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Diet and morphological variation in bison (*Bison bison*) from the Bighorn Basin, Wyoming, USA

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Cranial morphology has been used to examine ecological pressures on bison (*Bison bison*) populations and to place isolated crania within chronological and evolutionary contexts. This study analyzes 114 historic and 10 modern, ranched bison from the Bighorn Basin (Wyoming, USA) to assess morphological, dietary, and ecological changes before and after the 19th-century population bottleneck. Up to 26 morphological measurements were recorded on each specimen. Late Holocene bison from the region are morphologically consistent with contemporaneous populations elsewhere in North America. In contrast, modern ranched bison exhibit more curved horn cores, potentially reflecting management-related changes in herd dynamics. Stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) indicate that late Holocene Bighorn Basin bison consumed diets comparable to those of modern herds, both free-ranging, such as Yellowstone National Park, and ranched. Results offer insight into past variation in bison dietary ecology with the potential to inform modern conservation strategies for bison management.

KEYWORDS

bison, conservation paleobiology, cranial morphometrics, diet, stable isotopes

Introduction

In October 2024, the Department of the Interior released the Bison Shared Stewardship Strategy. This historic document co-authored with tribal members states, “We embrace the fact that bison conservation is inextricably linked with human, wildlife, and environmental health” (Baldes et al., 2024: 6). The North American bison or buffalo (*Bison bison*) is ecologically important (Geremia et al., 2019) and kin to many tribal groups in the northern Great Plains and Rocky Mountain regions (Oetelaar, 2014; Shamon et al., 2022). The near-extinction of the bison and subsequent conservation of bison in defined regions have impacted not only the ecosystems of these regions but also innumerable tribal groups.

As social isolation lifted in many parts of rural Wyoming following the first wave of COVID-19, the Meeteetse Museums launched this project the “Bison of the Bighorn Basin” in September 2020. The project was planned as a part of Wyoming’s Archaeology Awareness Month and called for community members to bring in privately collected bison crania found in the geographic Bighorn Basin. In addition to community-building and

providing educational resolution of the sometimes-blurry distinction between natural and archaeological resources, the project aimed to create a high-resolution dataset of cranial measurements of bison recovered from the physiographic Bighorn Basin and compare them with late Holocene morphological data from across the continent (McDonald, 1981; Widga, 2013).

Variations in cranial morphology have been studied in bison both in North America and Europe to investigate speciation (McDonald, 1981; Skinner and Kaisen, 1947; Wilson, 1978), herd dynamics (Guthrie, 1990; Gündemir and Szara, 2025), the effects of ecological and climate factors (Widga, 2013; Martin and Barboza, 2020b, Martin and Barboza, 2020a; Gündemir and Szara, 2025), and demographic information such as sex (Cannon, 1997; Cannon, 2007; Shackleton et al., 1975; Walker, 1992; Wilson, 1975, Wilson, 1978).

The Bighorn Basin provides an ideal location to learn about the morphology and diet of pre-bottleneck North American bison. Located in Northwestern Wyoming, the Bighorn Basin is ringed by the Pryor, Bighorn, Owl Creek, Absaroka, and Beartooth Mountains. On the western side of the Absaroka and Beartooth Mountains lies present-day Yellowstone National Park, home to the only bison herd to continuously occupy the same range in the lower 48 States (Cannon, 2008). The Bighorn Basin has a long history of bison, with at least 66 archaeological and historical sites containing bison (Martin et al., 2023). Notable among these is the Horner Site, which dates to between 10,500 and 11,500 years old (Frison and Todd, 1987). For indigenous groups in and around the Bighorn Basin, bison were a commodity but also considered a relative and of profound cultural significance (Frison, 2004; Brink, 2008; Kornfeld et al., 2010; Zedeño, 2017). Tribal use of bison in the Bighorn Basin continued until tribal movements were restricted in the late 1860s (Fort Bridger Treaty, 1868). The Bighorn Basin remained largely unsettled by Euro-Americans until the late 1870s, when cattle ranchers moved into the region. Historical accounts place the last wild bison sighting in the Bighorn Basin as late as 1898 (Osborne, 1995). These historic events, combined with the designation of large tracts of land as public, contributed to the accumulation of bison skeletal material that remained uncollected on the landscape.

Materials and methods

The lead author measured 114 historic bison crania sourced from members of the public (Supplementary Table S1) and ten modern bison (Supplementary Table S2) from both conservation and ranching herds across three localities. For this research, “historic” refers to bison that predate the population bottleneck event of the late 19th century, while “modern” refers to specimens from 21st-century conservation herds and ranching populations. The dataset of modern bison is compiled from three sources: legally harvested wild bison in Wyoming (n = 1), specimens from the Antlers Ranch outside of Meeteetse, Wyoming (n = 6), and specimens from the Hot Springs State Park conservation herd in Thermopolis, Wyoming (n = 3). Herd managers retained the modern skulls for distinguishing features, such as size or age, resulting in an inherent bias within the sample.

