DRIVERS OF MORPHOLOGICAL CHANGE IN BISON (*BISON BISON*):

CONSEQUENCES OF RISING TEMPERATURE, INCREASING DROUGHT, AND

ASSESSING VULNERABILITIES FOR MANAGING A KEYSTONE SPECIES

A Dissertation

by

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ABSTRACT

Body size of animals is plastic and dependent on environmental conditions that are changing globally. In this dissertation, I explore environmental traits as they relate to and drive body size change of North American bison (*Bison bison*) along the Great Plains. I examined 1) 40,000 years of body size change in the fossil record, 2) five decades of long-term ecological dataset of body size change at one location and one decade of body size differences among 19 locations along the Great Plains, 3) seasonal heat flux and growth rates of bison along the Great Plains, and 4) bison managers' vulnerabilities to environmental change. In the fossil record, I estimated body mass from a foot bone, the calcaneum, in 849 specimens that range over the 40,000 years and related that body and bone size to global temperature—reconstructed from the Greenland ice sheet. The rate of mass loss was 41 ± 10 kg per 1°C increase of global temperature. In the decadal dataset, I estimated asymptotic body mass of 19 herds from 6,400 observations of individual bison to relate body mass to average temperature and drought over the last five decades. Drought decreased asymptotic mass by -16 kg whereas temperature decreased mass between -1 and -115 kg, depending on location. I measured the seasonal effect of ambient heat load on growth of 700 *Bison* from 19 herds along the Great Plains from Saskatchewan (52 °N) to Texas (30 °N). *Bison* are better able to grow over summer when environmental heat loads are low. As seasons become warmer, reduction of body mass will likely alter reproduction to reduce annual growth of herds, the production of breed stock, and meat in the bison industry. I surveyed 132 bison

managers from North America that represent private, public, and NGO sectors to measure their perceptions, practices, attitudes, and values related to environmental change. I found that private and public/NGO sectors differed in adaptive capacity and thus the score for vulnerability. The private sector was less vulnerable than the public/NGO sector because the private sector had greater access to information exchange, external revenue, and grazing leases.

DEDICATION

I dedicate this to Rachel, the love of my life; without whom I would probably be a miserable slob of a mess. Our travels together through life have led us to this point where are both graduating with our doctorates at the same time and I am so proud of you and your many accomplishments! And to our dog, Koda; you are my bringer of snuggles, joy, and smiles at this intersection of the novel coronavirus COVID-19 pandemic and the conclusion of my doctoral studies. I love my little family.

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NOMENCLATURE

AACUC	Agricultural Animal Care and Use Committee
ABM	Asymptotic body mass (kg)
BM	Body mass (kg)
BM_E	Estimated body mass (kg) from photogrammetry
BS	Body size; refers to either body height or body mass
cwt	Cent weight (1 unit of 100 lbs)
dPDSI	Mean Decadal Palmer Drought Severity Index
DstL	Distal tuber length of the calcaneum (heel bone; mm)
GBr	Greatest breadth of the calcaneum (mm)
GDp	Greatest depth of the calcaneum (mm)
GISP2	Greenland Ice Sheet Project ice core
GL	Greatest length of the calcaneum (mm)
GP	Great Plains
H	Body height (m)
H_E	Estimated body height (m) from photogrammetry
IUCN	International Union for Conservation of Nature

IPCC	Intergovernmental Panel on Climate Change
IRB	Institutional Review Board
LGM	Last Glacial Maximum
MAP	Mean Annual Precipitation (mm)
MAT	Mean Annual Temperature (°C)
MDP	Mean Decadal Precipitation (mm)
MDT	Mean Decadal Temperature (°C)
NAM	North American model for wildlife management
NBA	National Bison Association
NGO	Non-Governmental Organization (meant as not-for-profit)
NOAA	National Oceanic and Atmospheric Administration
NPP	Net Primary Productivity
NPS	National Park Service of the United States
PDSI	Palmer Drought Severity Index
Q	Total surface heat loss (W)
q_{tot}	Total heat flux ($W \bullet m^2$)
SA	Surface area (m^2)
SCI	Santa Catalina Island, California

T_b	Body core temperature; *Bison* averages 38.4°C
T_a	Ambient air dry bulb temperature
ULT	Upper limit threshold; likely between 30°C for black *Bos taurus* and 35°C for black *Bos indicus*
USDA	United States Department of Agriculture
VSD	Vulnerability Scoping Diagram
WICA	Wind Cave National Park

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1. INTRODUCTION

1.1. Importance of studying body size and change of body size

Body size and body size change have been of significant interest because of the spectacular range of body size and disconcerting high rates of body size change of animals around the globe. Mechanisms and processes of life are essential to understand to improve estimates of expected consequences from the effects of climate change. Better management, conservation, and mitigation strategies to help organisms adapt to the effects of climate change can only develop from the progression of evidence-based data, information, knowledge, and wisdom. In this dissertation, I focus on exogenous environmental factors of weather and climate that affect growth and body size of bison for chapter 2, 3, and 4. Ultimately, implementing adaptation strategies hinges on the ability of conservation managers. In chapter 5, I follow up with a survey of vulnerabilities of bison managers to environmental change.

Body size has profound effects on both life history traits and physiological processes (Peters 1983, Hudson and White 1985, Barboza et al. 2009). Ontogenetic growth is the obvious primary mechanism of body size change of individuals, but here I focus on the drivers that affect mean mature body size and variable growth rates of adolescent bison. I assess the effects of latitude, global and local mean temperature, precipitation, and drought. Body size is a key functional trait for how animals interact with their environment, but their environment also shapes body size. Because of their considerably large body size, large grazing ungulates are ecosystem engineers—shaping and disturbing ecological processes in their wake. Halving body size of large animals, per se, would have drastic consequences that alter the size and strength of that ecological wake, but to what extent?

