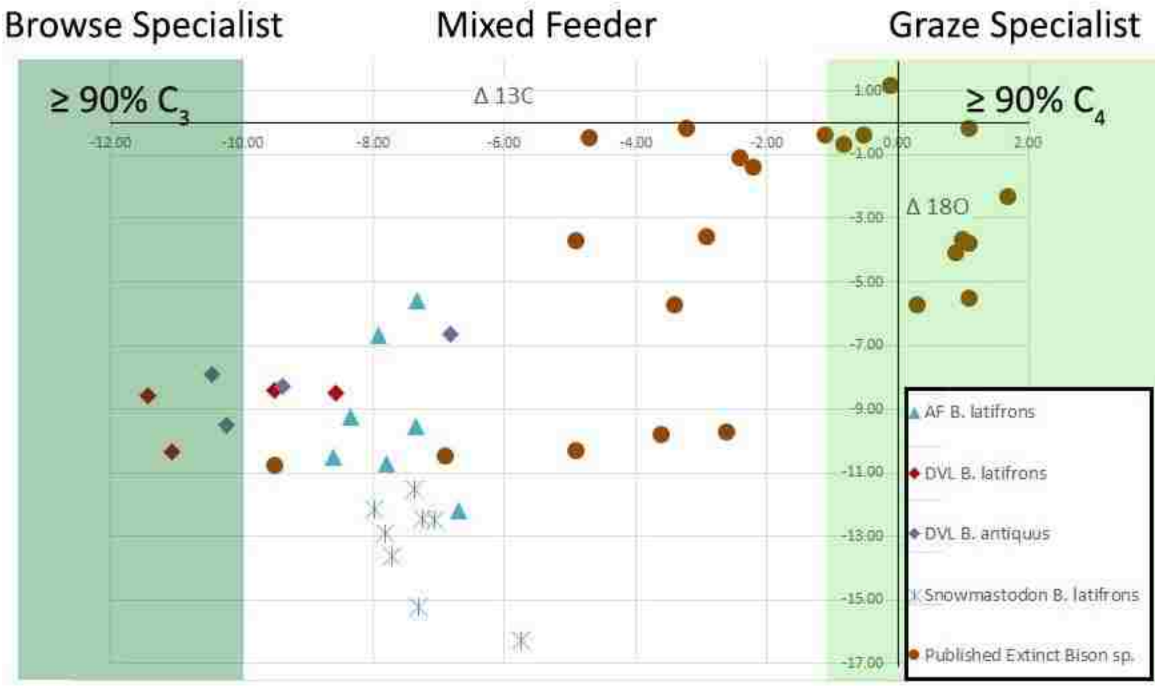


Figure 28: Scatterplot of all localities studied, illustrating isotopic space of individual animals from each population. Each point represents one bison. All points are *B. latifrons* with the exception of purple diamonds that represent *B. antiquus*, and unspecified *B. latifrons* or *B. antiquus* within "Published extinct *Bison* sp. Data." Note that the majority of points fall within the mixed feeder zone. (Includes data from: Connin, et al., 1998; Feranec and MacFadden, 2000; Yann and DeSantis, 2014.)

I isolated δ^{13}C values of individuals from each population to better illustrate the isotopic range of each study location (Fig. 29). AF and Snowmastodon *B. latifrons* exhibit similar mean range in δ^{13}C values, at ± 1.92 and ± 2.23‰, while DVL *B. latifrons* has a spread of ± 2.87‰. In addition, the populations at DVL generally displayed more depleted values than at the other locations. Previously published *B. latifrons* data from Nevada and Florida appear much more enriched, with Florida in particular having an even greater spread of ± 4.80‰.

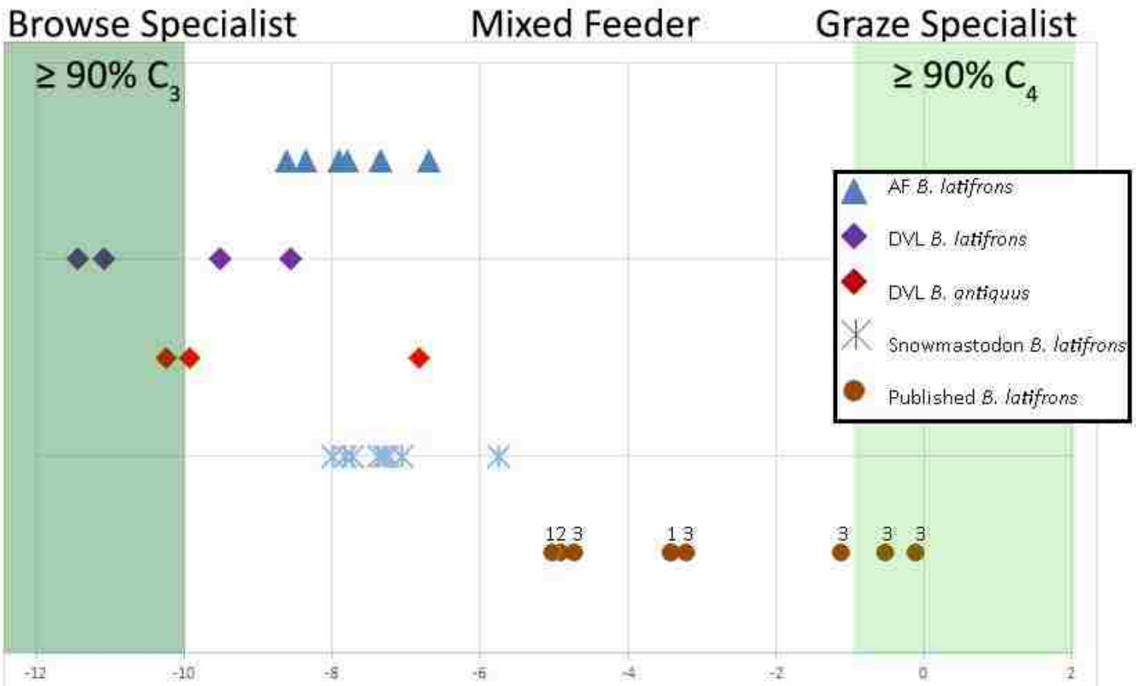


Figure 29: Mean δ^{13}C values of individuals. Note greater isotopic range and depleted δ^{13}C values in both taxa from the DVL population. Published *B. latifrons* are from Tule Springs, NV (1), and several from Florida (2,3) that display a highly enriched δ^{13}C signal. (Includes data from: [1]Connin, et al., 1998; [2]Feranec and MacFadden, 2000; [3]Yann and DeSantis, 2014).

To test the statistical significance of the variance between isotopic values of each bison population, I performed a series of Student's *t*-tests on the δ^{13}C data (Table 2). The outputs of the tests are in the form of P-values (highlighted in blue in Table 2), measured against t-values. In a two-tailed *t*-test, populations are statistically distinct with a 95% certainty when P-values are < 0.05. This statistical analysis suggests three levels of distinction between populations. AF *B. latifrons* are very distinct from DVL *B. latifrons* (Table 2A). Snowmastodon *B. latifrons* are very statistically distinct from either species at DVL (Table 2C, E, H). Population pairs with a lesser statistical distinction are DVL *B. antiquus* vs DVL *B. latifrons* (Table 2F), and the AF assemblage vs DVL assemblage (Table 2G). There is a statistical distinction, but to a much lesser degree between AF *B. latifrons* and Snowmastodon *B. latifrons* (Table 2B,).

Table 2: Results of Student's *t*-tests on δ^{13}C of bison populations in this study. All populations in this study are statistically distinct from one another at 95% certainty, with the exception of DVL *B. antiquus* vs AF *B. latifrons* (D). *B. latifrons* as a taxon is not statistically distinct from DVL *B. antiquus*, but more data are required to properly make this distinction (I). Note negative exponents in (A, C, G, and H). Yellow fields indicate statistical similarity.