Up to 26 measurements were taken on each specimen, depending on its completeness (Figure 1). These measurements follow Skinner and Kaisen (1947), and each measurement was assigned a number with the prefix “SK” (Table 1). Although subsequent researchers have used versions of the measurements (McDonald, 1981; van Zyll de Jong, 1986; Walker, 1992; Cannon, 2004, Cannon, 2007) published in Skinner and Kaisen (1947), the original version was used for this project. For consistency, one person measured all bison using forestry calipers (0–1016 mm), handheld digital calipers (0–155 mm), and a cloth tape measure. Morphology of bison in the Bighorn Basin (both historic and modern) was then compared with that of late Holocene *Bison bison* (n = 352) compiled by Widga (2007), referred to throughout as the “North American dataset.” Traditional linear metrics were used due to budgetary limitations and a desire to compare bison from a limited geographic range with the North American dataset Widga (2007).

Sex

Sexual dimorphism in bison, characterized by larger males and smaller females, allows cranial metrics to be used for sex



FIGURE 1

Specimen completeness ranged from fully preserved (left) to missing the frontals and premaxillary processes (middle) to just the base of the skull and horn cores (right). Missing horn cores were also common.

TABLE 1 Morphometric measurements adapted from Skinner and Kaisen (1947).

MEASUREMENT	DESCRIPTION
SK1	Horn Core Tip to Tip
SK2	Spread of Horn Cores on Outside Curve
SK3 (Left and/or Right)	Horn Core Length, Upper Curve, Tip to Burr
SK4 (Left and/or Right)	Horn Core Length, Lower Curve, Tip to Burr
SK5 (Left and/or Right)	Straight Length Horn Core
SK6 (Left and/or Right)	Vertical diameter of horn core
SK7 (Left and/or Right)	Circumference of horn core
SK8	Greatest width of auditory openings
SK9	Width of condyles
SK10	Occipital crest to top of foramen magnum
SK11	Occipital crest to bottom of foramen magnum
SK12 (Left and/or Right)	Transverse diameter of core
SK13	Width between horn cores
SK14	Width of cranium at narrowest point
SK15	Postorbital width
SK16	Width of orbitals at notch
SK17	Width of masseteric processes
SK18	Width of max-premaxillary suture
SK19 (Left and/or Right)	P2-M3
SK20 (Left and/or Right)	M1-M3
SK21 (Left and/or Right)	Overall length, occipital crest to tip of premaxilla
SK22	Length (bottom) foramen magnum to premaxilla
SK23	Length, occipital crest to tip of nasals
SK24	Length, occipital crest to nasal-frontal suture
SK25 (Left and/or Right)	Length beyond P2 to premaxilla
SK26 (Left and/or Right)	Length of nasal bone

differentiation due to relatively little metric overlap (Shackleton et al., 1975). For this study, five measurements were evaluated to separate small bulls from large cows (Table 2).

Morphology

Using analysis of variation (ANOVA), morphology was compared to the North American dataset (Widga, 2007) to see if there were specific differences. Horn Core Curvature Indices ((SK4/SK5) * 100) were calculated using Skinner and Kaisen (1947: 142).

TABLE 2 Measurements for sexing bison crania.

Measurement Description	Female (mm)	Indeterminate (mm)	Male (mm)
Spread of Horn Cores Tip to Tip (SK1)	<490	490 – 560	> 560
Spread of Horn Cores on Outside Curve (SK2)	<510	510 – 580	>580
Circumference at the Base of Horn Core (SK7)	<172	172 – 234, >200 most likely bull	>234
Greatest Width at Auditory Openings (SK8)	<212	212 – 534, >230 most likely bull	>234
Width of the Cranium Between the Horn Cores and Orbits (SK14)	< 224	224 – 258, > 240 most likely bull	> 258

Since the North American dataset only uses one measurement for both SK4 and SK5, while this paper presents left and right measurements, the average horn core curvature was calculated for comparison. When necessary, Tukey’s pairwise tests are used to clarify differences between groups.

Radiocarbon dating and stable isotopes

Stable isotope analyses have successfully reconstructed life histories from archaeological and paleontological bison specimens (Chisholm et al., 1986; Hobson, 1999; Hoppe, 2006; Cannon, 2007; Widga, 2013; McKetta, 2017). Twenty-three of the most complete bison from the historic dataset with the most reliable provenience were sampled for radiocarbon dating and stable carbon and nitrogen isotope analyses of collagen from bison bone. Five modern bison samples, all from the Antlers Ranch, were submitted for stable carbon and nitrogen isotope analysis to compare with historic specimens. These modern samples are limited in sample size (n =5) and to a ranch where bison receive supplemental food during seasons when food is scarce, but the authors felt it was important to compare historic and modern bison to see how similar their diets were and whether any differences warrant further investigation.

Radiocarbon dating (¹⁴C) and stable isotope analyses (δ¹³C and δ¹⁵N) were conducted at the University of California, Irvine W.M. Keck Carbon Cycle Accelerator Mass Spectrometer Lab. Dates were calibrated using OxCal 4.4 (Ramsey, 2024) using the Int20 Calibration Curve (Reimer et al., 2020) and reported with 2-sigma ranges (see Table 3). All samples had C:N atomic ratios ranging between 2.9 to 3.6, indicating collagen is well-preserved (Ambrose, 1991; Davies et al., 2019).