My focal taxon is bison for four reasons, 1) bison represent both wildlife and agricultural taxa and thus represents both public and private sectors, making the applicability of findings broad, 2) bison are widely-distributed throughout the grasslands, rangelands, savannas, and shrublands of North America from Arizona and Texas to Alberta and Manitoba, making implications generalizable, 3) bison have a deep history of climatic change in North America, having been here for over 160,000 years, contextualizing the findings, and 4) bison have a deep cultural connection for people, including national and tribal identity, iconic and symbolic status in the minds of many, emblematic of immense wealth of natural resources for nations, making finding relevant to many interested readers. In sum, bison are an ideal species to study because of their broad applicability. The bison coalition—the managers, habitats, and the species themselves—have been successful at saving the species from near extinction a century ago. What can we learn and apply from the bison system to help conservation a century from now?

1.2. Brief history of bison conservation

Bison play an integral role in origin stories of many native American cultures and are foundational to the original natural wealth of the United States. Seemingly overabundant, bison were over-hunted to near extinction (Figure 1.1A) in North America by unregulated over-harvest and livestock diseases like cattle fever in late 1890s and early 1900s (Hornaday 1889, Stoneberg Holt 2018, Aune and Plumb 2019, Barboza and Martin 2020). Their population plummeted from between 30–60 million down to less than 1,000 animals; establishing conservation efforts and organization in the late 1800s, such as the Boone and Crockett Club, the American Bison Society, and the National Park Service (Aune and Plumb 2019). Ownership of bison was transferred between sectors (Figure 1.1B) by force of treaty and later by various forms of fair-trade (U.S. National Archives & Records Administration 1803, Hornaday 1908, Nesheim 2012). Bison carcasses and hides were undervalued (Figure 1.1C: 1860s–1870s) as a common pool resource because the unregulated high-volume demand of bison leather for drive belts to propel the industrial revolution (Steller 1997, Reffalt et al. 2008, Snell 2010). Finally, depicted in (Figure 1.1D), there were other natural events such as the Little Ice Age, the Dust Bowl (Wanner et al. 2008, Cowan et al. 2017), social, economic, legislative authorizations about bison (Lueck 2002), and implementation of recovery efforts that have negatively and positively affected bison population over the last 220 years (Sanderson et al. 2008). In this dissertation, I focus on natural and social pressures, specifically climate change and bison manager vulnerability to environmental change.