A) AF Blat vs DVL Blat
t-Test: Two-Sample Assuming Unequal Variances
tstat > tcrit = statistically distinct

	Variable 1	*Variable 2*
Mean	-7.789455802	-10.4726167
Variance	1.172139897	6.117112305
Observations	35	30
Hypothesized Mean	0	
df	38	
t Stat	5.506965346	
P(T<=t) one-tail	1.35052E-06	
t Critical one-tail	1.68595446	
P(T<=t) two-tail	2.70104E-06	
t Critical two-tail	2.024394164	

B) AF Blat vs Snowmastodon Blat
t-Test: Two-Sample Assuming Unequal Variances
tstat < -tcrit = statiscially distinct

	Variable 1	*Variable 2*
Mean	-7.789455802	-7.315873
Variance	1.172139897	1.012002
Observations	35	63
Hypothesized Mean	0	
df	66	
t Stat	-2.127452625	
P(T<=t) one-tail	0.01856151	
t Critical one-tail	1.668270514	
P(T<=t) two-tail	0.037123019	
t Critical two-tail	1.996564419	

C) Snowmastodon Blat vs DVL Blat
t-Test: Two-Sample Assuming Unequal Variances
tstat > tcrit = statistically distinct

	Variable 1	*Variable 2*
Mean	-7.315873016	-10.472617
Variance	1.012002048	6.1171123
Observations	63	30
Hypothesized Mean	0	
df	34	
t Stat	6.730700837	
P(T<=t) one-tail	4.92258E-08	
t Critical one-tail	1.690924255	
P(T<=t) two-tail	9.84516E-08	
t Critical two-tail	2.032244509	

D) DVL Ant vs AF Blat
t-Test: Two-Sample Assuming Unequal Variances
-tcrit < tstat < tcrit = no significant difference

	Variable 1	*Variable 2*
Mean	-8.574667399	-7.7894558
Variance	7.50352013	1.172139897
Observations	23	35
Hypothesized Mean	0	
df	27	
t Stat	-1.309177544	
P(T<=t) one-tail	0.100753496	
t Critical one-tail	1.703288446	
P(T<=t) two-tail	0.201506992	
t Critical two-tail	2.051830516	

E) DVL Ant vs Snowmastodon Blat
t-Test: Two-Sample Assuming Unequal Variances
tstat < -tcrit = statistically distinct

	Variable 1	*Variable 2*
Mean	-8.574667399	-7.315873
Variance	7.50352013	1.012002
Observations	23	63
Hypothesized Mean	0	
df	24	
t Stat	-2.151538428	
P(T<=t) one-tail	0.02085495	
t Critical one-tail	1.71088208	
P(T<=t) two-tail	0.0417099	
t Critical two-tail	2.063898562	

F) DVL Ant vs DVL Blat
t-Test: Two-Sample Assuming Unequal Variances
tstat > tcrit = statistically distinct

	Variable 1	*Variable 2*
Mean	-8.574667399	-10.472617
Variance	7.50352013	6.1171123
Observations	23	30
Hypothesized Mean	0	
df	45	
t Stat	2.606680369	
P(T<=t) one-tail	0.006177789	
t Critical one-tail	1.679427393	
P(T<=t) two-tail	0.012355578	
t Critical two-tail	2.014103389	

G) AF Blat vs DVL sp.
t-Test: Two-Sample Assuming Unequal Variances
tstat > tcrit = statistically distinct

	Variable 1	*Variable 2*
Mean	-7.789455802	-9.64897832
Variance	1.172139897	7.487892604
Observations	35	53
Hypothesized Mean	0	
df	73	
t Stat	4.448024015	
P(T<=t) one-tail	1.52204E-05	
t Critical one-tail	1.665996224	
P(T<=t) two-tail	3.04408E-05	
t Critical two-tail	1.992997126	

H) Snowmastodon Blat vs DVL sp.
t-Test: Two-Sample Assuming Unequal Variances
tstat >tcrit = statistically distinct

	Variable 1	*Variable 2*
Mean	-7.315873016	-9.648978
Variance	1.012002048	7.4878926
Observations	63	53
Hypothesized Mean	0	
df	64	
t Stat	5.881776709	
P(T<=t) one-tail	8.06238E-08	
t Critical one-tail	1.669013025	
P(T<=t) two-tail	1.61248E-07	
t Critical two-tail	1.997729654	

I) All sites Blat vs DVL Ant
t-Test: Two-Sample Assuming Unequal Variances
-tcrit < tstat < tcrit = no significant difference

	Variable 1	*Variable 2*
Mean	-8.185230106	-8.5746674
Variance	3.858691473	7.5035201
Observations	128	23
Hypothesized Mean	0	
df	26	
t Stat	0.652344792	
P(T<=t) one-tail	0.259952524	
t Critical one-tail	1.70561792	
P(T<=t) two-tail	0.519905048	
t Critical two-tail	2.055529439	

There is no statistical distinction between AF *B.* latifrons and DVL *B. antiquus*, which suggests that the taxa behaved similarly at each of these locations. The large disparity between diets in AF *B. latifrons* and DVL *B. latifrons* (Table 2A), combined with a surprising lack of statistical distinction at 95% certainty between AF *B. latifrons* and DVL *B. antiquus* (Table 2D), suggests that in the presence of another large taxon with similar dietary needs, *B. latifrons* readily adjusts its diet to avoid competition. The isotopic data support this, as DVL *B. latifrons* possess a more depleted $\delta^{13}C$ signature than at the other sites in this study. Other contributors to this shift in diet may have been the presence of *Equus* or camel, both of which are specialized grazers.

When viewed as a taxon, *B. latifrons* does not possess a $\delta^{13}C$ signature different from that of the DVL *B. antiquus*, although more data from both species are required to confirm this similarity in diet.

8 - Discussion

The majority of individuals sampled in this study fall within the mixed-feeder range, with only four bison (two from each species) within the browse-specialist zone (Figs. 27, 28, 29). A compilation of data points from previous isotopic studies of extinct bison is included to compare my new data with the larger set. Most previous samples have not been identified to species level, but their temporal and geographic settings limit them to *B. latifrons* and *B. antiquus*. Bison have been included as portions of larger studies of fauna from Arizona, Florida, Nevada, and New Mexico. The majority of previously published data comes from multiple assemblages from AZ and FL, and suggests that bison of either species at these sites were primarily grazers (Connin et al., 1998 and Feranec and MacFadden, 2000).

The consistent pattern of stable carbon values with variable oxygen values at the American Falls and Snowmastodon sites indicates a pair of mutually compatible possibilities: the animals were mobile in pursuit of suitable environments and food sources, or they were exposed to a wide range of temperatures due to the increased seasonality of the site. Mobility apparently increased as the animals matured, as evidenced by increased variation in $\delta^{18}O$ values in the later-mineralizing (root) portion of the teeth. This positive covariance between oxygen and carbon isotopic systems in many animals (e.g., Figs. 15, 23, 26) strongly enforces my hypothesis that Pleistocene bison altered their diet and habitat in response to intra-annual weather variations. The close grouping of data points of both species at the DVL site (Figs. 27, 28) suggests that they experienced similar temperatures and utilized similar food sources.

The amount of C_3 browse in the diet of an individual *B. latifrons* varied with habitat and season, and my data show two distinct patterns. The first is a direct correlation between $\delta^{13}C$ and $\delta^{18}O$, which indicates that the animal's diet changed according to weather and seasons, as seen in teeth WSC 4039 and 21338C (Figs. 25, 26). This pattern most closely adheres to the hypothetical, idealized, nonmigratory bison tooth (Fig. 4), and manifests primarily in the DVL populations of both taxa. This is not to say that the patterns are identical, as there are several individuals that display correlation between both isotopic systems, but deviate at some point during enamel development (IMNH 17922, WSC 16708, 10492, 775) (Figs. 7, 20, 21, 24).