Samples for stable isotope analyses came from the petrous portion (n = 20) and zygomatic arch (n = 3) for the historic dataset. Modern samples were taken from the petrous portion (n = 3) and maxillary molars (n = 2). A correction of -1.5‰ was applied to all historic specimens to account for anthropogenic CO₂ added to the atmosphere in the 20th century (Tieszen, 1994). Collagen δ¹³C values were further corrected to an estimate of dietary input, -5.1‰ (Carlson et al., 2018). These corrected values are notated as δ¹³C_{diet}.

Bison forage can be divided into two plant groups based on their photosynthetic pathways: C₃ plants and C₄ plants. The δ¹³C of C₃ plants ranges between -35 and -22‰, with an average of -26.5‰, while C₄ plants range between -16 and -9‰, averaging -12.5‰ (Smith and Epstein, 1971; Chisholm et al., 1986; Carlson et al., 2018).

TABLE 3 Radiocarbon dates (¹⁴C) and stable isotope analysis of Bighorn Basin bison.

UCIAMS	BBHB ID	¹⁴ C age (uncal BP)	¹⁴ C age (cal BP)	μ	>30kDa collagen	δ ¹⁵ N	δ ¹³ C	%N	%C	C:N (atomic)	
248384	102	775 ± 15	724-673	695	4.8	7.8	-17.9	14.8	45.6	3.6	
248388	103	135 ± 20	273 - Modern	131	7.4	6.9	-19.3	15.5	44.9	3.4	
248394	104	220 ± 15	305-150	219	6.4	7.0	-18.6	14.9	43.8	3.4	
248383	105	155 ± 15	281	150	4.2	6.9	-19.3	14.7	45.8	3.6	
248380	116	115 ± 15	259-30	125	6.2	7.2	-20.0	14.5	44.5	3.6	
248392	118	150 ± 15	280-5	143	5.4	7.0	-19.3	15.0	44.9	3.5	
248389	119	180 ± 15	286	172	5.5	6.8	-18.7	14.7	44.9	3.6	
248393	120	155 ± 15	281	150	7.5	6.9	-19.8	15.3	45.1	3.4	
248404	127	140 ± 15	275 - Modern	131	4.0	7.1	-18.8	14.5	43.4	3.5	
248385	132	140 ± 15	275 - Modern	131	6.8	7.1	-17.5	15.4	45.7	3.5	
248397	133	225 ± 15	305-151	227	10.8	5.9	-18.7	15.6	43.5	3.3	
248398	134	150 ± 15	280 - Modern	143	4.6	6.7	-19.5	15.4	44.3	3.4	
248382	146	110 ± 15	258-32	126	5.9	6.5	-19.8	14.9	45.0	3.5	
248386	151	135 ± 20	273 - Modern	131	4.6	6.7	-18.1	14.8	43.7	3.4	
248381	154	285 ± 15	428-295	365	6.6	7.2	-18.7	15.1	45.1	3.5	
248387	165	370 ± 15	494-327	419	18.4	6.3	-18.6	15.6	44.1	3.3	
248391	197	150 ± 15	280 - Modern	143	4.9	6.5	-19.4	14.8	45.1	3.6	
248395	200	215 ± 15	303-150	212	4.2	7.3	-18.4	15.0	43.6	3.4	
248396	201	120 ± 15	263-26	124	6.0	7.1	-18.5	14.9	44.5	3.5	
248405	203	600 ± 15	644-549	601	4.1	7.9	-15.7	11.7	32.9	3.3	
248400	204	205 ± 15	298 - Modern	199	3.5	7.1	-16.8	14.4	41.9	3.4	
248399	205	175 ± 15	285	168	4.8	7.4	-19.4	15.0	43.8	3.4	
279305	212	185 ± 15	287	177	3.3	7.4	-18.5	14.6	43.1	3.4	
	M5	Modern				0.8	5.2	-20.4	14.1	38.6	3.2
	M6	Modern				8.8	6.3	-14.3	15.9	44.0	3.2
	M7	Modern				4.4	6.9	-20.5	14.8	43.9	3.5
	M8	Modern				6.6	6.6	-21.2	14.9	44.3	3.5
	M9	Modern				6.4	5.9	-22.9	15.0	45.4	3.5

uncal, uncalibrated BP; cal BP, calibrated BP; kDa, kilodalton; C:N (atomic), ratio of carbon atoms to nitrogen atoms measuring collagen integrity.

To calculate the proportion of C₃ and C₄ plants in a bison diet, this study uses an equation adapted from Carlson et al. (2018):

$$\% C3 = \left(\frac{(\delta^{13}C - 5.1 - (-12.5))}{-26.5 - (-12.5)} \right) \times 100$$

As herbivores that both graze and browse (Craine et al., 2015; Hecker et al., 2021; McDonald, 1981; Meagher, 1986; Widga, 2006), bison are expected to consume a mixture of the available plants in their range (Chisholm et al., 1986; Tieszen, 1994). Sagebrush and desert shrubland dominate the Bighorn Basin, flanked by juniper woodland that transitions into Engelmann spruce–subalpine or lodgepole pine forests (Knight et al., 2014). Annual rain in the Bighorn Basin ranges from less than 254 mm in the center to nearly 508 mm in the foothills surrounding the Basin (Knight et al., 2014). C₃ plants dominate this semi-arid environment, although C₄ plants are present during the summer months (Knight et al., 2014).