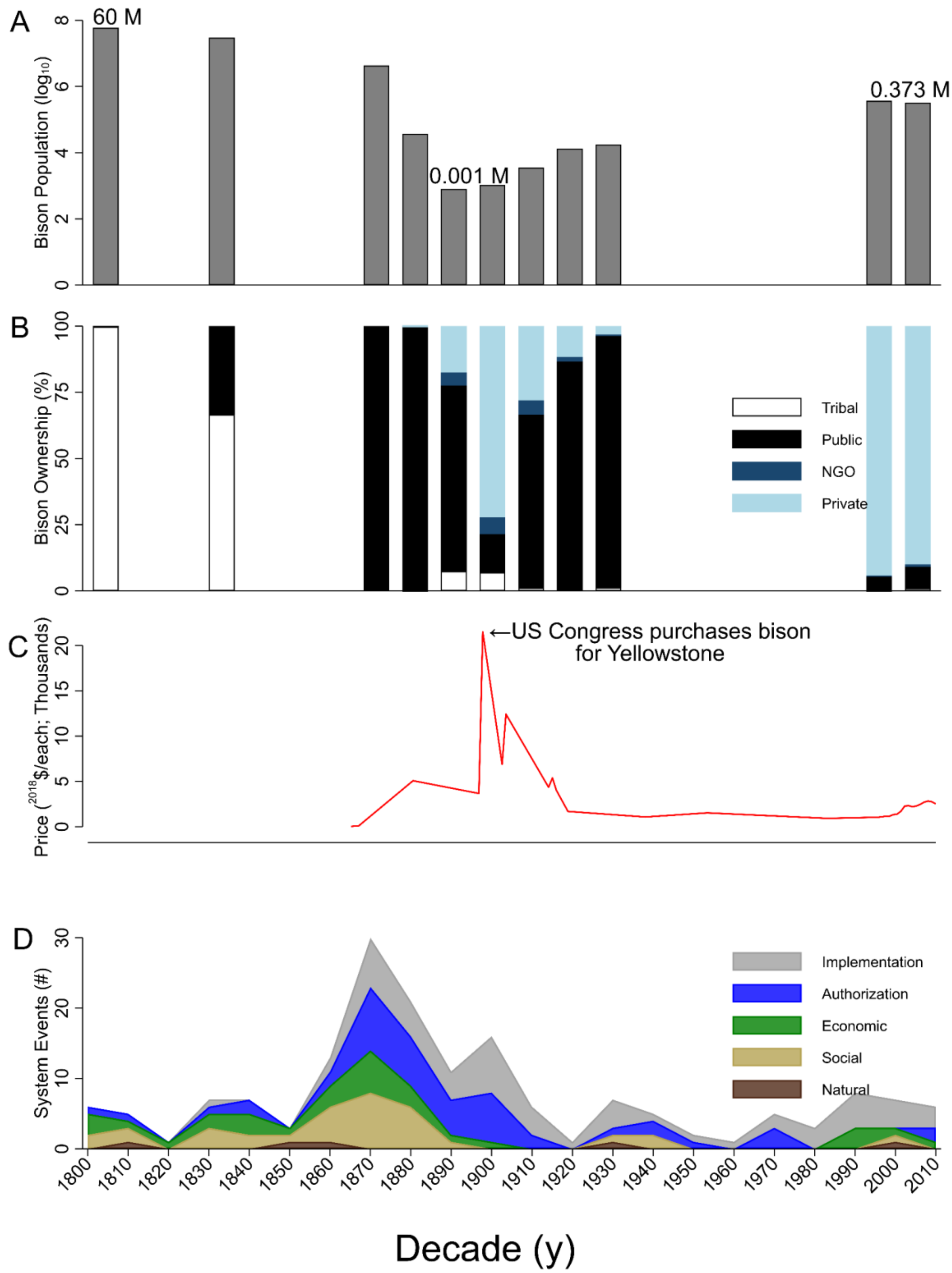

Figure 1.1. Stacked history timeline since 1800 CE of bison population, bison ownership, average carcass price, and bison system socio-ecological events. A) Log

bison population (log10; gray bars (Hornaday 1889, Garretson 1918, 1926). B) Bison ownership shows the relative share of bison population by sectors of Tribal nations (white bars), US government (‘public’, black bars), Non-governmental organizations like zoos (‘NGO’, navy bars), and private entities (light blue bars). C) Average carcass price of bison (red line) with all prices corrected to 2018 equivalent dollars (U.S. Bureau of Labor Statistics 2020) since 1820 CE (Hornaday 1889, USDA 2020). D) Conservation events ranging across domains of natural (brown), social (yellow), economic (green), legislation about bison (authorization, blue), and recovery efforts (implementation, gray; supporting data are in Appendix A).

1.3. Climate change

Within each subsequent chapter, I will include a section that describes the salient climate change consequences pertinent to the question at hand, but for here, I want to describe with a broad-stroke brush what is known in the literature about climate change and its consequences for large mammals.

It is expected global temperatures in the 21st century to rise between 2 and 4°C above the 20th century average (IPCC-AR5 2013); the globe is already 1°C warmer than the 20th century mean. Other studies have described decreasing body size as a universal consequence for mammals and birds in response to rising global temperature (Gardner et al. 2011, Joly et al. 2011, Weeks et al. 2019). Animals physiologically adapt to local climate and habitats. With climatic change, they must readjust their physiological baselines if they cannot alter their distribution to more favorable environments (Sejian 2013, Perdinan and Winkler 2014). Small mammals appear to adapt morphology and life history to environmental shifts within one to three generations (Mifsud et al. 2011, Crews and Gore 2012) but, the adaptive responses of large mammals to climate change are poorly understood. Most large bodied herbivores greater than 100 kg are long-lived, in excess of 10 years (Hoy et al. 2017), which exposes large taxa to several years of environmental stressors during growth that affect individual body size at maturity and the ultimate asymptotic size of the subpopulation. Consequently, researchers do not have enough understanding to project the effects of climate change for decisions of managing large herbivores.

The consequences of rising global temperature vary across geographic space and time, affecting timing of growing season and winter onset, shifting precipitation patterns, and increasing variability of extreme weather (Bloor et al. 2010, Wuebbles et al. 2017). The Great Plains, the primary range for bison, are predicted to warm (IPCC-AR5 2013, Wuebbles et al. 2017) and increase in drought severity (Fawcett et al. 2011, Cook et al. 2015, Cowan et al. 2017). *Bison* are resilient to short duration extreme weather events such as blizzards (Martin 2014), dry spells, or heat waves; but, chronic droughts and warming affect life history traits (Martin et al. 2018). Challenges that occur during the growing season negatively affect dietary uptake, storage, and use of energy and protein (Barboza et al. 2009).

1.4. Socio-ecological coupling of the bison system: consequences of body size change

Although we reduced native tallgrass prairies to about 1% of its original range and approximately 50% for mixed-grass and shortgrass prairies in the Great Plains, *Bison* are keystone species for native prairies (Knapp et al. 1999, Drummond et al. 2012). Bison are ecosystem engineers that alter their surrounding habitats and ecosystems through selective grazing (Fahnestock and Knapp 1994, Coppedge and Shaw 1998), wallowing (Polley and Collins 1984, Coppedge et al. 1999), transporting nutrients

(Plumb and Dodd 1993, Towne 2000), seed dispersal (Rosas et al. 2008), herd movement (Bergman et al. 2001, Van Vuren 2001), and physical disturbance of soil and vegetation (Coppedge et al. 1999, Coppedge and Shaw 2000, Allred et al. 2011). All the above combined traits differentiate bison from cattle, for example cattle do not create wallow holes like bison; wallows are essential to create vegetative heterogeneity over the landscape and ephemeral ponds for amphibian life cycles on the prairies (Polley and Collins 1984, Reinhardt 1985, Umbanhowar Jr. 1992, Gerlanc and Kaufman 2003). The above behaviors are also the primary mechanisms that produce extensive regulating and supporting ecosystem services such as erosion control, water preservation, carbon sequestration, and prairie restoration that people rely on to reduce floods and to produce food (Reeder and Schuman 2002, Allred et al. 2013, Kohl et al. 2013, Davenport 2018). Bison are good tools for prairie restoration and conservation. Bison are also a good tie to provisional services for people because of the production of meat, leather, bones, and hair-fiber.

1.5. Summary

In this dissertation, I use a step-wise approach to assess the drivers and consequences of *Bison* body size change, using 40,000 years of fossil *Bison* records, decadal scale long-term ecological datasets, and seasonal observations along the Great Plains from Saskatchewan to Texas. I also assess the vulnerabilities of bison managers from the private and public/NGO sectors.