At the DVL site, where the two species co-occur, *B. latifrons* exhibited more variability in its diet, possibly in response to the presence of *B. antiquus* (Fig. 29).

Fluctuations in the diet of *B. antiquus* do line up with the interpreted seasons shown in the idealized nonmigratory bison (Fig 4), but WSC 775 notably shows a preference for C_3 browse during a cold interval (Fig 24). Without more data, it is unclear whether this individual is representative of a larger herd or a solitary outlier, possibly a wandering bull.

The second pattern is a generally stable level of $\delta^{13}C$ despite fluctuations in $\delta^{18}O$. This pattern is primarily seen at the AF and Snowmastodon sites, and best illustrated by teeth IMNH 17917 and 17915 (Figs. 10, 11) and DMNH 58.446 (Fig. 13). This signal tells me that the animal consumed a similar diet regardless of season, which is a possible indicator of seasonal migration. Migration is likely, and my conclusions fit into a model of currently observed behavior of large herbivores.

In either scenario – seasonally changing diet or stable diet - *B. latifrons* consumed C_3 vegetation, but incorporated a non-trivial amount of C_4 plants into its diet.

My data support the hypothesis that *B. latifrons* was an indiscriminate feeder, and consumed C_3 and C_4 vegetation based on resource availability. This contradicts the long held view that the taxon was a C_3 browse specialist put forth by McDonald (1981). *B. latifrons* was more adaptable than previously thought, especially when in the presence of other competitors.

8.1 - A Hypothesis Regarding Niche Partitioning in *Bison*

During the multiple time intervals during which two taxa of bison coexisted in North America (Fig. 1), a recurring pattern occurs in which one taxon was adapted to steppe/savanna settings while the other taxon was adapted to tundra/woodland habitats (Table 3). Dietary analyses of fossil species are incomplete, and this study is focused on the paleoecology of *B. latifrons*, but inferences about the dietary habits of various taxa can be made based on the distribution of fossil localities. The distribution of these taxa suggest that as bison evolved in North America, each taxon selected its preferred habitat and followed these biomes as seasons and climate changed over time. However, the data I collected for *B. latifrons* portray the taxon as an indiscriminate feeder that opportunistically consumed both C_3 and C_4 vegetation. McDonald (1981) and others utilized fossil localities to place taxa into paleoecological context, but this new information suggests that bison were defined by their habitat rather than their diet.

Savanna/Steppe	**Woodland**
Bison priscus	*Bison priscus alaskensis*
Bison antiquus	*Bison latifrons*
Bison antiquus occidentalis	*Bison antiquus antiquus*
Bison bison bison	*Bison bison athabascae*

Table 3: "Couplets" of coexisting taxa. When two taxa of bison were contemporaneous, resource partitioning developed in the form of specialization of one taxon toward a savanna/steppe habitat and specialization of the other taxon toward a woodland habitat.

Resource partitioning remained a viable means of reducing competition between species, and may have been a driver of bison diversification. The range dynamics explored by

McDonald (1981) help to explain the distribution patterns of each species, particularly between *B. latifrons* and *B. antiquus*, but their function in a given niche may have been more malleable than previously thought.

B. latifrons was the most wide-spread species of bison throughout North America from its initial appearance in the Illinoian glaciation until its decline beginning in the Sangamon Interglacial. *B. latifrons* may have excluded *B. antiquus* from potential habitats due to competition, while successfully cohabitating these areas with other megaherbivores such as American mastodon. *B. antiquus* may have been pressured to find ecologic success in the more open plains, developing a preference for C_4 vegetation. The population density and range of *B. antiquus* increased throughout the Sangamon in response to the increase in its savanna habitat (McDonald, 1981). Increase in range is a strategy employed by growing populations, but several geographic and ecological barriers were in place during the Sangamon-Wisconsin transition which limited dispersal options. The Laurentide ice sheet closed off the northern corridor, and the Pacific Ocean prevented a further westward range shift.

During the late Wisconsin glaciation, *B. antiquus* underwent a significant northward range expansion (Fig. 2), in response to the northward expansion of suitable habitat. This range expansion coincided with the extinction of *B. latifrons*, the former presence of which may have inhibited synchronous habitation (McDonald, 1981). Over time, new taxa of bison emerged to take advantage of the expanding grasslands of North America (Geist, 1966; McDonald, 1981).

Extant bison exist as a pair of subspecies (*Bison bison bison* and *Bison bison athabascae*), but do not necessarily provide a reliable modern analogue for this niche partitioning model. The subspecies occupy different niches and geographic regions. Nor do they have access to their historical range and are kept within artificial boundaries. But similar niche partitioning behavior is seen among the two extant species of wildebeest. As a pair of large, ruminant species of bovids with expansive geographic ranges, wildebeest have the potential to be used as a paleoecological model for North American Pleistocene bison. The blue wildebeest (*Connochaetes taurinus*), the larger of the two species, inhabits a large geographic area throughout Angola, Botswana, Mozambique, Namibia, and Zimbabwe. These countries contain a variety of habitats, including savanna, semi-desert, and woodland (Andere, 1981; Estes, 1991; Ackermann, 2010). The black wildebeest (*Connochaetes gnou*) occupies a much smaller region of open grassland in South Africa (Estes, 1991; Codron and Brink, 2007). Both species are primarily grazers, but they have the ability to incorporate C_3 browse plants into their diets (Codron and Brink, 2007; Ackermann, 2010). The two species are often found to be sympatric; due to their similar dietary needs, there is selective pressure for these species to partition resources and minimize competition (Codron and Brink, 2007). Carbon isotopic studies of dentine collagen and feces by Codron and Brink (2007) showed that herds of blue wildebeest are more likely to adjust their diets in the presence of competitor species.

Codron et al. (2010) further examined the relationship between these co-existing species in both sympatric and allopatric populations. When allopatric, both taxa independently exhibit similar isotope niche breadths. However, in sympatric situations, black wildebeest have a narrower $\delta^{13}C$ range than blue wildebeest, which indicates a nearly exclusive diet of C_4 grasses. Blue wildebeest behave as a submissive species and must adapt their feeding behavior to contain a greater proportion of C_3 plants in order to minimize competition.

This relationship may mirror the late Pleistocene interaction between *B. latifrons* and *B. antiquus*, especially as seen in the DVL assemblage studied here. The allopatric population of *B. latifrons* at AF had an average $\delta^{13}C$ range of ± 3.1‰, and the Snowmastodon population had a

$\delta^{13}C$ range of ± 2.2‰. The DVL population of *B. latifrons* had a spread of ± 4.5‰, while the sympatric *B. antiquus* at DVL had a range of ± 8.5‰. The wider $\delta^{13}C$ range of both taxa at the DVL site indicates competitive pressure to adopt a broader diet to minimize competition. *B. latifrons* evolved first and had already radiated throughout a much larger region by the time *B. antiquus* arrived on the scene. Early interaction between the taxa may have been dominated by the northern competitive exclusion of *B. antiquus* prior to the Wisconsin glaciation (Fig. 2).

In both wildebeest and *Bison*, the larger taxon altered its diet in sympatric situations, while retaining a larger geographic range across multiple niches.

Isotopic evidence of this adaptability in bison helps to explain how two large taxa of megaherbivores were able to coexist throughout North America, but this hypothesis requires additional research and sampling of localities which contain both species of fossil bison contemporaneously.

Ultimately, it appears that niche partitioning between these two species was not sufficiently effective to permit them to coexist. *B. antiquus* was evidently the superior competitor, and *B. latifrons* became extinct.

