What and Why We Hunt: A Review of Archaeological Sites and Hunting Practices on the Northern Great Plains

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Abstract - We reviewed records of large herbivore faunal remains in archaeological sites on the Northern Great Plains (NGP) to describe the distribution and to evaluate the change in faunal composition and relative importance of species in the diet of hunters over time. We also reviewed historical documents of hunters and postulated what these changes infer about their underlying motivations and strategies. We summarized species distribution and composition of large herbivores (adults >44 kg) found at 637 archaeological sites on the NGP. These archaeological sites dated from the late Pleistocene, Holocene, and post-European contact (500 BP to present) time periods. Pleistocene archaeological sites contained large herbivores from four orders, nine families, and a suite of at least 26 species across 18 genera. Holocene sites contained large herbivores from one order, three families, 8 genera, and at least 10 species, which represented a 62% decline in species since the Pleistocene. Historic sites contained one order, three families, 5 genera, and at least 6 species of native herbivores, which was a 40% decline in species since the Holocene. Mean species and genera body mass between Pleistocene and Holocene sites declined by 81% and 78%, respectively. Mean species body mass declined (38%) and mean genera body mass remained relatively constant between Holocene and historic sites. Genus *Mammuthus* contributed 83% of the estimated total biomass for representative Pleistocene sites; with *Bison* and *Equus* making up 8% and 5%, respectively. The genus *Bison* contributed an estimated 89% and 76% of the total biomass estimated at Holocene and historic sites, respectively. Our results support a pattern of loss in the number of species to hunt and that the available large herbivores decreased in size during the Pleistocene and Holocene; these patterns appear to have continued into the post-European contact period. From the changes in megafauna composition of archaeological sites and historical records, inferences are drawn as to the motivations as to what and why particular species may have been hunted.

Introduction

Historically, evaluations of faunal remains in archaeological sites have focused on the composition and loss of species diversity since the Pleistocene. Causes of these losses have been debated for decades (Owen-Smith 1987), with one group of scientists attributing extinctions primarily to overhunting by humans (Martin 1984, Kay 2002), which removed megafaunal engineers that controlled the abundance of woody vegetation (Wright and Jones 2006; top-down model). Top-down effects involve species, or groups of species, at the top trophic level (i.e., driven by predation) influencing community structure and composition at lower trophic levels (Bunnell et al. 2014). For example, the loss of mammoths and other megafauna from over hunting may have allowed the conversion of mosaic, steppe grasslands and wood pastures to more uniform forests and prairies (Murchie et al. 2021). Another group of scientists advocate for the bottom-up model in which factors (i.e., driven by limited resources) influences community structure and composition at higher trophic levels (Bunnell et al., 2014). For example, the effects of climate change on vegetation leading to extinctions of species at higher trophic levels (Gingerich 1984, Guilday 1984, Rabanus-

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Wallace et al. 2017). Rabanus-Wallace et al. (2017) argued that increases in moisture and widespread formation of wetlands played an important role in altering the environment, and thus was an important factor that led to subsequent late Quaternary megafaunal extinctions. Additionally, critics of "overkill" (i.e., top-down) theory suggest Paleoindian hunters would have had to be extremely selective to produce the highly size-biased extinction pattern on megafauna composition (Zou et al. 2013).

Smith et al. (2018) argued that large-bodied mammals were driven to extinction or extirpated from most of the world during the late Pleistocene, and that this decline coincided with the global expansion of hominids. Scientists advocating the top-down model attributed this body size downgrading of mammals over time to prehistoric subsistence hunting. The decline in species numbers and downgrading of size was particularly noticeable in large herbivores (Smith et al. 2018). Recent studies suggest a more nuanced explanation that supports aspects of both the top-down and bottom-up models (Murchie et al. 2021, Fordham et al. 2022). Additionally, Murchie et al. (2021) found evidence that small refugia populations of Mammoths (*Mammuthus* spp.), and North American Horses (*Equus* spp.) persisted in the far north long after they were previously thought to have gone extinct.

Climate change, particularly during warming periods, has already been linked to extinction of megafauna (Slezak 2015). Moving forward, climate change will likely cause habitat loss and shifts in large herbivore distributions. Coupled with climate change, unregulated hunting has the potential of dramatically influencing large herbivore distribution and abundance. The potential for unregulated hunting is particularly true in areas where long-term social unrest can result in dramatically reducing wildlife populations (Bragina et al. 2015). Understanding human motivations as to which species are likely to receive the greatest pressure from unregulated hunting will be critical for setting conservation and management strategies to mitigate the impacts.

Studying what and why people hunt is a relatively new scientific discipline with most efforts revolving around surveying the public through questionnaires and focus groups (Duda et al. 1998). If we accept the argument of Smith et al. (2018) that selection of large-bodied mammals is a signature of human hunting, other inferences about human motivation for hunting might be made. For example, by looking back at what Paleoindian and historic hunters on the Northern Great Plains (NGP) harvested, we might derive inferences as to their motivations. Such motivations, and how they change over time, may have impacted their decision to select and harvest a particular species.

The intent of this paper is to (1) describe the distribution of archaeological records on the Northern Great Plains (NGP) and (2) evaluate temporal patterns of faunal composition and relative importance of species to the diet of hunters. To address these objectives, we reviewed data provided by FAUNMAP digital files and the recordings from authors in contemporary to historical times. We focused on large or "megafauna" herbivores (adults >44 kg; Martin 1984) to identify species composition, evaluate species diversity, estimate mean body size, and estimate total biomass of these mammals found in NGP archaeological sites.