Bison conservation, and wildlife conservation in general, during the 19th and 20th centuries was focused on saving species from un-regulated overharvest, predators, and cattle competition. Conservation during the 21st century will be to save the species from an indelible yet invisible threat of rising temperature and increasing drought. Ranges and assembly of animal and vegetation communities will shift because of changing climate. Cultural and social institutions may hinder re-organization of ecosystems and communities. I study the bison coalition to learn and apply what has been successful for the bison system for other wildlife and land conservation in North America. My aim is to provide actionable science to help re-frame conservation science to be more interdisciplinary and to improve concerted conservation efforts of both private working lands with public natural lands for the betterment of ecosystems and people.

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2. BISON BODY SIZE AND CLIMATE CHANGE*

2.1. Synopsis

The relationship between body size and temperature of mammals is poorly resolved, especially for large keystone species such as bison (*Bison bison*). *Bison* are well-represented in the fossil record across North America, which provides an opportunity to relate body size to climate within a species. We measured the length of a leg bone (calcaneal tuber, DstL) in 849 specimens from 60 localities that were dated by stratigraphy and ^{14}C decay. We estimated body mass (BM) as: $BM = (DstL/11.49)^3$. Average annual temperature was estimated from $\delta^{18}O$ values in the ice cores from Greenland. Calcaneal tuber length of *Bison* declined over the last 40,000 years, that is, average body mass was 37% larger (910 ± 50 kg) than today (665 ± 21 kg). Average annual temperature has warmed by 6°C since the Last Glacial Maximum (~24-18 kya) and is predicted to further increase by 4°C by the end of the 21st century. If body size continues to linearly respond to global temperature, *Bison* body mass will likely decline by an additional 46%, to 357 ± 54 kg, with an increase of 4°C globally. The rate of mass loss is 41 ± 10 kg per °C increase of global temperature. Changes in body size of *Bison* may be a result of migration, disease, or human harvest but those effects are likely to be local and short-term and not likely to persist over the long-time-scale of the fossil record.

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* Martin, J. M., J. I. Mead, and P. S. Barboza. 2018. Bison body size and climate change. Ecology and Evolution 8(9):4564–4574. DOI: 10.1002/ece3.4019. CC BY 4.0.

The strong correspondence between body size of bison and air temperature is more likely the result of persistent effects on the ability to grow and the consequences of sustaining a large body mass in a warming environment. Continuing rises in global temperature will likely depress body sizes of bison, and perhaps other large grazers, without human intervention.

2.2. Introduction

Variation in body size of American bison (Artiodactyla, Bovidae) has been a contentious topic for more than seven decades (Dary, 1974; Hill, Hill, & Widga, 2008; McDonald, 1981; Skinner & Kaisen, 1947). In North America, Skinner & Kaisen (1947) synthesized and synonymized 52 species of bison down to eight species using primarily skulls and horn cores which respond plastically to sexual selection. McDonald (1981) and Pinsof (1991) synthesized and synonymized those eight species of *Bison* to five, again based on cranial morphology. *Bison priscus* and *B. latifrons,* which denote sister taxa groups to the extant bison clade and represent the larger, more giant end of the body size spectrum, appear to go extinct circa 30,000 years ago. The extant bison clade in North America traditionally includes *Bison bison*, *B. occidentalis,* and *B. antiquus,* which represent a smaller body size in comparison to the larger, giant bison (*B. priscus* and *B. latifrons*). Yet, the skulls of these smaller species still represent plastic variation, likely due to sexual selection, not representative of overall body size. To avoid the issues surrounding problems with cranial morphology, our study here focuses on the post-cranial body size reconstruction, particularly of a mechanistic element to the structure of the skeleton. Our assessment is that the extant bison clade species may represent a linear chronospecies and is supported by recent ancient DNA assessments (Shapiro *et al.*, 2004; Froese *et al.*, 2017). Likely, *B. antiquus* and *B. occidentalis* did not go extinct, but through phenotypic and morphologic adaptation to changing climatic conditions, evolved into what is traditionally referred to as *B. bison* that we have throughout the Holocene and this is what we present below.

Extant *Bison* are one of eight ungulate genera to survive the most recent deglaciation in North America (Koch & Barnosky, 2006; Kurtén & Anderson, 1980; McDonald, 1981). *Bison bison* (the extant species in North America) has also survived a more recent near-extinction event by market hunters in the late 19th century (Dary, 1974; McDonald, 1981). Modern bison of the early 20th century bottleneck have rebounded in population to approximately 400,000 bison today because of conservation efforts from public and private sectors (Gates, Freese, Gogan, & Kotzman, 2010; United States Department of Agriculture, 2016). During the Holocene in North America, *Bison* had the largest distribution of any contemporary ungulate; from Pacific to Atlantic coasts and from arctic to the tropical ecoregions (Skinner & Kaisen, 1947; McDonald, 1981; Feranec *et al.*, 2009). Although it is often assumed that *Bison* are obligate grazers (occasionally referred to as hyper-grazers (MacFadden & Cerling, 1996; Leng, 2006)), *Bison* have shown to be adaptable and variable in diet selection (Miquelle, 1985; Feranec & MacFadden, 2000; Bergman *et al.*, 2001; Widga, 2006). *Bison* have inhabited North America (south of 55°N latitude) for approximately 200,000 years (Pinsof, 1991; Bell *et al.*, 2004; Barnosky *et al.*, 2014) and have occupied Beringia for nearly 300,000 years (McDonald, 1981; Shapiro *et al.*, 2004; Froese *et al.*, 2017).