8.2 - Summary and Conclusions

To test the hypothesis that *B. latifrons* was primarily a C_3 browser, I examined the paleoecology of the Pleistocene *Bison latifrons* in this study. I selected sites from Idaho, California, and Colorado in order to study the species in a variety of altitudes and latitudes. I analyzed carbon and oxygen stable isotopes collected from tooth enamel.

I collected 180 samples from 22 individuals. Nineteen of the individuals were from *B. latifrons* and three were from co-occurring *Bison antiquus*. I determined the $\delta^{13}C$ and $\delta^{18}O$ values of these samples, and I calculated the percentage of C_4 plants consumed by each animal. I determined mean values for each population to gain an understanding of their function within an assemblage, and I also examined the range and sequence of values within individual teeth to evaluate seasonal variations in diet.

I found *B. latifrons* to have been an indiscriminate mixed-feeder. This species consumed C_4 graze, but it also incorporated C_3 browse into its diet when required by its environment. Changes in intra-annual climate do not appear to have affected the plant types consumed, but the species was seen to adapt its diet based on availability of forage in its home range. I described several couplets of contemporaneous North American taxa, which utilized niche partitioning as a strategy to reduce competition with coexisting taxa. Extant wildebeest serve as a modern analogue for this behavior. Ultimately niche partitioning was not sufficiently effective to permit two species of large bison to coexist during the late Rancholabrean LMA, and *B. latifrons* went extinct.

Dietary plasticity in *Bison* was a strategy that was fundamental to their radiation throughout Pleistocene North America. It led to the continued ecological success of the genus through diversification up until the modern era.

8.3 - Future Work

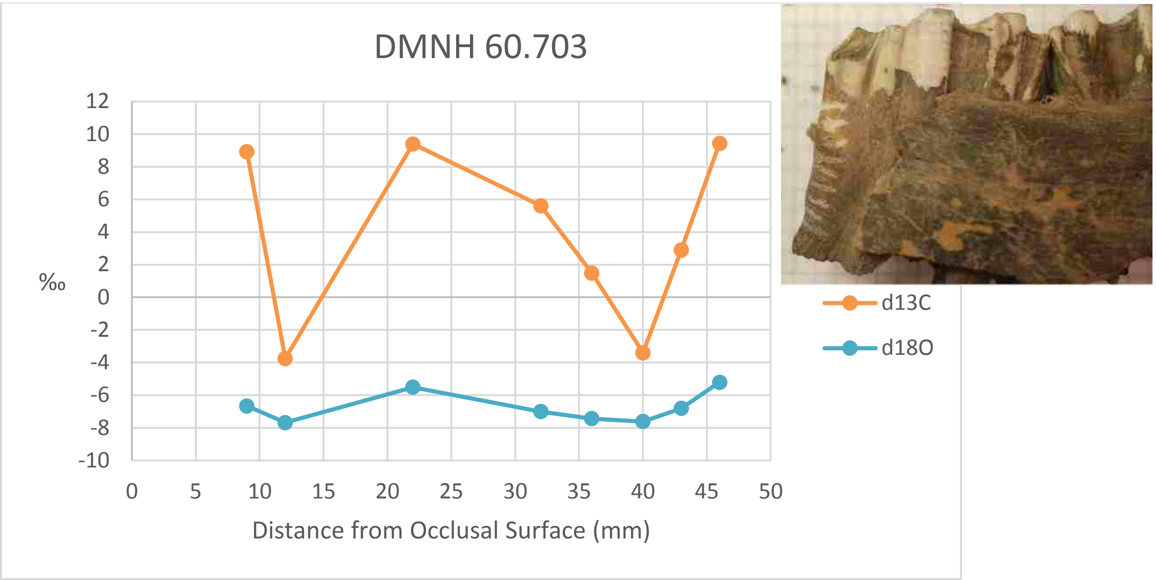
Further study of the assemblages examined here should include tooth microwear analysis, which serves as a proxy for diet at the time the locality was occupied (Rivals, 2011). This test has the capability of narrowing down the plants consumed by an animal to genus or species (Rivals et al., 2011). Analysis of strontium isotopes from tooth enamel would be a method of further testing the hypothesis that bison migrated in search of food sources, and would help estimate the range of individuals within each population. $^{87}Sr/^{86}Sr$ is an indicator of an animal's movement patterns throughout its life (Hoppe, et al. 1999). The ratio varies between habitats due to differences in bedrock and soil, and is recorded as a tooth mineralizes. Covariation among all three isotopic systems (carbon, oxygen, and strontium) could shed light on the hypothesis of seasonal migration of bison populations in pursuit of food sources in response to changing climate.

Regional differences in *B. latifrons* $\delta^{13}C$ signatures may be the result of differing plant communities or the presence of other megaherbivores that competed for resources. A broader dataset of serial $\delta^{13}C$ values sampled from various taxa across North America will help to pinpoint their dietary preferences and habits.

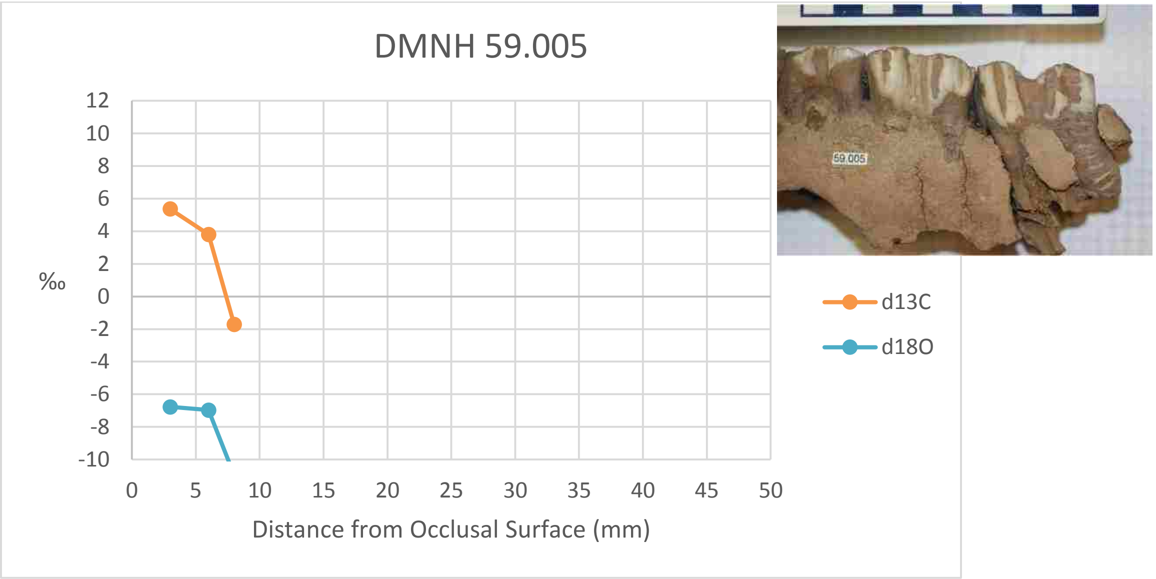
Appendix 1: Initial Snowmastodon Results

Initial results from the Snowmastodon site in Snowmass, CO were inconclusive. The data presented here are a representation of tooth enamel sample locations with especially anomalous samples removed. Samples determined to be problematic are those which had either lost too much mass during preparation, or were contaminated by water while in transition from carbonate device to mass spectrometer. Measured $\delta^{13}C$ values have a range between -5.34 to +8.93‰ VPDB, with a mean value of +0.93‰. The range in $\delta^{18}O$ values is -8.99 to -5.20‰ VPDB, with a site average of -7.49‰. Most teeth sampled at this location display positive covariation of the two isotopic systems. DMNH 56.322 (D4 A–F) and 60.022 (D6 A-H) are exceptions to this trend, displaying negative covariation toward the midpoint of the tooth, with a spike in oxygen values seen in DMNH 60.022. When several outlier data points were removed from charting DMNH 60.022, a positively covarying signal was seen, suggesting that the individual samples were not accurate representations of the tooth as a whole. DMNH 60.703 (D1 A-P) and DMNH 56.322 in particular display extreme variation in carbon values, on the order of ± 13‰, while oxygen values stay relatively consistent.