Stable nitrogen isotope analysis (δ¹⁵N) has been used to study weaning behaviors (Schurr, 1998; Ambrose, 2002), assess trophic

levels (Szpak, 2014), evaluate diet (Bird et al., 2021; Deniro and Epstein, 1981), and gauge nutritional stress (Ambrose, 1991, Ambrose, 2002; Funck et al., 2020). The dynamics of δ¹⁵N at the landscape level, however, are complex, with shifts attributed to numerous factors, such as water stress (Ambrose and Deniro, 1986) or diet (Bergmann et al., 2015; Berini and Badgley, 2017; Blackburn et al., 2021; Craine, 2021; Metcalfe, 2021). Research on bison δ¹⁵N suggests values vary with age, sex-group dynamics, and body size (Metcalfe and Olson, 2025).

Comparative analyses draw on both modern and historic datasets from various regions. The modern datasets include samples from the Bighorn Basin (n = 10), Theodore Roosevelt National Park (n = 5)—hereafter referred to as the modern Northern Plains (Davies et al., 2019)—and Yellowstone National Park (n = 15) (Feranec, 2007). Historic bison are derived from archaeological sites. Specimens referred to as “late Holocene Northern Plains” originate from North and South Dakota (n = 43) (Davies et al., 2019). Additional samples come from the Scoggin Site

($n = 5$), an archaeological site in the south-central portion of Wyoming. Previously reported radiocarbon dates from charcoal at the site place the Scoggin Site in the middle Holocene between 4,500 – 5,000 years B.P. (McKetta, 2017). Recent redating using bison petrous portions (Todd, 2024, p. 10) revises these dates, placing the site in the late Holocene (UCIAMS #288515, 3590 ± 20 uncal B.P.; UCIAMS #299516, 3910 ± 20 uncal B.P.). Regardless of this update in radiocarbon ages, Scoggin provides a temporal contrast to bison from later in the late Holocene, immediately before the population bottleneck.

Although regional bison datasets with broader temporal coverage do exist (Cannon, 2008; Cannon et al., 2023), they were not included in this study for the following reasons. This study intentionally employs a tight temporal scale, focusing on the late Holocene. This temporal constraint attempts to reduce the potential confounding effects of major climatic shifts, which could obscure relevant patterns or introduce unrelated variability. Stable isotope analysis comparisons were limited to the geographic areas bordering the Rocky Mountains – namely, the northern and central Plains. Future analyses will focus on smaller, regional datasets and varying time scales. All statistical analyses in this study were conducted using PAST version 4.17 (Hammer, 2024).

Results

Radiocarbon dating results

Radiocarbon dates (Table 3) place the study bison immediately before the 19th century population bottleneck event. Mass bison kills were increasingly common in the Rocky Mountains and Northern

Plains from 200–1500 cal BP (Reher, 1977; Kornfeld et al., 2010). This was a period of extensive changes both climatic, such as the Little Ice Age (500–250 cal BP) (Alt et al., 2024), and anthropogenic, including the re-introduction of the horse in Wyoming (268 ± 26 uncal BP) (Thornhill, 2021); and the westward expansion of European peoples and livestock (Dobson, 2013).

Morphometric results

Sex

Two bison (BBHB 181 and 182) were removed from morphometric analysis because of erroneous measurements. Of the remaining bison, 88.4% percent ($n = 99$) of the dataset are likely male bison, 8.9% ($n = 10$) females, and sex could not be assessed for 2.7% ($n = 3$) (Figure 2). This bias may be a result of how the project was advertised. In the early weeks of September 2020, to better engage local bison enthusiasts, advertising was framed as a competition—“How does your bison measure up?” As word spread, this may have biased the results, but people may also selectively recover large bison crania from the landscape. Similar biases have been documented in other cranial morphology studies on bison (Cannon, 2008), and many natural history museums have documented male bias in their collections (Cooper et al., 2019; Gower et al., 2019). Male bison have denser, larger crania (Guthrie, 1990) and are more likely to survive taphonomic processes of deposition, burial, erosion, and weathering. This bias should be considered in the interpretation of all results.

Cranial morphology

A principal components analysis (PCA) on the entire historic dataset (without separating by sex) showed four measurements

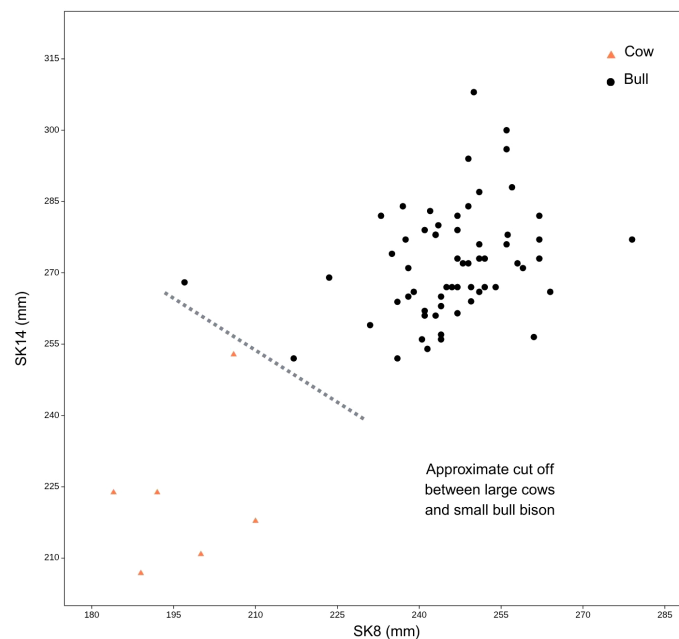


FIGURE 2
Two of the five metrics used for determining sex.