Materials and Methods

Distribution of archaeological sites

We obtained information on archaeological sites containing remains of species considered large herbivores (adults >44 kg; Martin 1984) from FAUNMAP (2018) digital files, a database documenting animal remains found at archaeological sites in the USA, Canada, and Mexico. Archaeological sites reported in FAUNMAP (2018) were locations where

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evidence of former human activity was found. Evidence of possible human occupation within sites included structural features, artifacts, fire hearths, and macro- and microscopic flora and faunal evidence of use by Paleoindians (Graham and Semken 1987, Mentzer 2012). To describe the distribution of archaeological sites on the NGP, we used data provided by FAUNMAP (2018) including the archeological site name, geologic age of the site (e.g., Pleistocene, Holocene, historic or post-European contact [hereafter referred to as post-contact]), location (state, county, map quadrangle, latitude, and longitude), and a summary of animal remains identified at the site. Precision for most locations is within the 7.5-minute series quadrangle (1:24,000 scale topographic maps that encompass ~140 km^2); therefore, locations provided are usually within 3.25 min (<15 km) of the actual archaeological site. Sites were grouped into the following time periods; the late Pleistocene (20,000 to 10,000 years before present [BP]), Holocene (10,000 to 500 BP), Holocene/post-contact (sites that archaeologists could not determine if they dated from the late Holocene or post-contact period), and post-contact (500 BP to present). We combined the Holocene/post-contact and post-contact sites under post-contact for the purposes of this study and hereafter refer to these periods as post-contact sites.

We focused on sites within the northern portion of the Great Plains level 1 ecoregion (Commission for Environmental Cooperation 1997). We defined the NGP as the Great Plains ecoregion found within the following political jurisdictions: Alberta, Saskatchewan, and Manitoba, CA; Montana, North Dakota, Minnesota, South Dakota, Wyoming, Iowa, and Nebraska, USA. We reviewed the published literature and writings of authors living during the post-contact period, including their journals and diaries, for comments about post-contact large mammals on the NGP.

Within the Great Plains ecoregion are also mountainous regions that support alpine and boreal forest communities not typically associated with the grasslands. In turn, species of mammals not typical of the Great Plains prairie ecosystem show up in some archaeological sites. Additionally, the climate has become warmer and drier since the Pleistocene (Mason et al. 2008, Seabloom 2020), perhaps as much as 6° to 9° C (Tierney et al. 2020, Bamforth 2021). It should be noted that one physical location may contain more than one archaeological site due to repeated occupation over time. Archaeological search efforts are often driven by the need to survey areas being considered for development (i.e., roads, pipelines, minerals, and energy development). Therefore, areas remote from current human development are often under-represented. Caution also needs to be stressed when attempting to interpret distribution of these animal remains, as pre- and post-European contact hunters may have moved artifacts some distance from the original kill site. Hunters prior to 500 BP would have traveled on foot, limiting how and what could be transported from one site to another. There also may be a bias favoring larger species. For example, the large thick bones from Mammoths may be more likely to remain intact and identifiable than the more delicate bones from smaller species, such as *Antilocapra americana* Pronghorn. Finally, pre-European contact (hereafter pre-contact) hunter-gatherers likely passively scavenged carcasses that predators killed or that died from other causes (e.g., accidents, disease). We believe this means of obtaining food would have been unpredictable, opportunistic, and limited in scope. It is not possible to decipher the difference between faunal remains obtained through hunting and scavenging. Thus, we assumed all faunal remains, except for domesticated animals, were the result of hunting, or in some cases, aggressive scavenging away from predators by humans (Dominguez-Rodrigo and Pickering 2003).

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Faunal composition and relative importance of species to diet

To help describe what herbivore species were hunted and how this changed over time, we used Simpson's index of diversity (Krebs 1985) to determine the relative diversity of animals harvested. Because archaeological faunal remains are frequently unidentifiable down to species, diversity was calculated at the genus level. Simpson's index of diversity (hereafter, diversity index) gives little weight to rare species/genera, with values closer to 1 representing high diversity and values closer to 0 representing low diversity (Krebs 1985). Although domestic herbivores (e.g., Cattle, Horses, Pigs) were reported in post-contact sites, we did not view them as "hunted" prey and only considered native free-ranging large herbivores for our analyses.

Following Smith et al. (2018), we summarized the body mass of species reported to derive their relative importance to prehistoric hunters as a food source. We obtained estimated body mass of several extinct mammals from online educational sites (Uchytell 2012; Illinois State Museum 2022). For some extinct species for which body mass were unknown, we estimated the approximate body mass from descriptions given in Kurten and Anderson (1980), Gidley (1900), and Gidley (1901). For example, Kurten and Anderson (1980) described mountain deer (*Navahoceros fricki*) as "… in a size range between Mule Deer and Wapiti with stocky limbs". Jensen (2000) estimated the average body mass of adult female and male Mule Deer (*Odocoileus hemionus*) to be 63 kg and 74 kg, respectively (mean 68 kg); and adult female and male Wapiti or Elk (*Cervus elaphus*) to be 225 kg and 316 kg, respectively (mean 270 kg). From these estimates, we assigned the body mass of 169 kg to Mountain Deer, the mean of Mule Deer and Elk body mass. It should be noted that recent work suggest that Mountain Deer may not have existed (Heffelfinger and Latch 2023). We derived estimated body mass of extant species from Jensen (2000), Jensen et al. (2013), Meagher (1986), Mitchell (1971), Nowak (1999), and Shackleton (1985). When known, estimated average body mass of adults (females and males) for each species were used to calculate mean body mass of species present at archaeological sites. Genera body mass were based upon the average body mass of species within each genus that were found at sites for each of the three time periods.