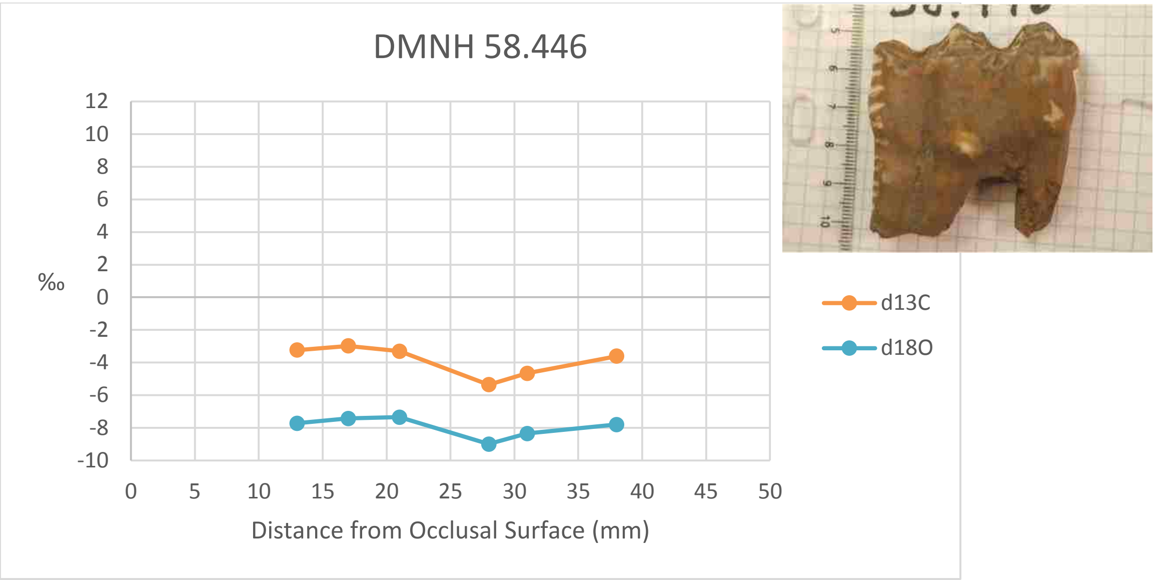
Due to these problematic results, I resampled teeth from the Snowmastodon site. My previous data are included here to illustrate the importance of proper collection and preparation of enamel tooth powder.



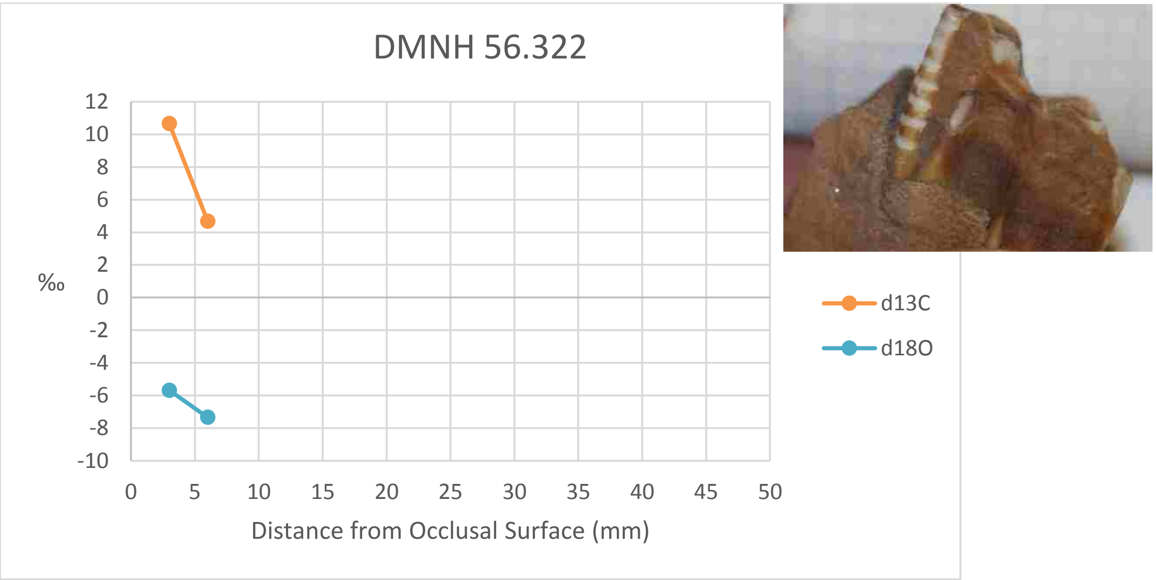
DMNH 60.703 displays high variability between sample points, particularly in carbon values. Oxygen values remain relatively constant by comparison.



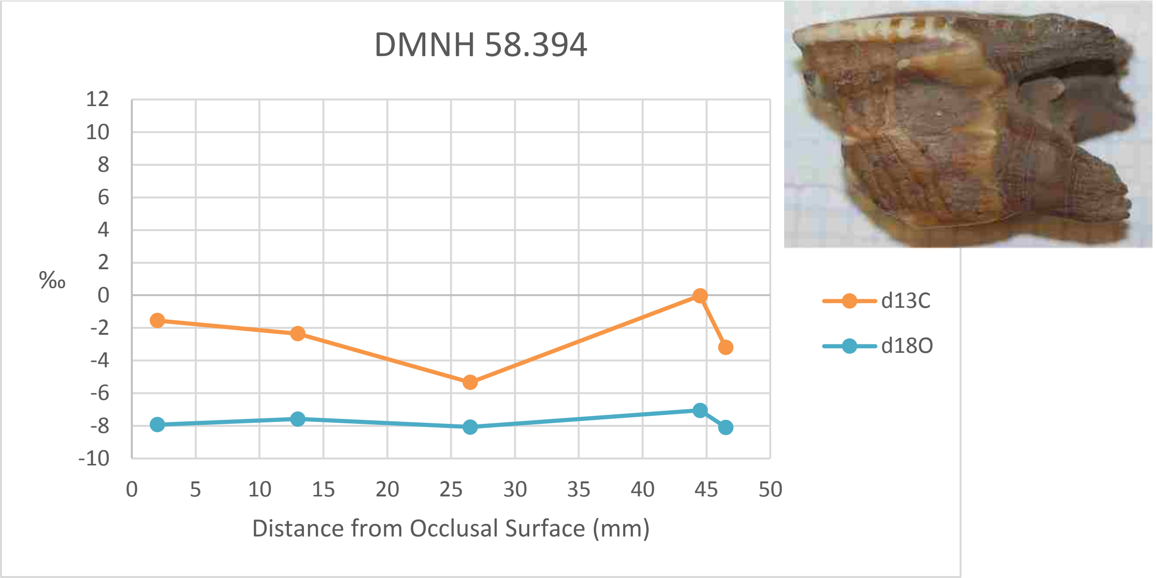
DMNH 59.005 exhibits positive covariation with a sharp negative drop in both isotopic systems 6mm from the occlusal surface.