were the primary drivers of variation, including Horn Core Tip to Tip (SK1; 70.8%) and Horn Core Max Width (SK2; 18.3%). All other cranial measurements (SK5 – 26) drove less than 10% of the variance of bison cranial morphology. To ensure the missing observations did not result in erroneous interpretations, a PCA was run with only bison containing complete measurements for SK1 – 16 ($n = 27$). The premaxilla was often damaged or missing, making measurements SK17–26 more difficult to obtain. Removing these measurements may remove younger bison from the analysis, but result in a clearer understanding of the drivers of variation. The resulting PCA reflected the same results as the PCA of the entire dataset. Horn Core Tip to Tip (SK1: 84.7%) drives the majority of the variance followed by Horn Core Max Width (SK2: 6.7%) and Horn Core Horn Core Length, Upper Curve, Tip to Burr (SK3: 3.4%), while all other measurements contribute little to the variance (SK4-16: 5.1%). Variation amongst *Bison bison* in the Bighorn Basin primarily occurs in their horn cores, consistent with other studies (Cannon, 2008, p. 51; McDonald, 1981; Skinner and Kaisen, 1947). Bison from the Bighorn Basin had statistically significantly larger horn cores in every measurement than bison from the North American dataset, except SK1 (Table 4). McDonald (1981) and (Cannon, 2008) also found horn core morphology to be a powerful discriminating variable for discerning taxonomy.

Bison from before the population bottleneck show comparable horn core curvature (Figure 3). The horn cores of the modern population are more curved. An analysis of variance (ANOVA) conducted on horn core curvature showed slight significance, $F(25.75) = 7.0$, $p \leq 0.000$. A Tukey's pairwise test showed significant differences between the modern population and the Bighorn Basin ($p \leq 0.000$) and North America ($p \leq 0.000$) datasets.

Stable isotope results

Late Holocene bison from the Bighorn Basin exhibit a mean $\delta^{13}C_{diet}$ value of -20.3‰ and range from -21.7 to -18.3‰ , with an average consumption of 7.9% C_4 plants in their diets. An ANOVA conducted on the percentage of C_4 between the six datasets was significant, $F(14.91) = 17.84$, $p \leq 0.001$. A Tukey's pairwise test, summarized in Table 5, showed significant differences between several populations, including the Scoggin site and all other

populations, as well as Yellowstone National Park and the late Holocene Northern Plains.

Late Holocene bison from the Bighorn Basin exhibit a mean $\delta^{15}N$ value of 7‰ and range from 5.9 to 7.9‰. An ANOVA conducted on the $\delta^{15}N$ showed significant differences ($F(13.1) = 48.77$, $p = 0.000$). A Tukey's pairwise test revealed these differences are significant ($p \leq 0.01$) between the modern Northern Plains dataset and late Holocene datasets of the Northern Plains and Bighorn Basin, as well as the Scoggin Site (Figure 4).

Discussion

Horn core plasticity

Bison horn cores respond to a series of both environmental (Cannon, 1997) and social (Guthrie, 1990) factors. If the observed trends are consistent with those in modern herds, the tendency for modern bison to exhibit higher horn core proportions (i.e., be longer and more curved) may result from several variables. As previously noted, an inherent bias from the modern dataset is that the bison tended to be especially large or long-lived. A larger, more representative sample would help evaluate the extent of this bias. The modern herds studied have controlled male-to-female ratios. In these settings, male bison do not need to compete for breeding access to the females and are sometimes segregated from the larger herd. Without the need to compete directly for mates, a herd structure where the short, upward pointing horn cores of *Bison bison* are advantageous, bull horn cores may become longer and more curved to visually signal reproductive fitness (e.g., Guthrie, 1990, p. 168-172). If modern bulls are not engaging in direct competition but still have access to females, then horn development may shift toward display features. The apparent difference between modern and historic bison could also result from bison spending time in different habitats (sensu lato Widga, 2013).