Faunal remains are frequently only identified to genera (Graham and Semken 1987). Therefore, we summarized the available information by both species and genera. To better quantify biomass of the generic or representative archaeological site and estimate relative importance of body size, we multiplied mean species and genera body mass by their frequency of occurrence to estimate total biomass. These estimates do not account for multiple individuals of the same species that may have been present at an archaeological site. Some species were subject to hunting tactics that permitted harvesting family units or herds (e.g., Mammoths and Bison; Frison 1991). Therefore, the contribution made by some species that are common to archaeological sites are probably underrepresented in total biomass estimates.

Results

As of 15 July 2018, FAUNMAP (2018) contained information recorded for 6791 archaeological sites, of which 637 sites located on the NGP were found to contain the remains of large herbivores (Fig. 1). There were 65 records from the late Pleistocene, 446 records from the Holocene, and 126 records from the post-contact period.

Of the 65 archaeological sites dating from the Pleistocene, there were 19 (29%) in Alberta, 17 (26%) in Nebraska, and 14 (22%) in Wyoming. Pleistocene archeological sites contained large herbivores from four orders (Artiodactyla, Edentata, Perissodactyla, and

Proboscidea), nine families (Antilocapridae, Bovidae, Camelidae, Cervidae, Tayassuidae, Megalonyclidae, Equidae, Mammutidae, and Elephantidae), and a suite of at least 18 genera and 26 species (Table 1). The most frequently occurring species were Plains Bison (*Bison bison)* (35%), Yesterday's Camel (*Camelops hesternus*) (12%), Mexican Horse (*Equus conversidens*) (11%), Caribou (*Rangifer tarandus*) (11%), and Pronghorn (9%; Table 1). The top three species contributing the most biomass were Imperial Mammoth (*Mammuthus imperator*) (19%), Columbian Mammoth (*Mammuthus columbi*) (17%), and Wooly Mammoth (*Mammuthus primigenius*) (11%; Table 1). The most frequent genera of large herbivores present were *Bison* (58%), *Mammuthus* (43%), and *Equus* (32%; Table 2). Diversity index for genera present for all NGP Pleistocene sites was 0.90. Mean body mass of species and genera found at Pleistocene sites was 1840 kg and 1034 kg, respectively (Tables 1 and 2). Estimated total biomass at representative Pleistocene sites for species and genera was 1698 kg, and 4504 kg, respectively. Genus *Mammuthus* contributed an estimated 83% of the estimated total biomass at Pleistocene sites with *Bison* and *Equus* contributing another 8% and 5%, respectively (Table 2).

Of the 446 archaeological sites dating from the Holocene, there were 125 (28%) in Saskatchewan, 83 (19%) in Alberta, 46 (10%) in Montana, and 43 (10%) in Manitoba (Fig. 1). Distribution of Holocene sites was primarily found to be along the periphery of the NGP and along major river systems. These sites contained large herbivores from one order (Artiodactyla), three families (Antilocapridae, Bovidae, and Cervidae), and a suite of 8 genera and at least 10 species (Table 3). The most frequent species were Bison (33%), Pronghorn
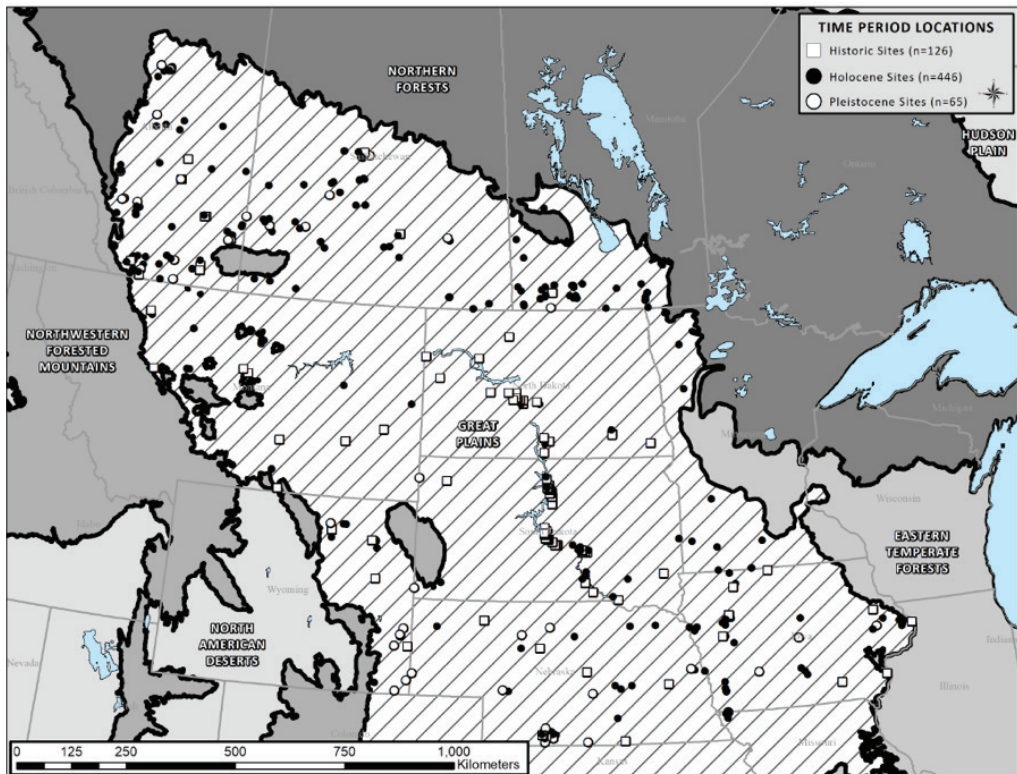

Figure 1. Location of archaeological sites on the Northern Great Plains dating from the late Pleistocene (20,000 to 10,000 BP; *n* = 65), Holocene (10,000 to 500 BP; *n* = 446), and historic/post-European contact (500 BP to 1900; *n* = 126).

