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Ancient DNA-based sex determination of bison hide moccasins indicates Promontory cave occupants selected female hides for footwear



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ABSTRACT

The thirteenth-century human occupants of the Promontory caves, Utah, distinguished themselves from surrounding Fremont populations by being successful hunting specialists of bison in a region normally peripheral for that species. The hunters' success is evident from the abundance of faunal remains excavated from the dry caves. The dry cave conditions also preserved hundreds of worn moccasins, which are of particular interest because of the Canadian-Subarctic style in which they are made, and for their potential to reveal more about the hunting strategies of their wearers. Here, we isolate ancient DNA from 38 Promontory Cave 1 (42BO1) moccasin and hide fragments and use these data to determine the species and sex of animals used to construct the moccasins. We found that moccasins from which we could isolate DNA were all made from bison and most (87%) were females. The strong female bias in our data, which we demonstrate is a significant departure from sex ratios in present-day bison herds, suggests that the occupants of the cave were purposefully targeting female bison for moccasin manufacture. Our study is the first to our knowledge to determine faunal sex ratios from an assemblage of archaeological leather and highlights another potential avenue for ancient DNA technologies to augment what can be learned from the archaeological record.

1. Introduction

Analyses of communal bison kills have been a focus of Plains archaeological research, especially for interpreting Indigenous hunting strategies from archaeological bone assemblages (e.g., Wilson, 1978; Johnson and Bement, 2009; Carlson and Bement, 2013). Age structures of archaeological bison assemblages have been characterized from tooth eruption sequences, occlusal wear patterns, cementum growth increments, fetal remains, and epiphyseal fusion (see Gifford-Gonzalez, 2018 for a summary). Inferences regarding the sex structure of hunted bison have been drawn from osteometric indices that differentiate the larger male from the smaller female bison (e.g., Hill et al., 2008; Driver and Maxwell, 2013). Knowing the age distribution and sex structure of animal remains in archaeological contexts can reveal nuances in the behaviors, social structures, and natural histories of prey species as well as the cultural practices associated with hunting (Payne, 1973; Weinstock, 2000; Pečnerová et al., 2017; Gifford-Gonzalez, 2018; Royle et al., 2018). Analyses of sex structure in archaeological bison assemblages can be used, for example, to evaluate the extent to which bison hunters were using sex-specific hunting strategies to target animals with greater nutritional value (Speth, 1983).

Bison are the most common large mammals in archaeological bone assemblages of the American Plains. While it is well known that people used every part of the bison (e.g., Ewers, 1958), osseous remains are most often preserved. Osteometric sex determination is often straightforward in bison, thanks to their strong sexual dimorphism, however

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smaller males and larger females add a degree of imprecision (e.g., Bedord, 1974; Walde, 2004). Sex determination can also be influenced by the condition of the remains preserved (e.g. Speller and Yang, 2016), the bone element preserved (Buonasera et al., 2020), the age of the animal at death, and by geographic and temporal variation in animal morphology (Gifford-Gonzalez, 2018). Determinations of sex that do not rely on morphological assessment, such as from DNA, have potential to improve understanding of Indigenous hunting strategies.

Genetic sex determination could also be used to determine the sex of perishable parts of hunted animals such as hide, from which sex is not easily distinguished, and animal parts with non-food uses that nonetheless may have influenced hunting strategies. For example, Indigenous peoples met critical shelter and clothing needs by hunting bison. Rawhide and leather from bison hides were essential for lodge covers, tipi liners, robes, tailored clothing, footwear, cordage, and items like travois baskets (Brink, 2008). Sexual dimorphism, animal age, and seasonality all influence skin thickness and hide pliability, which are aspects of bison morphology that humans considered (Brink, 2008; LeBlanc, 1999; Speth and Staro, 2012, 2013).

Here, we capitalize on the exceptional preservation of hundreds of worn moccasins excavated from the dry cave assemblages of the Promontory caves, Utah, to explore the sex assemblage of bison used for moccasins. We extract ancient DNA (aDNA) from 38 moccasin and hide fragments, among which 17 produced AMS ages between 703 ± 23 and 886 ± 27 radiocarbon years before present ($\sim 1135 \pm 27 - 1318 \pm 23$ AD; Table 1). We generate sufficient aDNA data from 23 samples to determine both species and sex of the animal hide and compare these data to new estimates of bison sex ratios from present-day herds. Our results represent the first use of molecular estimates of faunal sex ratio in archaeological soft tissue assemblages to better understand selection of materials by Indigenous people.