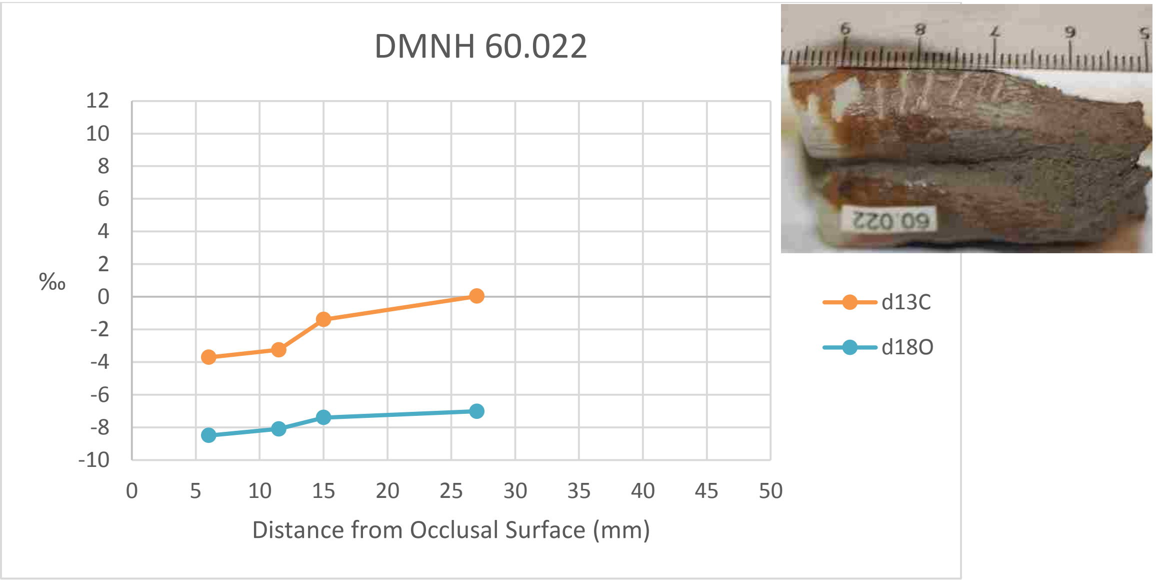
DMNH 58.446 exhibits positive covariation between isotopic systems throughout.



The majority of samples from DMNH 56.322 were discarded due to errors that occurred during preparation and analysis. D4B-D4D were combined due to low sample volume collected prior to analysis.



Positive covariation is seen in DMNH 58.394, while carbon values exhibit more positive values than oxygen.



DMNH 60.022 exhibits a positive covariation pattern throughout. Carbon values fall within the range of a C_4 specialist, while oxygen remains relatively constant.

Interpretation of Initial Snowmastodon Results

δ^{13}C values from the initial sampling average 0.93‰ even when outliers are removed, which is unusually high, even for extreme C_4 specialists. Positive δ^{13}C values are not expected in a biogenically fractionated apatite system (Feranec and MacFadden, 2000, Crowley, 2014). δ^{13}C values as high as positive 8.93‰ VPDB are prime indicators of a non-primary isotopic signal. δ^{18}O values seem reasonable with a site average of -7.49‰, but must be viewed skeptically in light of the highly positive carbon values. The equation of Koch (1998) indicates that the percentage of C_4 plants consumed is 95.21%, with several exclusively C_4 graze specialist individuals.

If the values were indeed correct, the teeth may have been subject to extreme diagenetic alteration, which accounts for the large shift and range in carbon values. The oxygen isotopic system is much more vulnerable to diagenesis than carbon, implying that if carbon has been altered, oxygen must have been altered even further. As discussed by Koch (1997), groundwater and meteoric precipitation tend to cause oxygen isotopic values to take on their values over time, typically in the positive direction. A homogenization of δ^{18}O is seen throughout the series, with a positive trend in both systems. This positive covariation between systems implies that a similar process must have acted upon all samples collected from the Snowmastodon site.

The other possibility for such a shift in isotopic values is human error and sample cross contamination. The Snowmastodon teeth were the first ones I sampled in this study, and during initial sampling I failed to account for cementum and secondary calcite on the surface of some of the teeth. The teeth recovered from the Snowmastodon site had a significant amount of secondary material on the surface, which I did not immediately recognize due to my inexperience with the sampling method. In most cases, the drilling depth was not sufficient to penetrate this layer, and enamel powder collected was typically light tan to brown in color. Further review of published literature (Crowley, 2012; Crowley and Wheatley, 2014) indicated that the surface of each tooth should be scoured using physical or chemical means prior to sampling for powder. These potential sampling errors were noted and accounted for in all subsequent sample collection.

I performed a second round of sampling at the Denver Museum of Nature and Science utilizing a refined collection method. Enamel powders collected during this process were uniformly white in color, which is characteristic of successful samples from other sites in this study.

Appendix 2: American Falls Formation Raw Isotopic Data

IMNH #	P #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
17906	P1A	5	-10.6	-13.6
	P1B	7.5	-7.5	7.0
	P1C	12	-6.0	-3.8
	P1F	27	-5.2	-7.5
	P1G	31	-7.4	-10.1

IMNH #	P#	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
17909	P2D	13.5	-7.8	-4.1
	P2E	17	-8.4	-10.2
	P2F	20.5	-7.5	-5.8

IMNH #	P#	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
17922	P3B	40	-7.9	-5.7
	P3C	45	-8.1	-12.4
	P3D	47	-7.2	-10.3
	P3E	50	-8.0	-14.4

IMNH #	P#	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
17931	P4A	11	-7.4	-9.4
	P4E	33	-6.4	-12.5
	P4F	38	-6.3	-14.7

IMNH #	P#	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
17930	P5C	19	-9.0	-6.0
	P5E	29.5	-7.9	-8.1
	P5F	35	-8.6	-9.8
	P5G	41	-7.8	-13.1

IMNH #	P#	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
17917	P6A	5	-6.5	-9.9
	P6B	9.5	-6.5	-12.0
	P6C	14	-6.8	-9.9
	P6D	18	-7.1	-11.9
	P6E	23.5	-7.5	-12.7
	P6F	28	-8.4	-6.8
	P6G	32	-8.0	-8.2
	P6H	37	-7.8	-5.1

IMNH #	P#	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
17915	P7A	9	-9.3	-11.1
	P7B	14	-9.3	-10.6
	P7C	18.5	-9.0	-11.9
	P7D	24.5	-8.7	-9.4
	P7E	29	-8.7	-8.7
	P7F	35	-8.5	-11.4
	P7G	41	-7.1	-11.6
	P7H	47	-8.2	-9.4

Appendix 3: Diamond Valley Lake Formation Raw Isotopic Data (*Bison latifrons*)

WSC #	H #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
16708	H1A	2	-21.8	-12.4
	H1B	5	-8.3	-10.1
	H1C	6	-9.2	-12.4
	H1D	9	-8.8	-10.5
	H1E	11	-9.2	-12.5
	H1F	13	-10.5	-10.2
	H1G	15	-10.7	-10.4
	H1H	16.5	-11.5	-9.9
	H1I	18	-10.7	-8.5
	H1J	20	-11.3	-9.3
	H1K	23	-10.9	-11.1
	H1L	25	-10.9	-9.7
	H1M	27	-10.7	-9.3
	H1N	29.5	-10.6	-8.7

WSC #	H #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
22135	H8A	2.5	-8.2	-8.5
	H8B	8	-9.7	-10.6
	H8C	12	-9.1	-10.0
	H8D	17	-9.7	-9.5
	H8E	22.5	-10.3	-7.1
	H8H	29	-9.3	-7.4
	H8J	36	-8.7	-7.6

WSC #	H #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
10492	H2A	3.5	-11.5	-8.7
	H2B	7.5	-11.4	-7.5
	H2C	12.5	-12.7	-9.5
	H2D	17.5	-11.4	-9.4
	H2E	24.5	-9.2	-8.9
	H2F	32	-12.4	-7.4

WSC #	H #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
22118	H7A	2.5	-8.8	-8.9
	H7B	7	-8.5	-8.1
	H7D	16.5	-8.4	-8.4