(19%), and Elk (12%). The most frequent genera of large herbivores present were *Bison* spp. (94%), *Odocoileus* spp. (28%), and *Antilocapra* sp. (19%). Diversity for genera present at these sites was 0.58. Mean body mass of species and genera found at Holocene sites was 351 kg and 232 kg, respectively (Table 3). Total biomass at Holocene sites for species and genera was 245 kg and 613 kg, respectively. The genus *Bison* spp. contributed an estimated 89% of the estimated total biomass at Holocene sites; with *Cervus* sp. and *Odocoileus* spp. contributing another 6% and 3%, respectively.

Of the 126 archaeological sites dating from the post-contact period, 70 (55%) were in North Dakota and South Dakota (Fig. 1). These sites contained one order (Artiodactyla), three families (Antilocapridae, Bovidae, and Cervidae), and a suite of 5 genera and at least 6 species of native herbivores (Table 4). The most common species were Bison (*Bison bison*) (61%) and Elk (41%). The most frequent genera of large herbivores present were *Bison* sp. (92%) and *Odocoileus* spp. (57%) with *Antilocapra* sp. and *Cervus* sp. sharing third place (41%; Table 4). Diversity for genera present at these sites was 0.72. Mean body mass of species and genera found at historic sites were 217 kg and 242 kg, respectively (Table 4). Total biomass at historic sites for species and genera was 675 kg and 706 kg, respectively. The genus *Bison* contributed 76% of the estimated total biomass at post-contact sites; with *Cervus* and *Odocoileus* making up another 16% and 6%, respectively (Table 4). Domestic livestock also occurred in 20 post-contact sites, including Cattle (Linnaeus) (*Bos taurus*), Goats (Linnaeus) (*Capra hircus*), Sheep (Linnaeus) (*Ovis aries*), Pigs (Linnaeus) (*Sus scrofa*), and Horses (Linnaeus) (*Equus caballus*).

Discussion

The NGP contains inclusions of elevated terrain that supported forests (e.g., Cypress Hills in AB and SK, Canada; Black Hills in SD, USA); thus, some species not commonly associated with prairie grasslands (e.g., Moose [Linnaeus] [*Alces americanus*] and Bighorn Sheep [*Ovis canadensis*]) were found at ≤2% of the sites. Additionally, climatic conditions that once allowed boreal and arctic species such as Caribou (*Rangifer tarandus*) and Muskox (*Ovibos moschatus*) to occur have warmed over the past 20,000 years, causing their southern range distribution to recede north. Distribution of Holocene sites was primarily found to be along the periphery of the NGP and along major river systems. Distribution of Holocene sites may be due, in part, to climate conditions. During the middle Holocene, the central portions of the NGP are thought to have been extremely harsh for human habitation due to warm and dry conditions, commonly referred to as the Altithermal (7500 to 4000 BP; Meltzer 1999). The Altithermal in turn would have influenced food foraging strategies (Meltzer 1999) and the composition of faunal remains found at these sites. As mentioned above, most historic archaeological sites were in North Dakota and South Dakota; particularly along the Missouri River. This may, in part, be an artifact of search effort due to the construction of dams for the Pick-Sloan Missouri River development plan (Knue 1991) and the requirement to conduct archaeological surveys for federally funded construction projects. The large number of sites located in Alberta and Saskatchewan may also be due to energy development. It is not known how regional differences might influence harvest composition and hunting strategies.

Pleistocene site contents were highly diverse in large herbivores; this is reflected by the high genera diversity index value of 0.90. During the Holocene, the number of orders, families, and genera declined. The 62% decline in the number of species between Pleistocene sites and Holocene sites (26 to 10 species, respectively) is comparable to

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Table 1. Estimated body mass of large herbivore species found at Pleistocene archaeological sites on the Northern Great Plains. Estimated live body mass value (LBM; kg) for extant species is the mean of adult male and female total body mass. Percent frequency is calculated from the number of sites containing that species divided by the total number of sites evaluated. Estimated biomass values is calculated by multiplying the estimated live body mass by the percent presence at Pleistocene archaeological sites.

Species	Author	Est. LBM (kg)	Frequency %	Est. Biomass (kg) [%]
Antilocapra americana	Ord	51[1]	12	6 [0.3]
Bison bison	Linnaeus	578[2]	55	318 [18.0]
Bison latifrons	Harlan	1998[3]	2	40 [2.3]
Bootherium bombifrons	Harlan	424[4]	6	25 [1.4]
Ovibos moschatus	Zimmrmann	305[5]	5	15 [0.9]
Ovis canadensis	Shaw	83[6]	3	2 [0.1]
Camelops hesternus	Leidy	699[3]	12	84 [4.7]
Hemiauchenia macro-cephala	Cope	300[5, 7]	3	9 [0.5]
Cervalces scotti	Lydekker	708[7]	3	21 [1.2]
Cervus elaphus	Linnaeus	271[8]	3	8 [0.5]
Navahoceros fricki	Schultz and Howard	170[7, 8]	2	3 [0.2]
Odocoileus hemionus	Rafinesque	68[8]	2	1 [0.1]
Odocoileus virginianus	Zimmrmann	68[8]	2	1 [0.1]
Rangifer tarandus	Linnaeus	57[5]	12	11 [0.6]
Sangamona fugitive	Hay	220[7]	3	7 [0.4]
Platygonus compressus	LeConte	45[4]	3	1 [0.1]
Megalonyx jeffersonii	Jefferson	999[4]	2	20 [1.1]
Equus complicatus	Leidy	400[7]	2	8 [0.5]
Equus conversidens	Owen	300[7, 9]	11	33 [1.9]
Equus giganteus	Gidley	1150[7, 9]	2	23 [1.3]
Equus scotti	Gidley	681[7, 9]	3	20 [1.2]
Mammut americanum	Kerr	4540[4]	2	91 [5.1]
Mammuthus columbi	Falconer	9988[3]	3	300 [16.9]
Mammuthus imperator	Leidy	11000[3]	3	330 [18.6]
Mammuthus jeffersonii	Osborn	6356[4]	2	127 [7.2]
Mammuthus primigenius	Blumenbach	6356[4]	3	191 [10.8]
Mean Total Biomass		1840		1698