Despite conservation efforts, modern bison face increasing temperatures and increasing variability in climate (IPCC Working Group 1, 2014). Global temperature in the 21st century is expected to rise between 1 and 4°C above the 20th century average (IPCC Working Group 1, 2014). Past global and regional climates can be reconstructed by using isotopic markers from ice cores and marine sediments and by using limnological data such as species of pollen and diatoms, and charcoal in geological context. Currently, the longest and highest resolution records for reconstructing past atmospheric conditions are stable isotopes of Oxygen (^{18}O) from continental ice sheets in Greenland (< 120,000 years (Alley *et al.*, 1993)) and Antarctica (< 800,000 years (Jouzel *et al.*, 2007)). Values for $\delta^{18}O$ from the Greenland Ice Sheet Project (GISP2) index decadal temperatures that would have been experienced by *Bison* in the Northern Hemisphere.

Species that are affected by climate change may alter their distribution and adapt through changes in morphology, physiology, behavior, and life history (Smith *et al.*, 2010, 2014). Small mammals appear to be able to adapt morphology and life history to environmental shifts within one to three generations (Mifsud *et al.*, 2011; Crews & Gore, 2012). However, the adaptive responses of large mammals to climate change are poorly understood. In comparison with small mammals, large species can better avoid harsh environments by moving long distances, tolerate austere conditions with large bodies, and recover over multiple seasons to reproduce over long lifespans (Barboza *et al.*, 2009). Impacts of climate change on animals are twofold: direct effects of temperature on the animal (i.e., energetic load as heat) and indirect effects of temperature on the animal's food supply (Figure 2.1). Warm temperatures advance the seasonal growth of grasses to reduce the availability of nitrogen for growth of cattle and bison (Craine *et al.*, 2009, 2010, 2012; Craine, 2013). Ambient air temperature directly affects the costs of thermoregulation of the animal in cold winters and the ability to lose excess heat in warm summers (Speakman & Król, 2010; Long *et al.*, 2014). Seasonal patterns of air temperature affect the onset, duration, and intensity of plant production that sets the quantity and quality of food for growth and reproduction of herbivores from spring through autumn (Huston & Wolverton, 2011; Albon *et al.*, 2017).

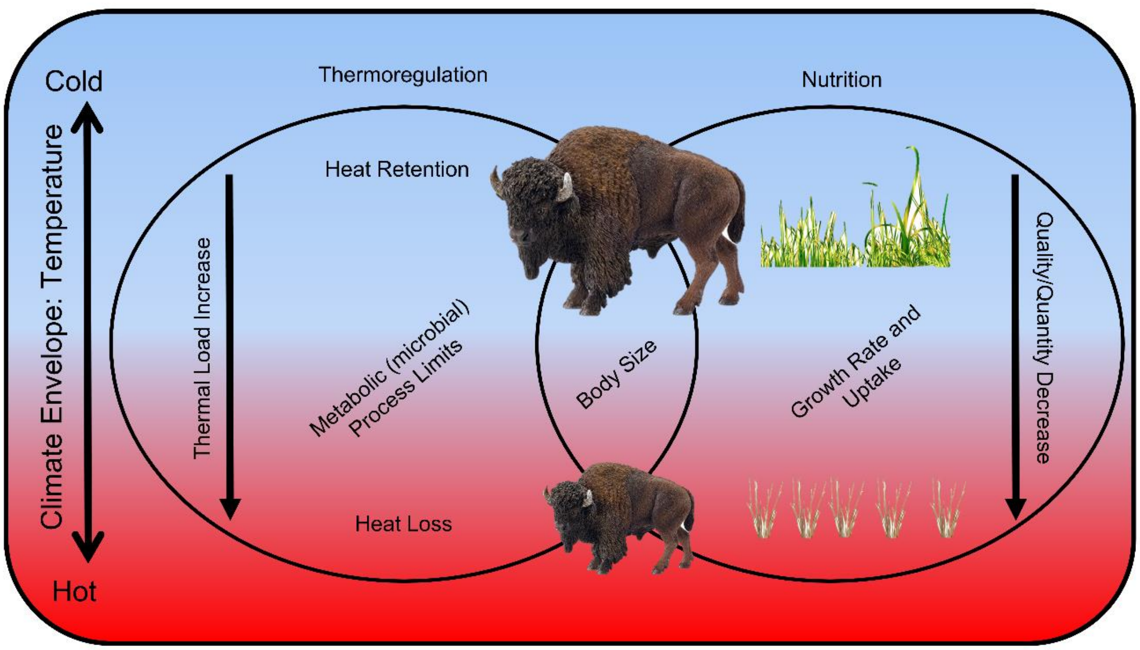

Figure 2.1. Conceptual model of the direct and indirect effects of elevated ambient temperature on body size of *Bison*. Reprinted from Martin et al. (2018).

At least four biological concepts attempt to explain the phenomenon of changing body size. Cope's Rule recognizes the tendency of vertebrate animals to increase body size over geological time scales (Stanley, 1973). Bergmann's Rule emphasizes the positive relationship between body size and latitude, which suggests that the ability to retain body heat favors larger bodies at cooler temperatures. The Metabolic Theory of Ecology emphasizes the allometric scaling of body size and the underlying relationships between the volume of animals and the surfaces that are exposed to the environment (Brown & Sibly, 2006). The Heat Dissipation Limit Theory emphasizes heat load as a driver of body size because metabolism can produce excess energy (heat), which may be more difficult to dissipate as body size and metabolic work increase (Speakman & Król, 2010). However, these relationships alone are not sufficient to accurately project the effect of climate change on the body size of large species. Although the fossil record provides abundant evidence of changes in the body size of vertebrate animals (i.e., dinosaurs, proboscideans) that have been linked to global shifts in climate (Sander *et al.*, 2011), taxa differ in the direction, rate, and extent of response to global warming and cooling (Lovegrove & Mowoe, 2013). Among large mammals, changes in body size at a continental scale declined quickly with rising temperature but rose more slowly with cooling over the past 100 million years (Evans *et al.*, 2012).