2. Background

2.1. The Promontory cave context

The early Promontory Phase on Promontory Point, Utah (Fig. 1), marks a discontinuity in the late period archaeological record of the northeastern Great Basin (Ives, 2014and Ives et al., 2021). The dry cave conditions preserved hundreds of worn and discarded moccasins, as well as mittens, bison robe fragments, gaming pieces, matting, basketry, cordage, bows, arrows, stone tools, ceramics, and hide processing tools (Ives et al., 2014; Yanicki and Ives, 2017). The early Promontory Phase deposits have provided 95 Bayesian modelled AMS dates (including those in Table 1) that suggest an occupation extending from 1248-1290 CE (Ives et al., 2014, 2021). Intriguingly, the rich material culture preserved in the caves differs from local Fremont expressions. At the time the caves were occupied, local Fremont populations relied on wild food resources from wetlands, some large game hunting, intensive small game capture, and wild seed processing. The substantial archaeological deposits resulting from this sudden and brief occupation of Promontory Cave 1, alternatively, include scant evidence of small game animals and wild seed processing and instead reveal a strong large game hunting focus (Ives et al., 2014a,b).

Promontory collections excavated in 1930–31 and 2011–2014 unearthed thousands of items, but significant midden deposits remain in the caves today. Promontory Cave 1 was subject to looting prior to Steward's 1930–31 work. The most recent excavations of Cave 1 unearthed more than 30,000 whole and fragmentary faunal remains dominated by bison, pronghorn antelope, elk, deer, and sheep (Ives and Janetski, in press). These and Steward's (1937) excavations (as well as other collecting activities) recovered more than 340 worn out moccasins from Caves 1 and 2. Hallson (2017) used a modelling approach to estimate that 1660 to 3160 (mode ~2400) moccasins and 1.6–1.8 million whole and fragmentary faunal remains probably comprised the original contents of the site (full explanation of modelling in Supplement 1).

These moccasins are constructed with the hide of multiple animals, most commonly bison, but also deer, pronghorn antelope, and rarely elk or bear (Steward, 1937). Reilly (2015) drew from Hallson's analysis to estimate that 120 to 540 bison hides would be required to make the discarded moccasins in Cave 1.

Promontory cave 1 was closely connected with local hunting and butchering activities. The saddle terrain above Caves 1 and 2 constrained game animal passage and was well suited for small-scale communal hunting and ambush strategies. Various artifacts associated with hunting and processing have been recovered both in the saddle passage and within the caves (Supplement 1). Cave 1 contains heavy, low food utility items (bison skulls and articulated lower limbs) as well as other articulated elements indicating that the cave occupants brought butchering units directly into Cave 1 for further processing (Supplement 1). There is, therefore, a rather close relationship between Cave 1 and the kill locale above it.

Julian Steward (1937) proposed that the unusual assemblage at the Promontory caves reflected the presence of Apache or Navajo ancestors midway between a Subarctic point of origin and ultimate Southwestern and southern Plains homelands. In particular, the soft-soled, fine leather moccasins Steward recovered from the Promontory caves were made in a fashion characteristic of Dene (Athapaskan) and Algonquian speakers in Subarctic Canada. The moccasins were unlike contemporary Fremont moccasins (Fremont, Hogup, and hock style moccasins, which were coarsely executed on poorly tanned leather) and also unlike later Numic forms (Aikens, 1970; Hatt, 1916; Steward, 1937; Ives, 2014).

More recent excavations have reinforced some of Steward's suspicions. Steward was correct in his attribution of the moccasin pattern to the Subarctic region. In fact, archaeologists recovered a 1400-year-old antecedent moccasin form from a southern Yukon ice patch within the northern Dene homeland (Ives et al., 2014a,b; Hare et al., 2012). Other Promontory Cave 1 artifacts provide evidence for a Subarctic and northern Plains heritage: unique stone hide softening implements (*chi-thos* or tabular bifaces still in use today in the Subarctic, yet unknown in Fremont assemblages), instances of intricate plat sinnet weaving (in a style used in the Subarctic for moccasin garters, mitten strings and birch bark vessel handles otherwise unknown among Great Basin fiber perishables), a probable dog travois basket, and extra-local obsidian.