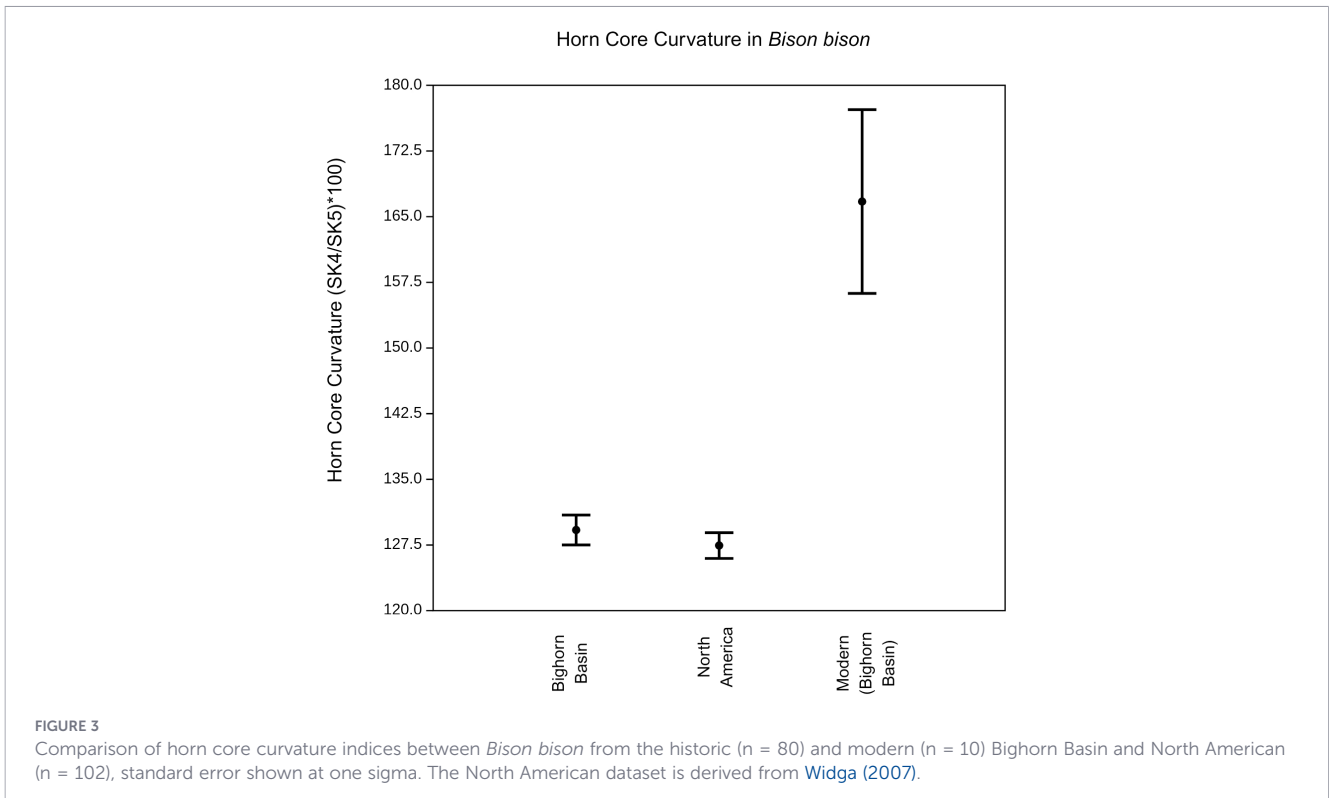
Bison diets in the Bighorn Basin

Stable carbon isotope results align with the expectation that bison diets will reflect a mixture of the C_3 and C_4 plants available in the area (Hoppe, 2006; Bouvier, 2022) and are comparable to contemporaneous bison from the Northern Plains (Davies et al., 2019). Significant differences occur in the percentage of C_3 plants between the diets of late Holocene bison and those from the Scoggin Site (middle to early late Holocene). Bison from the late Holocene Bighorn Basin consumed the most C_3 plants (92.1%), followed by those on the Northern Plains (90.6%), with bison from the Scoggin site consuming only 74.3% on average. Greater consumption of C_4 plants is expected for a herd further south, where the availability of C_4 plants increases (Lohse et al., 2014; Carlson et al., 2018). The greater consumption of C_4 plants may reflect the variability of the middle Holocene, when the climate shifted toward warmer, drier conditions (Knight et al., 2014; Davies et al., 2019), but systematic redating of the site as recommended by Todd (2024) would help to clarify these relationships.

TABLE 4 Significance of the most variable measurements between Bighorn Basin and National dataset.

Measurement	Bighorn Basin Mean \pm SD (n)	North America Mean \pm SD (n)	t (p)
Horn Core Tip to Tip (SK1)	590.4 \pm 66.8 (51)	559.3 \pm 83.1 (249)	2.9 (0.004)
Spread of Horn Cores on Outside Curve (SK2)	609.6 \pm 69.3 (51)	547.7 \pm 118.3 (41)	2.9 (0.004)
Horn Core Length, Upper Curve, Tip to Burr (SK3)	198.9 \pm 33.2 (*84)	169.3 \pm 38.6 (261)	6.8 (0.001)
Horn Core Length, Lower Curve, Tip to Burr (SK4)	241.4 \pm 51.8 (*83)	186.9 \pm 53.9 (102)	6.9 (0.001)

* indicates the average value of left and right side measurements.



Bison from both late Holocene populations consumed high amounts of C₃ plants but incorporated some C₄ plants into their diets. This is a departure from the diets of Yellowstone National Park bison, where no C₄ plants are observed (Feranec, 2007). Bull bison have been observed consuming a higher percentage of C₄ plants than cow bison (Post et al., 2001; Blackburn et al., 2021). The Bighorn Basin δ¹³C dataset is derived from male bison, so the mean 7.9% of C₄ plants in bison diets from the area may represent the upper range of C₄ plants utilized by bison in the area during the late Holocene.