The relationship between body size and temperature of mammals is poorly resolved especially for ecological keystone species of large mammals, such as bison (Knapp *et al.*, 1999). *Bison* modify ecosystems through selective grazing (Fahnestock & Knapp, 1994; Coppedge & Shaw, 1998), wallowing (Polley & Collins, 1984; Coppedge *et al.*, 1999), transporting nutrients (Plumb & Dodd, 1994; Towne, 2000), herd movements (Bergman *et al.*, 2001; Van Vuren, 2001), and physical disturbance of soil and vegetation (Coppedge & Shaw, 2000; Allred *et al.*, 2011). Fossilized skeletal elements can be used to study body size over long time frames. Our study focuses on the calcaneum (the heel bone; Figure 2.3), an anatomically functional element, that is conserved evolutionarily. We used the calcaneum to estimate body mass, whereas previous authors have focused on skull metrics (Skinner & Kaisen, 1947; McDonald, 1981) that are more susceptible to sexual selection and vary widely among species. In contrast, sexual dimorphism in bison, while noticeable in modern contexts, is lost in the fossil record without adequate comparison of other representatives of the correct species at that time. Moreover, using osteometrics and ratios on post-cranial elements are unable to determine the intermediate-sized individuals within a fossil population, stated another way, mature females and immature bulls overlap in size and all immature individuals overlap in size (Lewis, Buchanan, & Johnson, 2005). *Bison* are well-represented in the fossil record across North America, which provides an opportunity to relate body size to climate within a taxon over the last 40,000 years. In this paper, we used the historical and pre-historical record of *Bison* to test the hypothesis that large-scale changes in climate drive changes in body size.

2.3. Materials and Methods

We used curated specimens from modern and fossil *Bison*. Martin et al. 2018 Supplementary Data S1 lists specimen numbers and sponsoring collections. Physiographic and chronological information about localities is summarized in Martin et al. 2018, Supplementary Data S2 and osteometric information about specimens at each locality is summarized in Martin et al. 2018, Supplementary Data S3: https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1002%2Fece3.4019&file=ece34019-sup-0001-DataS1-S3.xlsx). I assembled a database of 2,400 *Bison* calcanea representing 60 localities (geological strata at geographic locations) in North America (Figure 2.2; Martin et al. 2018, Supplemental Data S2). We used determinations of radiocarbon age only after 1990 for consistent accuracy of radiometric estimates (Martin et al. 2018, Supplemental Data S2) that were calibrated using OxCal Online Tool (https://c14.arch.ox.ac.uk/) by employing the IntCal13 curve (Reimer *et al.*, 2013). Calibrated ages and errors are reported in S1; ages and errors in analyses are assumed accurate but not precise due to variability of the radiocarbon curve (Reimer *et al.*, 2013). Specimens lacking adequate chronologies or osteometrics (< 3 measures) were omitted from subsequent analyses, thus providing 1,169 samples.

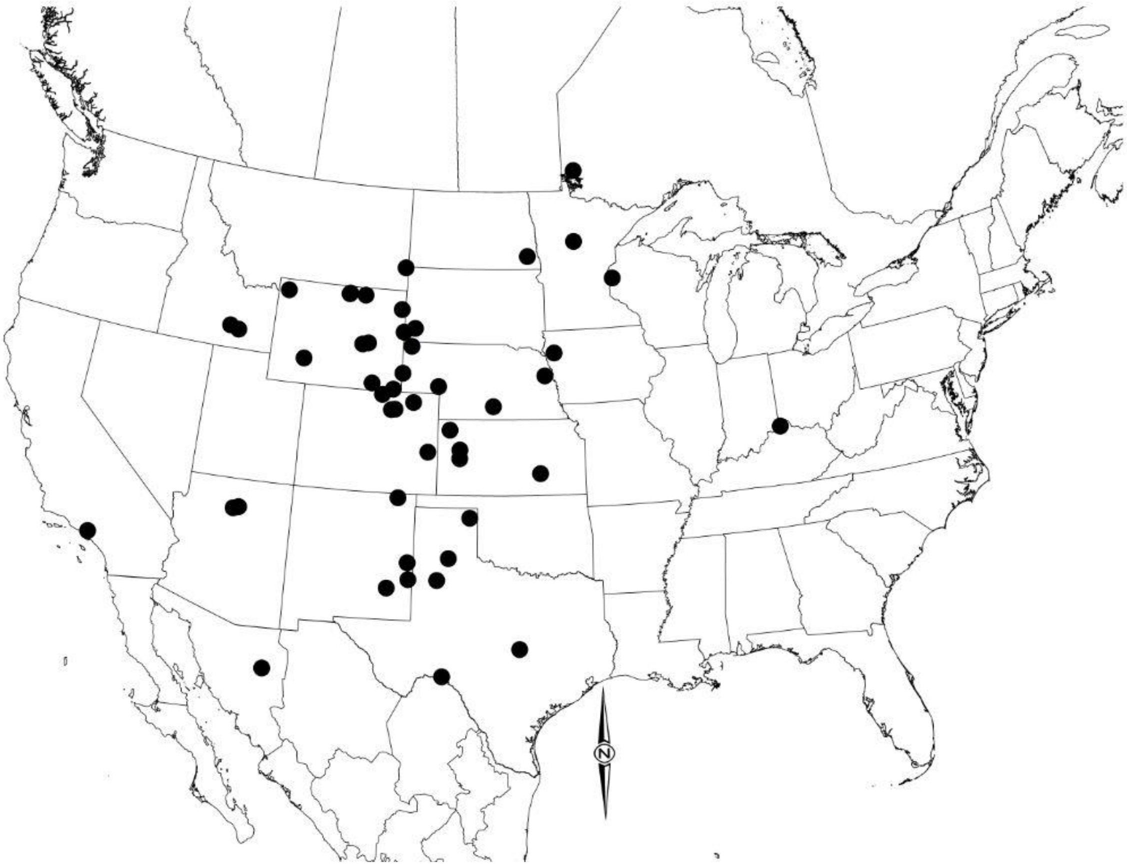

Figure 2.2. Localities (*n* = 60) of fossil specimens in North America that correspond with body mass estimates of bison with calibrated age. Sites are further described in S2. Reprinted from Martin et al. (2018).