Appendix 4: Diamond Valley Lake Formation Raw Isotopic Data (*Bison antiquus*)

WSC #	H #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
775	H3A	4	-8.2	-9.2
	H3B	7.5	-7.2	-7.9
	H3C	10	-9.9	-10.8
	H3D	16	-14.2	-8.8
	H3E	21	-12.4	-10.0
	H3F	26	-11.7	-10.4
	H3G	31	-8.1	-9.2

WSC #	H #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
4039A	H4A	3.5	-11.0	-9.0
	H4B	7.5	-10.3	-8.3
	H4C	11.5	-5.7	-4.5
	H4D	17	-9.4	-9.6
	H4E	20	-10.5	-9.9
4039B	H5	7.5	-10.5	-7.9

WSC #	H #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
21338C	H6A	4	-6.2	-6.4
	H6B	8	-9.0	-8.7
	H6C	11	-6.7	-6.2
	H6D	16	-7.6	-10.6
	H6E	21	-6.4	-5.6
	H6F	26	-6.9	-6.1
	H6G	30.5	-7.2	-5.1
	H6H	34.5	-6.8	-4.1
	H6I	38.5	-1.1	-3.1
	H6J	42.5	-10.3	-10.7

Appendix 5: Snowmastodon Round 2 Raw Isotopic Data

DMNH #	D #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
60.703	D*1A	2.5	-6.30	-12.70
	D*1B	5	-7.90	-13.30
	D*1C	7	-7.80	-13.70
	D*1D	9	-9.10	-14.60
	D*1E	11	-8.70	-15.60
	D*1F	13	-6.80	-14.00
	D*1G	15.5	-7.10	-13.40
	D*1H	18	-7.10	-13.60
	D*1I	20	-8.7	-11.8

DMNH #	D#	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
58.446	D*2A	5	-8.60	-12.20
	D*2B	8	-7.30	-10.40
	D*2C	9.5	-6.70	-9.50
	D*2D	12	-7.6	-11.7
	D*2E	14	-7	-11.7
	D*2F	15	-6.7	-12.6
	D*2G	16.5	-7.4	-13.4
	D*2H	18	-6.9	-14.3
	D*2I	20	-7	-16.2

DMNH #	D #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
59.005	D*3A	3	-7.50	-12.70
	D*3B	6	-8.20	-14.40
	D*3C	8	-7.7	-15.2
	D*3D	10	-6.7	-15.8
	D*3E	12	-7.4	-17.4
	D*3F	14	-6.3	-15.8

DMNH #	D #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
56.322	D*4B	3	-5.6	-15
	D*4C	5.5	-6.7	-15
	D*4D	9	-4.7	-12.8
	D*4E	12.5	-6.6	-12.8
	D*4F	15.5	-7.9	-12.1
	D*4G	18	-7	-10.4
	D*4H	22	-7.9	-10.7
	D*4I	25	-8.4	-11.8
	D*4J	27.5	-8.7	-11.7

DMNH #	D #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
p58.394	D*5A	3	-7.70	-15.20
n67.512	D*5B	5.5	-6.90	-15.20
	D*5C	7.5	-7.8	-15
	D*5F	16	-7.2	-12.7
	D*5G	18.5	-7.7	-10
	D*5H	21	-9.1	-9.1
	D*5I	23	-9.1	-9.7
	D*5J	25	-8.3	-10.2

DMNH #	D #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
p60.022	D*6A	0.5	-6.50	-16.00
n67517	D*6B	2	-5.8	-16.8
	D*6C	4	-5.7	-17.4
	D*6D	6.5	-5.5	-16.5
	D*6E	8	-5.2	-16
	D*6F	10	-5.8	-15

DMNH #	D #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
67505	D*7A	1	-8.60	-12.90
	D*7B	3	-8	-12.3
	D*7C	5	-7.8	-13.1
	D*7D	8.5	-7.7	-13.1
	D*7E	11	-7.7	-13
	D*7F	12.5	-7.1	-13.1

DMNH #	D #	Distance (mm)	$\delta^{13}C$	$\delta^{18}O$
67503	D*8A	0.5	-6.20	-12.20
	D*8B	3	-6.1	-12.5
	D*8C	5	-7.3	-12
	D*8D	7	-6.8	-12.9
	D*8E	9	-6.8	-11.8
	D*8F	11	-7.4	-11.8
	D*8G	12	-8.5	-11.6
	D*8H	14.5	-7.8	-10.4
	D*8I	17	-8.8	-10.7
	D*8J	19	-8	-9.2

Appendix 6: Individual Tooth Sample Weights

Actual Sample #	Sample ID #	Weight (mg)	Average Wgt Collected (mg)	Avg. Wgt all Samples (mg)
IDAHO				
IMNH 17906	P1A	9.144	2.822	1.598
	P1B	0.185		
	P1C	0.815		
	P1D	0.51		
	P1E	2.107		
	P1F	3.328		
	P1G	3.662		
	P1H	0		
IMNH 17909	P2A	0.662	0.660	
	P2B	0.267		
	P2C	0.25		
	P2D	0.325		
	P2E	1.613		
	P2F	1.185		
	P2G	0.67		
	P2H	0.31		
IMNH 17922	P3A	0.385	0.828	
	P3B	0.807		
	P3C	1.292		
	P3D - Chunk	27.407		
	P3E - Chunk	35.15		
IMNH 17931	P4A	1.739	1.584	
	P4B	1.301		
	P4C	1.171		
	P4D	0.734		
	P4E	2.348		
	P4F	2.212		
IMNH 17930	P5A	0.58	1.249	
	P5B	0.379		
	P5C	1.682		
	P5D	0.743		
	P5E	1.79		
	P5F	2.365		

	P5G	1.204	
IMNH 17917	P6A	1.41	2.447
	P6B	2.942	
	P6C	1.162	
	P6D	1.442	
	P6E	2.602	
	P6F	1.99	
	P6G	3.114	
	P6H	4.915	
IMNH 17915	P7A	2.937	4.369
	P7B	4.471	
	P7C	3.503	
	P7D	3.533	
	P7E	3.541	
	P7F	5.73	
	P7G	7.449	
	P7H	3.785	

Actual Sample #	Sample ID #	Weight (mg)	Average Wgt Collected (mg)	Avg. Wgt all Samples
CALIFORNIA				
L2726-16708	H1A	1.011	2.473	3.120
	H1B	1.457		
	H1C	1.078		
	H1D	1.924		
	H1E	1.524		
	H1F	1.274		
	H1G	1.655		
	H1H	2.255		
	H1I	1.798		
	H1J	2.091		
	H1K	2.128		
	H1L	2.780		
	H1M	3.528		
	H1N	2.609		
L2726-10492	H2A	3.276	4.161	
	H2B	2.853		
	H2C	2.930		
	H2D	4.450		
	H2E	6.371		
	H2F	5.087		
L2726-775	H3A	1.880	2.181	
	H3B	2.227		
	H3C	1.957		
	H3D	2.959		
	H3E	1.794		
	H3F	2.455		
	H3G	1.995		
L2726-4039A	H4A	2.120	1.977	
	H4B	2.463		
	H4C	1.790		
	H4D	1.902		
	H4E	1.611		
L2726-4039B	H5	3.415	3.415	
L2726-21338C	H6A	1.933	2.801	

	H6B	1.644	
	H6C	2.644	
	H6D	1.889	
	H6E	2.805	
	H6F	2.758	
	H6G	2.365	
	H6H	3.169	
	H6I	4.941	
	H6J	3.858	
L2726-22118	H7A	3.705	4.348
	H7B	4.639	
	H7C	3.584	
	H7D	5.463	
L2726-22135	H8A	3.789	3.601
	H8B	2.911	
	H8C	2.661	
	H8D	3.353	
same individual	H8E	4.813	
	H8F	3.576	
	H8G	3.421	
	H8H	4.993	
	H8I	2.760	
	H8J	3.142	
	H8K	4.190	