The populations examined generally exhibit broad δ¹⁵N variability, except for modern Northern Plains bison, which display a more constrained isotopic range. At the population-level, historic bison from the Bighorn Basin possess the highest

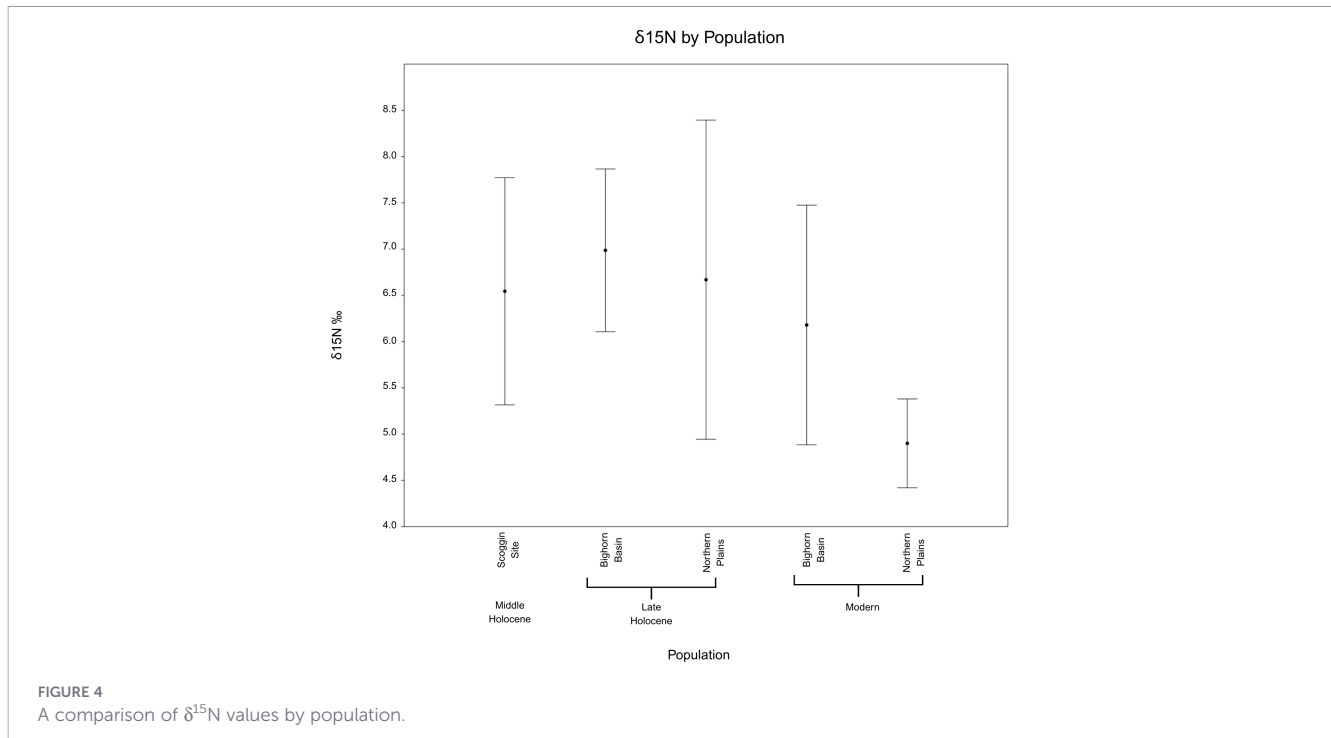
mean δ¹⁵N values. The complexity of the nitrogen cycle and expected fractionation warrant investigation into several potential causes of the increased mean δ¹⁵N of bison from this study over contemporaneous bison in the Northern Plains. These differences could result from diet or habitat.

Elevated mean δ¹⁵N values in the bone collagen of historic Bighorn Basin sample could reflect dietary differences between the mixed grass prairie of Theodore Roosevelt National Park (Morgan, 2020) and the sagebrush steppe of the Bighorn Basin (Knight et al., 2014). It might also reflect differences between bulls and cows. In Yellowstone National Park, bull bison show higher δ¹⁵N values than cows from the same area, indicating lower-quality diets (Berini and Badgley, 2017). In contrast, research from Elk Island National Park

TABLE 5 Tukey's pairwise p-values from ANOVA test of %C₄ with lower left half values indicating Tukey's Q and upper right half values indicating p-values.

	LH BHB	LH Northern Plains	Scoggin	Yellowstone	Modern Bighorn Basin	Modern Northern Plains
LH Bighorn Basin	n= 23	0.999	***0.018	0.051	0.998	0.995
LH Northern Plains	0.257	n= 43	***0.016	***0.014	0.999	0.984
Scoggin	4.639	4.704	n= 5	***0.000	0.234	***0.040
Yellowstone National Park	4.103	4.762	7.07	n= 14	0.219	0.766
Modern Bighorn Basin	0.595	0.480	3.155	3.205	n= 5	0.973
Modern Northern Plains	0.787	0.962	4.233	1.885	1.077	n= 5

***, significant values at p ≤ 0.05.



found a negative correlation between body size and $\delta^{15}\text{N}$, with bull bison displaying lower $\delta^{15}\text{N}$ than cows (Metcalfé and Olson, 2025). These contrasting findings indicate that sex-based dietary differences are context-dependent and warrant further investigation. As a result, the elevated mean values observed in the historic Bighorn Basin bison cannot confidently be attributed to sex-based dietary differences. Other contributing dietary elements could include seasonal changes in diet, such as the selection of nitrogen-fixing forbs and shrubs in the early and late growing season (Bergmann et al., 2015; Blackburn et al., 2021; Craine, 2021), or a diet composed of relatively more wetland plants (Metcalfé, 2021). Bison graze on initial growth following fires both today (Shaw and Carter, 1990) and in the past (Roos et al., 2018), possibly contributing toward elevated $\delta^{15}\text{N}$ (Pate and Anson, 2008; Turner et al., 2011; Dunnette et al., 2014).