Our research was inspired by a significantly anomalous δ^{13} C value from the ankle wrap of one Promontory Cave 1 moccasin (FS305) that triggered more detailed exploration of a bison isotopic landscape (Metcalfe et al., 2021). Isotopic evidence indicated that the leather for the ankle wrap came from a bison that was probably killed several hundred kilometers away, in an arc extending from northern Arizona to eastern Colorado, or even farther (Metcalfe et al., 2021). As part of that study, we used ancient DNA to determine that the bison whose hide comprised the ankle wrap leather was female. This test sample provided the impetus for the present sex-determination study to examine sex-biased strategies in selecting hides for moccasin construction.

2.2. Bison herd compositions and hunting strategies

Parity in bison sex ratio at birth is a reasonable working assumption, although with a tendency toward a slight male bias (Reynolds et al., 2003). Fuller (1962), Haugen (1974), and Rutberg (1986) all observed more male than female calves in a single generation (53–62% male). Wolff (1988) estimated equal proportions of male and female offspring at birth in a 260–360 animal bison herd in Nebraska but observed that bison cows may put more nursing energy into male calves. We analyzed a large body of bison calf sex ratio data from Elk Island National Park in Alberta, Canada, and found that of 3348 bison calves recorded between 1963 and 2019 the proportion of male calves was 52% (Table S1).

It is possible that sex ratios at birth change over a cow's lifetime. Rutberg (1986) found that bison cows with no offspring in a previous year produced more male than female calves. Green and Rothstein

Table 1

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Promontory samples and sequencing statistics. FS# refers to the originally assigned field sample number for 2011–2014 testing in Promontory Cave 1 (42BO1). "Library prep" refers to the Santa Cruz (SC) or Meyer-Kircher (MK) protocol used in processing. Rx ratio refers to the proportion of reads aligned to the X chromosome versus autosomes. The expected alignment ratio (Rx) is 2:1 for males and 1:1 for females, as males have only one X chromosome.