Actual Sample #	Sample ID #	Weight (mg)	Average Wgt Collected (mg)	Avg. Wgt all Samples (mg)
COLORADO				
DMNH 60.703	D1A	15.745	3.828	2.864
	D1B	22.233		
	D1Aa	0.790		
	D1Ab	1.121		
	D1Ba	0.899		
	D1C	2.437		
	D1D	1.079		
	D1E	1.860		
	D1F	1.029		
	D1G	1.560		
	D1H	1.849		
	D1I	3.242		
	D1J	2.707		
	D1K	2.262		
	D1L	4.437		
	D1M	2.634		
	D1N	2.425		
	D1O	2.005		
	D1P	2.424		
DMNH 59.005	D2A	3.698	4.030	
	D2B	4.343		
	D2C	2.570		
	D2D	2.632		
	D2E	2.602		
	D2F	7.256		
	D2G	5.631		
	D2H	3.632		
	D2I	4.331		
	D2J	2.548		
	D2K	5.090		
DMNH 58.446	D3A	3.174	2.914	
	D3B	3.465		
	D3C	3.761		
	D3D	5.103		
	D3E	3.573		
	D3F	2.560		
	D3G	2.041		

	D3HI	1.386	
	D3JK	1.163	
DMNH 56.322	D4A	0.877	2.222
	D4B	1.516	
	D4CD	0.892	
	D4E	6.739	
	D4F	2.480	
	D4G	0.830	
DMNH 58.394	D5ABC	1.971	1.327
	D5DEFG	1.236	
	D5HI	1.577	
	D5J	LOST	
	D5K	0.911	
	D5LM	0.939	
DMNH 60.022	D6A	0.832	2.112
	D6B	7.073	
	D6C	0.799	
	D6D	1.766	
	D6E	1.334	
	D6F	2.118	
	D6G	1.422	
	D6H	1.555	

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Education:

Graduate	**Master of Science - Geoscience** University of Nevada Las Vegas, Department of Geoscience Expected Graduation: August 2015 Advisor: Dr. Stephen M. Rowland Thesis Project: Stable Isotope Analysis of *Bison latifrons* and Paleoecological Inferences GPA: 3.6
Undergraduate	**Bachelor of Science in Geology** University of Nevada Las Vegas, Department of Geoscience Graduation: December 2012 Geoscience GPA: 3.0

Graduate studies: Mammalogy, Biogeography, Stable Isotope Geochemistry, Quaternary Topics Seminar, Earth Systems Change, Instrumental Techniques in Geoscience, Carbonate Depositional Systems, Research methods, Metallic Ore Deposits, Volcanology, Posters and Time Management

Undergraduate studies: Paleoclimatology, Principles of Sedimentation and Stratigraphy, Quaternary Paleoecology, Fossil Record and Paleontology Lab, Introductory and Advanced Field Camps, Mineralogy, Structural Geology, Igneous and Metamorphic Petrology, Historical Geology

Additional Academic Experience:

UNLV Geoscience Course Audit 2015: Tectonics and Structures, focus on Neotectonics and Paleoseismology
ExxonMobil Short Course 2014: Multi-disciplinary Subsurface Integration in Exploration and Production
ExxonMobil Short Course 2013: Basin and Play Analysis/Mapping

Related Skills: Proficient with Adobe Photoshop and Illustrator, Microsoft Excel and Powerpoint, familiar with SEM imaging equipment, working knowledge of FORTRAN programming

Work Experience:

May 2015-Present	National Park Service Geologist Intern Supervisor: Vincent Santucci
Jan. 2015-Present	Valley of Fire State Park - Paleontological Survey Survey of Triassic-Jurassic vertebrate and plant fossils Supervisor: Dr. Joshua Bonde
March 2014-Present	Esmeralda County Paleontological Survey and Excavation Survey and excavation of Gomphothere, preparation and display in museum Supervisor: Dr. Joshua Bonde
Sept. 2014- Dec. 2014	UNLV Department of Geoscience Graduate Teaching Assistant: Paleontology Laboratory Supervisor: Dr. Stephen M. Rowland
Jan. 2014- May 2015	UNLV Department of Geoscience Lead Graduate Teaching Assistant: Historical Geology Supervisors: Dr. Ganqing Jiang, Dr. Joshua Bonde
Sept. 2013- Dec. 2014	UNLV Geoscience Educational Outreach Presentations for secondary education students and interest groups Supervisor: Dr. Jean Cline
July 2011- Survey Jan. 2015	Tule Springs Fossil Beds National Monument - Paleontological Survey and excavation of vertebrate and invertebrate specimens Supervisor: Dr. Joshua Bonde
Jan. 2013- May 2013	UNLV Honors College Graduate Assistant Research assistant, database management
Aug. 2011- Dec. 2012	UNLV Paleontology Laboratory Research assistant, maceration and preparation of specimens, web design Supervisor: Dr. Stephen M. Rowland

Dec. 2005-	Best Buy Inc.
Aug. 2012	Department Senior

Awards:

May 2014	GSA Rocky Mountain/Cordilleran Section – Outstanding Graduate Poster Award
March 2014	UNLV Graduate & Professional Student Research Forum – Platform Session Honorable Mention
Jan. 2014	Edwards & Olswang Geology Scholarship
Jan. 2014	Bernarda French Scholarship
Dec. 2013	UNLV Graduate & Professional Student Association Travel Grant
April 2012	UNLV Geosymposium 2012 – 2nd Place Undergraduate Poster

Research and Presentations:

Hardy, F., Rowland, S. 2015, *Bison latifrons* paleoecology: Dietary plasticity in megaherbivores, 10th Annual UNLV Geosymposium

Hardy, F., Bonde, J. 2015, Welded beast of the Sump: Gomphothere skull reconstruction, 10th Annual UNLV Geosymposium

Hardy, F., Bonde, J. Stomping around the Sump: Miocene pygmy Gomphothere from Esmeralda County, Nevada, 2015 Geological Society of Nevada Symposium

Hardy, F., Rowland, S. 2014, Rumble in the Pleistocene: *Bison latifrons* paleoecology and megafaunal competition, Technical Session 45, Geological Society of America Annual Meeting. v. 46, No. 6, p. 133

Hardy, F., Rowland, S. 2014, Great Basin *Bison latifrons*: Stable Isotope Paleoecology, Technical Session 6, Geological Society of America Rocky Mountain/Cordilleran Section Meeting. v. 46, No. 5

Hardy, F. 2014, Stable Isotope Paleoecology of an Ice Age Bison, Platform Session B, 16th Annual UNLV Graduate and Professional Student Research Forum

Hardy, F., Rowland, S. 2013, Isotope Geochemistry and Paleontology of a Giant Long-horned Bison from the Snowmass Village Fossil Site, CO, 8th Annual UNLV Geosymposium

Hardy, F., Rodriguez, M., Bonde, A., Rowland, S. 2012, Paleontology of a Late Pleistocene Long-Horned Bison from Lincoln County, Nevada, 7th Annual UNLV Geosymposium

Hardy, F., Rowland S. 2011, Gastropod Paleoecology of the Pleistocene (Rancholabrean) Wilkin Quarry Site, Lincoln County, Nevada, 6th Annual UNLV Geosymposium

Rowland, S., Hardy, F., McLaurin, B. 2011, The Wilkin Quarry Rancholabrean Biota of Lincoln County, Nevada, 71st Annual Meeting Society of Vertebrate Paleontology

Professional and Academic Affiliations:
UNLV Geosymposium Committee - Abstracts with Programs Chair
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