Estimated body mass of species derived from [1]Mitchell (1971), [2]Meagher (1986), [3]Uchytell (2012), [4]Illinois State Museum (2022), [5]Nowak (1999), [6]Shackleton (1985), [7]Kurten and Anderson (1980), [8]Jensen (2000), and [9]Gidley (1901).

that previously reported in the literature for North America (e.g., 73%; Martin 1984). However, the extinction of five genera on the NGP (18 to 13 genera, 27%) was less severe than reported for North America north of Mexico as a whole (44 to 13, 70%; Martin 2002). The vastness of the open prairie on the NGP may have provided partial refugia for some genera as suggested by Kay (2002).

With the loss of species and genera, the genera diversity for the Holocene declined to 0.58. When we compared mean species and genera body mass between Pleistocene to Holocene sites, they declined by 81% and 77%, respectively. In comparison, Smith et al. (2018) reported that the mean mass of nonvolant terrestrial mammals in North America declined from 98.0 to 7.6 kg during this period, a 92% decline. The genera responsible for the greatest proportion of the decline since the Pleistocene was Mammoths, with a mean for the genus estimated to be 8425 kg and frequency of occurrence of 43%. Mammoths contributed at least 83% of the potential biomass to the average Pleistocene site. The loss of this single genera becomes the primary factor influencing not only mean species and genera body mass

Table 2. Estimated body mass of large herbivore genera found at Pleistocene archaeological sites on the Northern Great Plains. Estimated live body mass value (LBM; kg) of extant species is the mean of adult male and female total body mass. Percent frequency is calculated from the number of sites containing those genera divided by the total number of sites. Estimated biomass values is calculated by multiplying the estimated live body mass by the percent frequency at archaeological sites.

Genera	Mean Est. LBM (kg)	Percent Frequency	Est. Biomass (kg) [%]
Antilocapra	51[1]	12	6 [0.1]
Bison	578[2, 3]	58	338 [7.7]
Bootherium	424[4]	6	26 [0.6]
Ovibos	305[5]	5	14 [0.3]
Ovis	83[6]	3	3 [0.1]
Camelops	699[3]	18	129 [3.0]
Hemiauchenia	300[5, 7]	3	9 [0.2]
Cervalces	708[5]	3	22 [0.5]
Cervus	271[8]	3	8 [0.2]
Navahoceros	170[5, 8]	2	3 [0.1]
Odocoileus	68[8]	11	7 [0.2]
Rangifer	57[5]	12	12 [0.3]
Sangamona	220[4]	3	7 [0.2]
Platygonus	45[4]	3	1 [Trace]
Megalonyx	999[4]	2	15 [0.2]
Equus	633[5, 7]	32	204 [4.7]
Mammut	4540[4]	2	70 [1.6]
Mammuthus	8425[3, 4]	43	3629 [82.8]
Mean Total Biomass	1034		4504

Estimated body mass of species derived from [1]Mitchell (1971), [2]Meagher (1986), [3]Uchytell (2012), [4]Illinois State Museum (2022),[5]Kurten and Anderson (1980), [6]Shackleton (1985), [7]Nowak (1999), [8]Jensen (2000), and [9]Gidley (1901).

but also estimated total biomass at archaeological sites. The relative importance of Mammoths may be higher than this, as members of genera are thought to have been hunted in family units (Frison 1991); although this assumption has been challenged (Hoppe 2004). When reviewing 33 Clovis sites (ca. 13,500 BP) across the USA and Canada, Waguespack and Surovell (2003) reported a similar pattern with Mammoths and Mastodons (*Mammut* spp.) being present in 79% of all assemblages.

The next most important component of Pleistocene hunting efforts appears to be Horses (*Equus* spp.). Members of Bison (*Bison* spp.), Camel (*Camelops* spp.), and Pronghorn (Antilocapridae family) had a relatively high frequency of occurrence but were estimated to contribute only a minor component to the potential total biomass of a site. Although American Mastodons (*Mammut americanum*) were very large herbivores (4540 kg), the distribution and numbers of these forest-dwelling relatives of the Mammoths made them far

Table 3. Estimated body mass values of large herbivores found at Holocene archaeological sites on the Northern Great Plains. Estimated live body mass value (LBM; kg) of extant species, is the mean of adult male and female total body mass. Percent frequency is calculated from the number of sites containing that species divided by the total number of sites evaluated. Estimated biomass values is calculated by multiplying the estimated live body mass by the percent frequency at archaeological sites.