	Table in Text																
FS #	Radiocarbon Lab #	Sample N	/letadata			ect e	Total read pairs processed	Reads aligned to:			Reads uniquely aligned to:			Percent	Cattle X	Rx	Predicted
		δ13C	14C Date	cal AD (2σ)	Object type			Cattle	Deer	Sheep	Cattle	Deer	Sheep	endogenous (Unique Cattle aligned reads/ Total read pairs)	chromosome aligned reads	ratio	Sex based on Rx
305	OxA-25234	-12.5	725 ± 24	1267–1288	Ankle Wrap	SC	2,585,396	71,906	30,144	34,594	30,355	2244	1087	2.78	3271	0.86	Female
235					Moccasin	SC	2,392,792	42,777	18,361	18,979	20,446	3130	986	1.79	1837	0.81	Female
1677	OxA-30544	-19.49	818	1210–1278	Moccasin	SC	3,494,342	563,799	188,076	221,286	290,352	8580	7717	16.13	24,941	0.83	Female
1244	OxA-28320	-19.73	$\pm 26 \\ 742 \\ \pm 23$	1263–1286	Moccasin	SC	1,360,746	10,399	4815	4557	5209	1392	395	0.76	458	0.83	Female
1290	OxA-30782	-19.65	804 + 28	1219–1278	Moccasin	SC	2,683,825	24,890	9543	10,620	11,949	1090	297	0.93	1120	0.85	Female
945	OxA-28316	-19.57	$^{\pm 28}_{\pm 24}$	1272–1290	Moccasin	SC	2,627,479	55,922	21,678	24,307	26,666	2149	1233	2.13	2550	0.86	Female
1340					Moccasin	SC	3,440,009	48,708	18,683	22,118	23,572	2158	1769	1.42	2211	0.86	Female
1408	OxA-30701	-20.1	$\begin{array}{c} 783 \\ \pm \ 23 \end{array}$	1225–1279	Moccasin	SC	2,758,066	19,376	10,091	9452	8174	2098	378	0.70	900	0.88	Female
1145					Moccasin	MK	8,181,119	570,071	226,942	270,394	254,041	14,060	13,796	6.97	26,507	0.88	Female
291					Moccasin	SC	2,707,406	15,937	6461	6914	7716	1092	309	0.59	749	0.89	Female
799	OxA-26097	-19.73	741 ± 23	1263-1286	Moccasin	SC	3,699,976	70,198	24,634	29,026	35,187	1610	1280	1.90	3386	0.91	Female
1120	OxA-28314	-19.3	$\begin{array}{c} 751 \\ \pm 24 \end{array}$	1257–1284	Hide	МК	1,219,721	225,889	89,773	107,336	97,491	3360	3078	18.52	10,901	0.92	Female
131					Moccasin	SC	3,318,920	16,128	69,645	7208	7744	1530	406	0.49	794	0.94	Female
1505	OxA-30542	-18.98	$\frac{886}{\pm 27}$	1052–1278	Moccasin	MK	153,966	3747	1874	2041	1423	261	120	2.43	185	0.94	Female
1433					Moccasin	SC	2,079,796	18,703	9429	9395	7601	1873	358	0.90	926	0.95	Female
117					Moccasin	SC	2,449,758	247,088	92,728	113,797	110,879	2787	3233	10.09	12,274	0.95	Female
126					Moccasin	SC	2,207,673	22,420	9709	10,463	9825	1305	328	1.02	1135	0.97	Female
173	OxA-25183	-19.6	706 ± 25	1272–1290	Moccasin	SC	2,276,168	14,442	6908	7194	5945	1109	240	0.63	811	1.09	Female
303					Moccasin	SC	2,827,506	18,227	7627	7478	9744	1954	740	0.64	742	0.76	Female
1676	OxA-30705	-18.34	841	1222-1277	Bison	SC	6,275,013	252,860	99,292	110,608	116,168	6233	3955	4.03	10,513	0.78	Female
			± 23		Robe			-	-	-	-						
1675	OxA-30703	-20.76	763 ± 23	1249–1281	Bison Robe	SC	3,106,197	28,294	10,010	11,659	14,236	970	412	0.91	786	0.52	Male
1596	OxA-30702	-20.51	777	1226-1280	Moccasin	SC	364,820	7795	3608	4127	2956	327	153	2.14	194	0.46	Male
1223	OxA-28319	-19.8	± 23 703	1274–1290	Moccasin	SC	3,453,590	136,372	51,118	63,274	64,955	4120	5503	3.95	5586	0.61	Male
801	OxA-26098	-19.34	± 23 777	1227–1279	Moccasin	SC	396,709	2791	1711	1430	1188	548	118	0.70	112	NA	NA
225			\pm 22		Moccasin	SC	362,272	1334	918	619	620	443	38	0.37	64	NA	NA
305					Moccasin	SC	366,720	684	1144	496	118	584	41	0.19	29	NA	NA
263					Moccasin	SC	415,957	501	442	190	258	286	19	0.12	24	NA	NA
1318					Hide	SC	393.194	175	360	80	80	285	7	0.04	8	NA	NA
1568					Moccasin	SC	291.637	589	325	247	308	135	19	0.20	25	NA	NA
1117					Moccasin	SC	320.699	809	437	364	373	151	13	0.25	40	NA	NA
291					Moccasin	SC	386.328	1628	817	776	765	243	57	0.42	78	NA	NA
116	OxA-25180	-19.01	730	1265–1287	Moccasin	SC	319,580	1871	1160	954	752	394	38	0.59	63	NA	NA
168			± 26		Moccasin	SC	416,765	1071	1019	1708	146	379	731	0.26	57	NA	NA
130					Moccasin	SC	429.686	711	554	343	300	271	14	0.17	44	NA	NA
615					Moccasin	SC	483,442	2165	1032	918	1119	330	65	0.45	76	NA	NA
969	OxA-28317	-20.3	752	1257-1283	Moccasin	SC	479,421	605	550	314	251	311	26	0.13	33	NA	NA
500	5 2001/	20.0	± 23	120, 1200	Man		400 504	105	071	71	(7	000	10	0.00	50		
568					Moccasin	SC	429,584	135	271	71	67 274	220	12	0.03	5	NA	NA
1431					wioccasin	30	238,429	840	307	312	3/4	242	19	0.33	33	INA	INA



Fig. 1. The location of the Promontory caves in Utah and the geographic distribution of Dene (Athapaskan) languages in North America.

(1991) reported that, while female bison often favor caring for males, calves of older females were nearly always female.

Bison social groups do not have equal sex ratios. Bison spend much of their early lives in matriarchal herds, with cows and calves forming the largest component of the herd. These herds vary in their proportions of cows, yearlings, and calves (Van Vuren and Bray, 1986; Larter et al., 2000; Delgiudice et al., 2001; Bradley and Wilmshurst, 2005; Fuller et al., 2007). Males leave the cow-calf herd around age four (Olson, 2005), forming small bachelor groups or living as isolated bulls. Bulls are most likely to rejoin cow-calf herds temporarily during the mid to late summer rut (mating season) (Brink, 2008), but may also join cow-calf herds outside of the mating season (Olson, 2005).