2.3.1. Species and body mass estimation

Fossil calcanea were reported as belonging to one of three species of *Bison* (e.g., *B. bison*, *B. antiquus*, and *B. occidentalis*) in collection databases based on associated diagnostic elements with specific shape and morphological landmarks (e.g. horn cores, (Skinner & Kaisen, 1947; Balkwill & Cumbaa, 1992)). Some of the specimens were originally identified as *Bison bison antiquus*, (*nomen dubium*), which has been synonymized with *B. antiquus* (McDonald, 1981). Six standard linear measurements were taken on the calcaneum (Olsen, 1960; Von Den Driesch, 1976; Miller & Brotherson, 1979; McDonald, 1981; Hill, 1996): distal breadth of calcaneal tuber (DstBr), greatest breadth of calcaneum at the sustentaculum (GBr), distal depth of calcaneal tuber (DstDp), distal length of calcaneal tuber (DstL), greatest length of calcaneum (GL), and greatest depth of calcaneum at the sustentaculum (GDp, Figure 2.3). We used DstL to estimate live body mass (BM; Equation 2.1) by the relationship of Christiansen (2002, p. 688).

Equation 2.1 $\mathbf{BM} = \ (\boldsymbol{DstL/11.49})^{\mathbf{3}}$

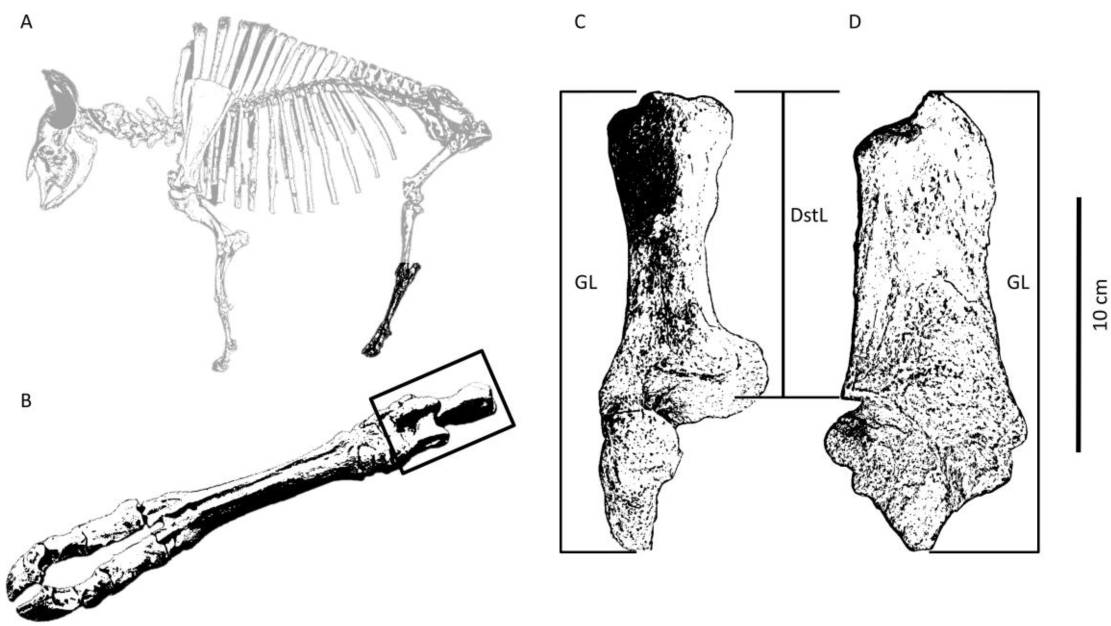

Figure 2.3. Standard metrics on a typical fossil calcaneum from a *Bison* (A) hock (B) shown in dorsal view (C) and medial view (D). Two measures for assessing body size of bison are illustrated: GL; greatest length, DstL; distal tuber length).

Additional measures of the calcaneum are described by von den Driesch (1976) and Hill (1996). Reprinted from Martin et al. (2018).

2.3.2. Paleotemperature proxy

We assume that global temperature is relative to the Greenland Ice Sheet Project (GISP2) ice core paleotemperature proxy data (Grootes *et al*., 1993). Proxy data from reconstructing global paleoclimatic temperature in °C was derived from GISP2 $\delta^{18}O$ values (‰; Grootes *et al.*, 1993; Alley, 2000; Alley & Ágústsdóttir, 2005) and were related to average age of the locality. The global temperature anomaly was derived by scaling the GISP2 data to the estimated Last Glacial Maximum temperature, which was on average 6°C colder than the 20th century average global temperature.