A final possibility is that variation in mean $\delta^{15}\text{N}$ reflects differences in the elevation gradients used by bison. Bison faunal material has been found throughout the Rocky Mountains (Fryxell, 1926; Cannon, 1997; Cannon, 2004; Cannon, 2007; Tirlea et al., 2022) and within the Absaroka and Beartooth Mountains on the periphery of the Bighorn Basin (Lee and Puseman, 2017; Widga et al., 2024). The bison at these sites were likely escaping heat, pests, and parasites of lower elevations during the summer months (Benedict and Barboza, 2022; Dixon, 2022; Tirlea et al., 2022). Nitrogen occurs in relatively higher amounts in forested areas than in grassland ecosystems (Asner et al., 1997). Bison moving from the Bighorn Basin to the surrounding mountains would pass through forests and up to the alpine tundra where nitrogen concentrations are high (Seastedt and Vaccaro, 2001; Knight et al., 2014). Plant growth in the alpine is restricted (Fisk et al., 1998) and thus is not likely to comprise a significant component of the bison diet;

however, readily accessible water may provide the mechanism for elevated $\delta^{15}\text{N}$ levels. This explanation would require more research, including comparison with the stable isotope ratios of bison recovered from ice patches. Both modern herds have lower $\delta^{15}\text{N}$ values, possibly resulting from supplementary food (i.e., higher-quality diets) or changes in the composition of range plants.

Future research

The interpretation of many of this study's findings could be improved by a more comprehensive study of bison morphology and stable isotope ratios. A more exhaustive dataset of bison morphology, including privately managed ranches and conservation herds of varying sizes and under different management practices, could help elucidate whether patterns noted here are the result of diet, herd structure, or other variables. The effect of management practices on horn core development and morphology could help better interpret bison from archaeological sites. Sampling from female bison could clarify sex-based differences in diet as reflected by isotopic values. An understanding of the seasonal abundance and distribution of C_3 and C_4 plants available in the Bighorn Basin would better contextualize $\delta^{13}\text{C}$ values and inform interpretations of habitat use. A comparison of bison from low-elevation sites with those recovered from ice patches could test hypotheses about seasonal use of ice patches, yielding information helpful for interpreting archaeological recoveries. An investigation of the effect of fire history on $\delta^{15}\text{N}$ in bison warrants further study. Though not evaluated here, fire could contribute to elevated $\delta^{15}\text{N}$, as observed in late Holocene bison from the Bighorn Basin.

Conclusion

A dataset of this size covering a distinct geographic region could not have been gathered without the local community's involvement. Late Holocene bison in the Bighorn Basin are morphologically comparable to other populations, though with statistically larger horn cores. Though based on small modern sample sizes, this study suggests management in the Bighorn Basin and Northern Plains allows bison to maintain diets similar to those of late Holocene bison. Variations in modern herd demographics and social dynamics may influence changes in horn core morphology, particularly related to sex ratios within the herd; however, further research with larger sample sizes is necessary to substantiate these associations.

Stable isotope analyses show late Holocene bison consumed primarily C₃ plants but had elevated $\delta^{15}\text{N}$ values. While nitrogen cycling is complex, the elevated $\delta^{15}\text{N}$ values in Bighorn Basin bison may reflect dietary differences between males and females, the seasonal use of high elevations, or post-fire grazing. These results, while shaped by limitations in sex distribution, offer insight into past variation in bison dietary ecology and may inform modern conservation strategies for bison management across the public, private, Tribal, and nonprofit NGO sectors in the Bighorn Basin and Wyoming more broadly.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because vertebrate skeletal material was the focus of this research, and no ethical approvals were required.

Author contributions

AP: Data curation, Project administration, Writing – review & editing, Writing – original draft, Funding acquisition, Formal analysis. CW: Writing – original draft, Investigation, Writing – review & editing, Conceptualization. JM: Writing – original draft, Methodology, Writing – review & editing. IO: Writing – review & editing, Writing – original draft, Methodology. JB: Writing – review & editing, Methodology. KC: Investigation, Writing – original draft, Project administration, Writing – review & editing, Formal analysis,

Methodology. LT: Investigation, Conceptualization, Writing – review & editing, Resources.

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Conflict of interest

Author KC was employed by the company Cannon Heritage Consultants. Author LT was employed by the company Greybull River Sustainable Landscape Ecology, Inc.

The remaining author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that generative AI was not used in the creation of this manuscript.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2026.1759337/full#supplementary-material>

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