Communal hunters often targeted cow-calf herds (Brink 2008). Such hunts rely on finding a herd that is neither too small, in which agile, dangerous animals can escape, nor too large to manage safely. During late summer and early fall, the favorable body conditions of cow-calf herds as well as their tendency to bunch when threatened made them favorable targets (Brink, 2008; Speth, 2013).

To determine what sex ratios might be expected in a cow-calf herd, we estimated the proportion of females in cow-calf herds based on observational data from two present-day bison populations (Supplement 2). We estimated that cow-calf herds living in the Henry Mountains of Utah included up to 77% females (data from Van Vuren and Bray, 1986). Similarly, cow-calf herds in Elk Island National Park, Alberta, comprise up to 78% females (Supplement 2, Tables S1, S2). These calculations may over-estimate the proportion of females as, for example, we assume that non-calf males are not present despite that young males comprise part of the herd (Olson, 2005), and that calves are in equal sex ratio at birth. We also do not consider the impact of licensed hunting of male bison in the Henry Mountains herd. Considering these assumptions and the limitations of observing only modern populations, we treat our estimates of 77-78% female bison in a cow-calf herd as a maximum and assume the actual proportion of females is probably lower in most encounter circumstances for hunters.

The physiological status of bison differs seasonally among males and females and probably influenced their desirability as prey for human hunters (Speth, 2010). In the late winter and early spring, both male and

female bison are in their poorest condition. During this time, females carry late term calves that they must nurse once born (late April-early May). Breeding males have been in relatively poor condition since the rut. Both male and female physiological conditions decline with the poorer winter foraging conditions. In the late winter and early spring, non-pregnant and non-lactating cows would be prime hunting targets. Once green-up occurs, however, bison quickly recover. Cows are in optimal condition by late summer or fall when calves from the previous spring are weaned and gestation after the rut begins (Brink, 2008). In 1830, William Ferris reported the condition of bison in the Bear River valley east of Promontory Point. He commented on the poor status and nutritional value of bison prior to the spring phenological burst and noted how rapidly female bison then became *the* most desirable hunting target after the spring green-up (Phillips, 1940; Speth, 2010; Brink, 2008).

Frison's (1978) "overwintering model" suggests that bison cows were targeted in the fall and early winter to prepare meat, fat, and hides and store provisions for winter. Cow hides are in the best condition during late fall and early winter (Brink, 2008). In fact, during fall and winter, meat from bulls could have been so low in fat that protein poisoning would be a serious risk if these animals were an exclusive source of food (Brink, 2008; Phillips, 1940; Speth, 2020). However, while cow-calf herds were probably a preferred target in many cases, late precontact hunters in New Mexico in some instances focused on male bison during spring, when their condition was superior to late term and calving females, Speth (1983, 2010, 2013; Speth and Rautman, 2004). Seasonality indices for Promontory Cave 1 are still being assessed, but there is evidence for occupation in all seasons. It is possible that seasonal hunting activities conducted from the caves would meet the provisions of the overwintering model, contributing to a fall and early winter presence.

While most bison-related archaeological literature devotes attention to bison as food, this literature also acknowledges their role as a source of other raw materials and hide in particular. In Plains contexts, Indigenous peoples hunted pronghorn antelope and deer specifically for their hides to use for finer garments, such as dresses and tunics, during times of year when the hide was thin and suitable for producing soft leather (e. g. Grinnell, 1972). Bison, in contrast, were valued in some instances for their unusually heavy hides, with different parts of a hide sometimes exceeding 10 mm in thickness (Brink, 2008). The thick neck hides of bulls was prized for objects such as shields (Brink, 2008; LeBlanc, 1999; Speth and Staro, 2012, 2013). Heavy hides are, however, difficult to sew. While the skill levels apparent in the Promontory moccasin assemblages vary, several moccasins feature exquisite sewing, and the grained, softened bison leather is uniformly of high quality, typically 2.5-3.5 mm in thickness. Bison leather patches for worn sole portions were often thicker (4.0-7.0 mm). Rare instances of Promontory moccasin vamps or insets of antelope or deer have thicknesses in the 1.0-2.0 mm range. The quality and craftsmanship of the moccasins indicate that cave artisans sought leather that was sufficiently thick and durable to withstand the rough, arid terrain in which they lived, yet thin and supple enough to allow the characteristic intricate seaming and stitching of the moccasins (Fig. 2). It is notable that, on the Plains, spring was the traditional time for securing raw materials for lodge coverings, as bison hides are naturally thinnest in the spring (e.g., Brink, 2008; Southesk, 1969).