Genera	Species	Est. LBM (kg)	Percent Frequency	Est. Biomass (kg) [%]
Antilocapra		51[1]	19	8 [1.6]
	Antilocapra americana	51[1]	19	10 [4.1]
Bison		578[2]	94	546 [89.3]
	Bison bison	578[2]	33	192 [78.4]
	Bison antiquus	1598[3]	<1	3 [1.2]
Ovibos		305[4]	<1	<1 [0.1]
	Ovibos moschatus	305[4]	<1	<1 [0.3]
Ovis		83[5]	<1	<1[0.1]
	Ovis canadensis	83[5]	<1	<1[0.2]
Alces		402[6]	1	5 [0.6]
	Alces americanus	402[6]	1	4 [1.6]
Cervus		271[7]	12	37 [5.5]
	Cervus elaphus	271[7]	12	33 [13.5]
Odocoileus		68[7]	2	17 [3.1]
	Odocoileus hemionus	68[7]	2	1 [0.4]
	Odocoileus virginianus	68[7]	2	1 [0.4]
Rangifer		57[3]	<1	<1 [Trace]
	Rangifer tarandus	95[4]	<1	<1 [0.2]
Mean Total Genera Biomass		232		613
	Mean Total Species Biomass	351		245

Estimated body mass of genera and species derived from [1]Mitchell (1971), [2]Meagher (1986), [3]Uchytell (2012), [4]Nowak (1999), [5]Shackleton (1985), [6]Jensen et al. (2013), [7]Jensen (2000).

less common (present at about 2% Pleistocene sites contributing about 1.6% of the genera biomass), with their range primarily east of the Mississippi River and in the Southwestern states of Arizona and California (Mead and Meltzer 1984). In current day Nebraska, Mammoths outnumbered mastodons 20 to 1 (Voorhies 1994).

Holocene sites on the NGP are most striking for their loss of genera diversity (0.90 to 0.58). The largest species procured by hunters decreased in size by 93% with the shift from Pleistocene Mammoths (8425 kg) to the Holocene Bison (578 kg). During the Holocene, Bison became the basis for subsistence hunting with a high frequency of occurrence (94%) and contributing an estimated 89% of the potential biomass to the average Holocene site. Again, the contribution Bison made to the overall dietary protein base of this dataset is likely underestimated because Bison were more likely procured using jumps, pounds (circular corrals), and driving them onto thin ice where Bison were killed in numbers, versus members of the Deer family, where individual animals were hunted and killed individually (Frison 1991). Deer (*Odocoileus* spp.) and Elk frequency of occurrence made a 2- to 3-fold increase between the Pleistocene and Holocene but contributed little to the estimated total biomass.

Three species disappeared from historic sites that were present in Holocene sites. The Ancient Bison (Rhoads) (*Bison antiquus*) went extinct during the Holocene, while loss of Caribou and Muskox (*Ovibos moschatus*) may simply be due to climate change and/or fewer sites registered during the historic period ($n = 126$) versus the Holocene period ($n = 446$). These three species were only found at one site during the Holocene. Diversity

Table 4. Estimated body mass values of native large herbivores found at post-European contact archaeological sites on the Northern Great Plains. Estimated live body mass value (LBM; kg) is the mean of adult male and female total body mass. Percent frequency is calculated from the number of sites containing that species divided by the total number of sites evaluated. Estimated biomass value is calculated by multiplying the estimated live body mass by the percent frequency at archaeological sites.

Genera	Species	Est. LBM (kg)	Percent Frequency	Est. Biomass (kg) [%]
Antilocapra		51[1]	41	21 [3.0]
	Antilocapra americana	51[1]	41	21 [3.1]
Bison		578[2]	92	532 [76.0]
	Bison bison	578[2]	92	532 [78.9]
Ovis		83[3]	2	1 [0.2]
	Ovis canadensis	83[3]	2	2 [0.2]
Cervus		271[4]	41	112 [15.9]
	Cervus canadensis	271[4]	41	112 [16.6]
Odocoileus		68[4]	57	39 [5.6]
	Odocoileus hemionus	68[4]	4	3 [0.4]
	Odocoileus virginianus	68[4]	8	5 [0.8]
Mean Total Genera Biomass		242		706
	Mean Total Species Biomass	217		675

Estimated body mass of genera and species derived from [1]Mitchell (1971), [2]Meagher (1986), [3]Shackleton (1985), and [4]Jensen (2000).

increased from 0.58 to 0.72 from Holocene to post-contact sites. While Bison representation at Holocene and post-contact sites remained stable at 94% and 92%, respectively, the presence of Pronghorn, Elk, and Deer (*Odocoileus* spp.) increased; thus, in turn increasing the genera diversity during the historic period.

Knowing the thought processes of prehistoric hunters (>500 BP) is not possible, but inferences might be drawn by a review of what was harvested. It would appear that over the past 20,000 years, the motivations and strategies used by hunters have changed over time. During the Pleistocene and Holocene, the primary motivation for hunting seems to have been simply to obtain food; the strategies used appear to be (1) focused on species that provided the best opportunity to successfully harvest and (2) the size of the food reward. During the Pleistocene, the composition of harvested species was highly diverse (0.90). This diversity suggests that Pleistocene hunters may have taken advantage of any opportunity to obtain protein that presented itself. Secondly, the genera *Bison, Mammuthus*, and *Equus* occurred at the highest frequencies. Modern counterparts to these genera have social structures based upon larger family units and herds. Our results support Frison (1991) in that the social structure of these species may have predisposed these animals to being driven in groups off cliffs, or into corrals and water bodies where hunters could swarm on individual animals and kill them. Kornfeld et al. (2010) suggested Pleistocene hunters may have also taken advantage of terrain by maneuvering Mammoths into deep, steep-walled arroyos. Some selection for large body size also may have played a role into how much effort was placed on procurement of an animal. Juvenile Mammoths were apparently the preferred target of long-term, systematic exploitation (Kornfeld et al. 2010). Mammoths were the largest herbivore hunted during the Pleistocene, perhaps averaging >8000 kg.