Since seasonal and physiological differences among hide qualities, and undoubtedly many other nuances, were known to Plains Indigenous peoples, the choices that they made when hunting bison for their hide or when selecting individuals for hide-working could skew the sex ratio of bison in an archaeological assemblage.

3. Materials and methods

3.1. Samples

The hide samples in our study were excavated from Promontory Cave 1, Utah, between 2011 and 2014 (Fig. 1). Miscellaneous hide fragments recovered from these Promontory sites could have been part of, or intended for, moccasins, thong sandals, drum tops, bags, clothing, mittens, or other items (Steward, 1937).

We processed two hide fragments, two bison robe fragments, and 34 moccasin samples at the University of California, Santa Cruz Paleogenomics Lab (PGL) (Table 1). Two samples are from the same moccasin (FS 305) but were sampled from different pieces of leather: the moccasin body and ankle wrap. Isotopic results indicated that the body portion was consistent with local bison whereas the ankle wrap leather originated from a different, non-local bison (Metcalfe et al., 2021).

We sent 17 samples of hide artifacts also used for aDNA analysis for



Fig. 2. A complete Promontory moccasin (UMNH.A.8011.18, FS 42Bo1.801.1) from Cave 1, with its sole (body) folding upwards to meet its vamp and inset, creating a puckered, round toe. In this case, the ankle wrap remains attached to the moccasin, along with laces for tying it. Photographed courtesy of the Natural History Museum of Utah.

radiocarbon dating at the Oxford Radiocarbon Accelerator Unit. Ages for the radiocarbon dated samples are presented in Table 1, reported for the first time here; they range from 703 ± 23 to 886 ± 27 radiocarbon years before present and are part of a larger data set of 95 Bayesian modelled AMS dates indicating that the early Promontory Phase occupation of Cave 1 took place between 1248 CE and 1290 (Ives et al., 2014, Ives et al., 2021). The Bayesian modelled age range for the Cave 1 occupation (and associated hunting) covers a period of 25–42 years (95.4% confidence). While this is a narrow time frame from an archaeological perspective, an occupation duration of one or two human generations plus the very large projected number of moccasins in Cave 1 significantly diminishes the prospect that many (if any) of the moccasins in our much smaller sample come from the same hide.

3.2. DNA extraction, library preparation, and sequencing

We extracted DNA from hides and prepared the extracted DNA into genomic libraries for sequencing following protocols developed for working with degraded DNA (Fulton and Shapiro, 2019). Prior to extraction, we washed all samples with ultrapure water to remove surface debris. We extracted DNA following Dabney et al. (2013) and included one DNA extraction negative (no sample). Following extraction, we purified darkly colored extracts with polyvinylpolypyrrolidone in columns to remove PCR inhibitors following Arbeli and Fuentes (2007).

We generated Illumina sequencing libraries following either Meyer and Kircher (MK) (2010) or, for the most recently processed samples, the Santa Cruz Reaction (SCR) (Kapp et al., 2021) (Table 1). The SCR is a single-stranded library preparation approach that more efficiently converts extracted DNA into sequenceable molecules compared to double-stranded approaches like MK (Kapp et al., 2021); we therefore prepared SCR libraries from samples initially prepared following MK with remaining extract. For three samples the MK preparation exhausted the DNA extract. For MK libraries, we labeled each molecule on both ends via a dual indexing PCR (iPCR) using KAPA Hifi (Roche, Pleasanton, CA, USA), unique indexes, and TruSeq Illumina sequencing primers, which we amplified in the modern DNA lab for 25 cycles. Following SCR library preparation, we performed quantitative PCR for each library to determine the optimal cycle number for dual indexing PCR, as described in Kapp et al. (2021). We cleaned all indexed libraries with a 1.5x concentration of SPRI beads (Beckman, Indianapolis, IN, USA). We quantified library concentration with a Qubit fluorometer (Thermo Fisher, Waltham, MA, USA) and pooled libraries at equimolar ratios. We sequenced all libraries and negative controls across several Illumina Miseq 2 \times 75bp and NextSeq 2 \times 150bp runs at the PGL.

3.3. Data analysis

We trimmed reads of adapters, removed low quality reads (-q 15), removed reads smaller than 25 base pairs (-L 25), and merged reads using SeqPrep2 (https://github.com/jeizenga/SeqPrep2). We then used prinseq v.0.20.4 (Schmieder and Edwards, 2011) for complexity filtering and removal of duplicate reads. We mapped all reads with a minimum quality threshold of 30 (-q 30) using BWA (aln -l 1024; version. 0.7.12-r1039) to cattle (Bos taurus ARS-UCD1.2_Btau5.0.1Y bosTau9+Y), bighorn sheep (Ovis canadensis; NCBI CP011912.1), and roe deer (Capreolus capreolus CCMK01) nuclear genomes. We used cow rather than bison because the highest quality Bison genome (Oppenheimer et al., 2021) was made from an F1 cattle/bison hybrid and lacks an X chromosome. We used a python script to confirm species assignment by counting the number of reads uniquely aligned to each of the three genomes. Finally, we confirmed species assignment and assessed contamination using MapDamage, a program that measures the distribution of expected ancient DNA damage patterns.

We then determined sex for all samples for which at least 150 reads aligned to the cattle X chromosome following Flamingh et al. (2020), which used a script adapted from Mittnik et al. (2016). Sex was predicted based on the number of reads aligned to autosomes compared to the X chromosome, normalized by the assembled chromosome length. The expected alignment ratio (Rx) is 2:1 for males and 1:1 for females, as males have only one X chromosome.

To develop an understanding of the natural range of observed Rx of bison data aligned to a cattle genome, we analyzed previously generated sequencing data from four female bison and four male bison (Table S3), using female data generated by Wu et al. (2018) (SRR6448737) and Yang et al. (2020) (SRR12514558, SRR12514559, and SRR12514560). and male data generated by Oppenheimer et al. (2021) (SRS7735511), Heaton et al. (2016) (SRS1620843), and two individuals presented here for the first time (NAGP 14568/LIB100490/SRR15221439 and NAGP 5852/LIB100491/SRR15221438; see Supplement 3 for details of data generation). For all eight samples, we trimmed adapters with Seqprep2 and performed complexity filtering with prinseq, as above. To simulate ancient DNA data, we trimmed all reads to 58 and 40 base pairs, which was the average and mode fragment size, respectively, from the alignments of our Promontory samples to cattle. We aligned the trimmed reads to the bosTau9+Y genome as above. The minimum number of reads that aligned to the cattle genome of any Promontory sample was 3747, so we subsampled 3747 aligned reads from each present-day data set ten times, with replacement, to visualize variation in alignment proportions by random sampling of reads. We then used the Flamingh et al. (2020) script to calculate Rx for these eight bison of known sex. Lastly, we used a Fisher's Exact test to compare the proportion of moccasin samples found come from female hides with known proportions of female bison at birth, and within a cow-calf herd.

4. Results

4.1. Sequencing results

We generated 153,966 to 8,181,119 read pairs per sample (average 1,879,334 reads: Table 1). We generated 333,501 read pairs for our negative control. Of the initial 38 samples processed, 23 samples yielded higher endogenous contents, with at least 3000 reads aligned to any of the three genomes (Table 1). Based on the number of reads uniquely aligned to each of the cattle, deer, and sheep genomes, all 23 samples were identified as *Bison*. These 23 samples had endogenous contents of 0.49%–18.42% (average 3.56%; Table 1). The 23 sequenced libraries had 3747–570,071 reads aligned to the cattle genome (average 108,804 reads; Table 1). The extraction negative control had 269 reads aligned to cattle, 509 aligned to deer, and 143 aligned to sheep.

The remaining 15 samples not used in further analysis were identified based on the number of reads uniquely aligned to each genome as either bison or deer (Table 1), although deeper sequencing would be required to verify taxonomic identity. It is possible that alignments to deer may be due to the use of deer brain for tanning the hides.

4.2. Expected Rx

To determine the expected range of Rx values for male and female bison aligned to cattle, we modelled ten bootstrapped observed Rx values for each of our eight modern reference bison (4 males and 4 females; Fig. 3). Observed Rx for females ranged from 0.77 to 1.20 when trimmed to 58 bp (0.72–1.13 at 40bp), and for males 0.38 to 0.61 when trimmed to 58bp (0.40–0.61 at 40bp).