Mammoths appear to have offered several benefits for the Pleistocene hunter. Mammoths were a relatively common species, appear to have had a social structure vulnerable to hunting (Frison 1991), and provided a large food reward. As a result, Mammoths contributed perhaps >80% of the harvested biomass for a Pleistocene hunter on the NGP. In contrast, although mastodons offered the large reward of >4500 kg, opportunities to harvest these animals appears to be limited due to their distribution on the NGP, which was limited to what is now Nebraska and appear to have been more solitary animals living in forested areas (Kurten and Anderson 1980). Although similar in size to Mammoths, our results suggest Mastodons contributing <2% of the harvested biomass on the NGP; less than that contributed by the much smaller *Bison, Equus*, and *Camelops*. There is little definitive evidence that Horses and Camels were systematically hunted (Kornfeld et al. 2010). Furthermore, there is debate regarding if Clovis hunters specialized on hunting Mammoths or were generalists (Bamforth 2021); perhaps Paleoindian hunters were both. During the Pleistocene, opportunity and the size of the reward appear to be the primary factors influencing what was hunted and harvested. Cannon and Meltzer (2008) discuss the tradeoffs between subsistence strategies of early Americans in patchy environments from various regions. Caution is needed when comparing our results with those from regions outside the NGP.

With the extinctions and downgrading of body size in available animals, the harvest of Holocene hunters on the NGP is marked by reduced opportunities with only eight genera of large herbivores present and lower diversity (0.58). During the late Holocene (ca. 1800 BP in western NGP and 1500 BP in eastern NGP), bows and arrows tipped with small points were first adopted by Paleoindians on the NGP, and the use of atlatls with large and heavy points rapidly disappeared (Blitz 1988). However, there is no clear evidence that this shift in technology to a weapon with increased distance and accuracy was due to changes in game available (Blitz 1988). Bison, with a herd social structure that allowed multiple animals to

be killed at a site, provided both opportunity and rewards. The percent frequency of Bison remains at Holocene sites was 94%, coupled with a mean live body mass of approximately 580 kg, resulting in Bison contributing approximately 90% of the biomass harvested. There is an abundance of evidence from bone beds that Bison have been killed in mass since the Pleistocene (Kornfeld et al. 2010). Thus, our estimate of Bison biomass harvest is probably an underestimate since multiple individuals being harvested at a single site was not taken into account by the percent frequency. Members of the Deer family contributed most (9%) of the remaining harvest biomass during the Holocene.

Pre-contact hunters often depicted big game with large antlers and horns on pictographs (Frison 1991), and large cairns of Elk antlers constructed by plains tribes have been documented (Thomas and Ronnefeldt 1982). For a nomadic hunter traveling on foot, harvesting animals for the sole purpose of obtaining large horns or antlers is assumed to have been of little or no value to Paleoindians other than for making tools. However, Frison (1991) reported one Holocene archaeological site of a ceremonial nature, containing the skull caps of several large antlered Mule deer. Opportunity and the size of the biomass reward appear to continue be the primary factors influencing the harvest during the Holocene.

During the post-contact period, Bison contributed the bulk of the biomass harvested (76%). Although more difficult to harvest, Elk had a frequency of 41% and contributed about 16% of the harvest biomass. Genera that were socially less vulnerable to harvest (*Odocoileus* spp.) and/or provided limited reward, such as Pronghorn, more than doubled in their frequency of occurrence. Some of this increase may be due to evidence of these smaller species being able to remain intact and identifiable. Fire use by indigenous hunters may have also played a role by altering the vegetative structure as prairie shifted from grass to grass-forbs dominance when used in procurement of Bison and Deer (McClain et al. 2021). That said, during historic times (500 BP to present), technology appears to have influenced the increase in overall diversity of hunter harvest. This increase in diversity is likely attributed to new opportunities provided by the introduction of the domestic Horse (Linnaeus) (*Equus caballus*) to the NGP between 1720 and 1770 and fur trade rifle, which arrived about 1800 (Waldman 1985). The Horse and rifle would have increased opportunities to harvest Deer and Pronghorn and thus, increasing the prevalence of these smaller herbivores. Procurement of Bison and, to a lesser extent, Pronghorn could be achieved by using jumps and corrals, whereas successfully running an Elk off a cliff or into a corral was less likely until hunters acquired the Horse and rifle (Frison 1991, McCabe 2002). Game-sinks and refugia between warring tribes on the NGP also point to the value of the Horse for hunting (Martin and Szuter 1999, 2002); however, the theory of game sinks has also been questioned (Lyman and Wolverton 2002).

During the early and mid-1800s, commerce began to play a greater role in the frequency of Deer and Elk remains found in post-contact archaeological sites and their subsequent decline. There exists a long history of hide hunting and Deer hides being used as a medium of exchange (Young 1961). In northwestern Montana, even as recently as 1900, Deer hides were considered legal tender and were worth $0.50 USD each (Allen 1971). As an example of the potential impact of commerce, Prince Maximilian of Weid reported that the American Fur Company at Fort Union (near present day Williston, North Dakota, USA) exported 20,000 to 30,000 Deer hides in 1833 (Thomas and Ronnefeldt 1982). By 1867, Charles Larpenteur, a fur trader at Fort Buford (3 km east of the then abandoned Fort Union), reported trading only 1800 Deer hides (Larpenteur 1989). Unregulated subsistence and market hunting that was also supported by U.S. government policies to restrict Native Americans to reservations (e.g., U.S. Army provided free ammunition to hide hunters; National Park Service 2021), introduction

of Cattle-borne diseases (Koucky 1983, Flores 1991), and the rush of European settlement in the 1870s and 1880s resulted in the near extirpation of all large herbivores throughout the NGP. The near extermination of all large herbivores on the NGP, also followed the downgrading pattern observed by Smith et al. (2018). The order of species to be nearly extirpated from the NGP began with Bison between 1880 and 1885 (McHugh and Hobson1972), followed by Elk between 1870 and 1890 (Murie 1979), Mule Deer and White-tailed Deer (*Odocoileus virginianus*) between 1890 and 1910 (Young 1961, McCabe and McCabe 1984), and finally Pronghorn between 1900 and 1915 (O'Gara and McCabe 2004).

The demise of the Bison herds illustrates the interplay of new opportunities and commercial motivations that influenced hunters (Rinella 2009). During 1830 to 1870, Metis hunters on the northern plains were motivated to hide hunt by the demand of eastern markets for hair-on robes used for fashionable blankets and coats. Technology also changed this business model around 1870 by dramatically changing the cost-benefit ratio of killing Bison. The industrial age factories needed leather belting to run machines in the eastern mills. In turn, tanneries shifted to a chemical tanning process that used flint-hides without hair. By market demand shifting to flint-hides, hide hunting went from a seasonal to a year-round operation. Bison numbers on the NGP soon dropped from the tens of millions to a few thousand (McHugh and Hobson1972, Rinella 2009). By 1883, the last remaining large Plains Bison herd was in Butte and Harding counties of present-day South Dakota; that herd was quickly extirpated. In the late 1880s and early 1890s, individual and small isolated herds were hunted for "souvenir" hides that would bring $100 to $200 each, the equivalent of a month's wages for a common laborer (Rinella 2009).

If not for imposition of regulated hunting seasons and the development of what was to become the North American Model of Wildlife Conservation (Geist et al. 2001), the extinction and downgrading of large herbivores would have continued, perhaps resulting in no native herbivores on the NGP over 44 kg. Even with the establishment of hunting regulations and the North American Model of Wildlife Conservation, it has been noted that antler and horn size for several species of trophy ungulates has declined between 1900 and 2008; this being, in part, attributed to intensive and/or selective harvest pressures (Monteith et al. 2013). During the post-contact period, introduction of new technologies (i.e., the Horse and rifle) allowed hunters to procure species that had formerly been difficult to harvest. In the early 1800s, market hunting for hides and meat became an added motivation for selecting large mammal species. With the arrival the railroads in the late 1860s on the NGP, shifts in technology (i.e., tanning processes, increased accuracy of guns and ammunition), commercial markets, introduced diseases, and to some extent European style trophy hunting (Roosevelt 2000), the harvest rates far surpassed sustainable taking of native free-ranging herbivore populations. As a result of these cumulative motivations and pressures, unregulated subsistence and market hunting nearly extirpated all herbivores >44 kg from the NGP by 1900.

The patterns of downgrading in the size of herbivores that we observed with this dataset from the NGP mimic those of Smith et al. (2018). The impacts of current climate change on large ungulates are poorly understood (Mysterud 2013). That said, climate change, particularly warming climates, have also been identified as influencing megafauna extinction (Slezak 2015). Warming climates may shift range distributions of Moose (*Alces americanus*) and other NGP herbivores north, as was seen during the Holocene with Muskox and

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Caribou. Changes in moisture and temperature regimes may alter the ranges of disease host vectors, such as terrestrial gastropods (Nicolai and Ansart 2017) and insects (Schmidtmann et al. 2011), and in turn current distributions of associated diseases such as Brain Worm (Dougherty) (*Parelaphostrongylus tenuis*) and epizootic hemorrhagic disease. Introduced invasive plants, such as cheatgrass (Linnaeus) (*Bromus tectorum*) continue to spread, changing the frequency of fire and degrade the carrying capacity of grasslands for mule deer and pronghorn (Jensen et al. 2023).

Today, the cumulative impacts of habitat loss, climate change, and new diseases (bottom-up model factors) are all rapidly changing and exerting negative influences on large herbivores that have not been seen before. These cumulative changes may, in turn, make what in the past has been considered minor human disturbance much more impactful. There may be a cautionary tale provided by these results for future decision makers regarding wildlife management. Following the collapse of the Soviet Union in 1991, central government control of the economy and government institutions disappeared (e.g., per-capita plummeted, land was privatized, government funding for wildlife management vanished). Within 10-years Roe Deer ([Linnaeus] *Capreolus capreolus* and [Pallas] *C. pygargus*), Red Deer (*Cervus elaphus*), Moose, Wild Boar (*Sus scrofa*), Brown Bear (Linnaeus) (*Ursus arctos*), and Eurasian Lynx (Linnaeus) (*Felis lynx*) populations declined; demonstrating how quickly and widespread wildlife populations can be impacted during period of social unrest (Bragina et al. 2015). Even in stable countries, there is the potential for significant impacts on wildlife populations. As declining hunter participation raises concerns for funding the management of wildlife populations (U.S. Fish and Wildlife Service 2018), and alternative funding sources are considered (Hohensee et al. 2017), tightening budgets may pressure some agencies to reduce monitoring of these species. This might be particularly true for game hunted with what some consider "primitive" equipment (i.e., archery and muzzleloader rifles), and/or for subsistence hunting. Currently, and into the foreseeable future, large herbivore populations will be facing the traditional top-down factors (e.g., human harvest, predation). In addition, large herbivores and other wildlife will be dealing with several new bottom-up factors such as climate change, loss of habitat (Jensen et al. 2023), pesticides (Berheim et al. 2019), and chronic wasting disease (DeVivo et al. 2017, Mathiason 2022). If pre-contact hunters armed with spears and atlatls, in combination with climate change, were contributing factors capable of exterminating up to 62% of the large herbivores on the NGP when these new bottom-up and top-down pressures were not an issue; how quickly could poorly regulated hunting, coupled with this host of new negative impacts facing game species extirpate localized herbivore populations with modern weaponry? Vigilance in following the North American Model of Wildlife Conservation (Geist et al. 2001) and proper funding of wildlife management programs are essential for the maintenance of future game populations, regardless, if harvested by subsistence hunters or for recreational sport. It would seem therefore that we need to learn from our past, identify current public concerns, explain the science in a non-threatening manner, and broaden our base of support for sound management (Prot 2015).

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