4.3. Sex determination of promontory hides

Of the 38 samples processed, one hide, two robe fragments, and 20 moccasins yielded data with at least 3000 reads aligned to the cattle genome and 150 reads aligned to the cattle X chromosome and were used for further analysis (Table 1). The Rx of these samples fall into two clusters, one spanning 0.76 to 0.97, and the other 0.46–0.61 (Table 1)



Fig. 3. Rx values for modern reference bison and Promontory samples. Blue dots describe the male range of Rx values and red dots describe the female range of Rx values. Modern data points reflect ten independent subsamples of 3747 reads from each of eight modern bison. All data sets are aligned to the cattle reference genome. The expected alignment ratio (Rx) is 2:1 for males and 1:1 for females, as males have only one X chromosome. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(Fig. 3). The separation between the two clusters is consistent with two distinct categories indicated by the expected Rx analysis described above. Of the 23 samples, three fall into the male cluster and 20 (87%) fall into the female cluster (Fig. 3). The observation of 87% female hides is significantly higher (Fisher's Exact test p < 0.00001) than the expected 48% female bison if hide collection for moccasins was conducted randomly (based on Elk Island National Park data). A value of 87% female is not significantly higher than the expected 77% female in a cow calf herd (p = 0.0967) based on Fisher's Exact testing.

5. Discussion

The people living on Promontory Point, Utah, from 1248–1290 CE selectively used hides from female bison to produce leather moccasins and other hide belongings. Of the 23 bison hide samples from Promontory Cave 1 from which we could recover sufficient ancient DNA, 87% are from female bison. The shallow depth of sequencing in our experiment made it impossible to determine explicitly the minimum number of hides represented. While it is possible that some samples came from moccasins made from the same hide, we believe that the majority derive from different individuals. One sample, the FS 305-ankle wrap, is known from previous isotopic work to have originated at a distant site (Metcalfe et al., 2021), and three of our samples are male, so we can conclude with certainty that several bison are represented in our sample set. Additionally, the range of dates generated from our samples, and the large number of moccasins present in Cave 1 make it highly unlikely that our samples derive from only a few individuals.

While our results strongly support the conclusion that the people of Promontory Point were preferentially using female bison hides to make moccasins, they do not by themselves prove that people were selectively targeting female bison during the hunt (as opposed to choosing female hides from a more diverse sex assemblage of hunted bison). These results would remain consistent, however, with selective hunting of cow-calf herds at Promontory Point. Future analyses of sex ratios of osseous remains preserved in the caves will provide additional insights into hunting strategies specifically, and their relationship to the selective use of hides.

Our results add to the body of previous work demonstrating selective targeting of hides, including preference for the thicker hide from a bull's neck for constructing shields (LeBlanc, 1999), the soft skin of deer or pronghorn antelope (e.g., Grinnell, 1972) and juvenile caribou (Binford, 1978) for clothing, and the springtime thinner hides of bison for lodge coverings (e.g., Brink, 2008; Southesk 1969). Similar choices were made regarding footwear; in the Subarctic, moose was a preferred raw material for moccasins because it met requirements for both durability and pliability (e.g., Helm and Lurie, 1961; Thompson, 1990). The hide of female bison (and perhaps juvenile males) provided both the durability necessary for footwear and suppleness and pliability to allow the gathering and fine sewing of the Promontory moccasin style.

6. Conclusion

Promontory people selected female bison hides to make moccasins. Future analyses of the sex ratio of other artifacts, such as osseous remains, or in determining if male hide leather was used for other purposes (e.g., travois baskets, of which there is a Promontory example), in the Promontory caves could reveal more about the nature of these selective practices.

Genetic sexing of faunal materials provides an alternative and more precise tool compared to morphological analysis to determine sex ratios in zooarchaeological assemblages, facilitating studies of prehistoric hunting strategies. In addition, where perishable goods, such as materials made from hide or other rapidly degrading materials are preserved in the archaeological record, genetic sexing provides what may be the only approach to determine the sex of animals used to produce these goods. These data can provide new insights into critical non-dietary aspects of prehistoric life (e.g., see Ball, 1970 and Betinez and Nye, 1959 for the indispensable importance of moccasin footwear for Apache peoples).

The Promontory cave archaeological records represent a significant discontinuity from preceding and contemporary late Fremont assemblages. This study reveals another characteristic of the Promontory record: Promontory cave occupants exercised a high degree of selectivity in the raw material they used for their extensive and sophisticated hide processing tradition, suggesting yet another way that the early Promontory Phase cave occupants differed from their neighbors.

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Data availability

Alignments of the 23 successfully identified samples to cattle, deer, and sheep is available in DRYAD (https://doi.org/10.7291/D17T1F). Raw data is not uploaded as it could contain human DNA of the Promontory Cave occupants.

Declaration of competing interest

The authors have no conflicts of interest to report.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2021.105533.

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