2.3.3. Statistical analyses

We used mixed model regressions for each metric of the calcaneum to compare species as a fixed effect with *B. bison* as the base for the comparison (Stata v14.2, 2015, StataCorp, College Station, TX, USA). Similarly, mixed models were used to compare DstL with other calcaneal metrics with species as a fixed effect. The fixed effects of species, temperature, and latitude were included in the model to analyze DstL and estimates of body mass from measures of DstL (Christiansen, 2002). We used two estimates of temperature in the models: GISP2 temperatures and the relative global temperature anomaly. All mixed models included site as a random effect to account for repeated measures within each location. We used the robust 'sandwich estimator' to relax assumptions of normal distribution and homogeneity of variance for the regression (Bolker *et al.*, 2009; Rabe-Hesketh & Skrondal, 2012). Pairwise group comparisons among predicted margins from each model were made with Bonferroni's correction (α = *0.05*).

2.4. Results

Species significantly affected all metrics of calcaneal size (Table 2.1), that is, specimens from *B. antiquus* were larger than those of *B. bison*. Similarly, the intercept of the positive relationship between the depth or breadth of the calcaneum and its tuber length (DstL) was greater for *B. antiquus* than for *B. bison* (Table 2.2). Estimated body mass decreased over time from *B. antiquus* (802 ± 183 kg) to *B. occidentalis* (678 ± 105 kg) to modern *B. bison* (479 ± 177 kg; (Figure 2.4).

Table 2.1. Summary statistics [$\overline{x}$ ± SD (*n*)] calcaneal osteometrics (mm) of *Bison*. Abbreviations: GL; greatest length, DstL; distal tuber length, DstBr; distal tuber breadth, DstDp; distal tuber depth, GBr; greatest breadth, GDp; greatest depth. Upper case letters indicate significant pairwise differences ($p < 0.05$) between species within each measure (row). † = Extinct.

Parameter	*Bison bison*	*B. occidentalis*†	*B. antiquus*†
GL	142.1 ± 12.2 (428) A	155.9 ± 8.7 (35) B	161.8 ± 11.3 (568) C
DstL	88.4 ± 12.0 (273) A	100.7 ± 5.3 (36) B	106.2 ± 8.0 (540) C
DstBr	36.17 ± 3.8 (164) A	38.3 ± 4.1 (35) B	41.5 ± 4.7 (569) B
DstDp	39.3 ± 3.5 (164) A	42.2 ± 3.5 (38) B	44.3 ± 4.5 (589) C
GBr	48.0 ± 4.5 (433) A	50.3 ± 4.2 (33) B	55.2 ± 5.2 (545) B
GDp	55.5 ± 4.5 (400) A	58.3 ± 4.6 (34) B	63.7 ± 5.0 (563) B

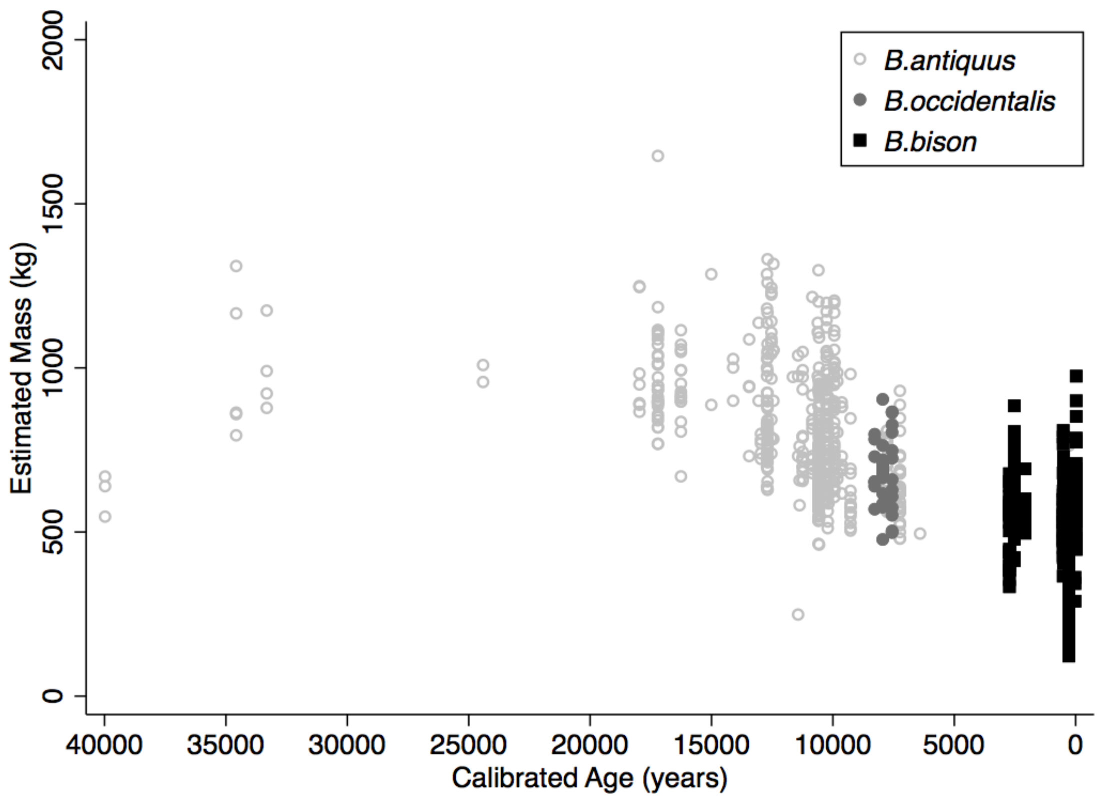

Figure 2.4. Average body size of fossil bison measured as calcaneal lengths (DstL) and body mass at 60 localities in North America from 40,000 years ago (left) to today (right). Reprinted from Martin et al. (2018).

Table 2.2. Regression relationships for estimating distal tuber length in *Bison*. (DstL) from other measures of the calcaneum (GL, DstBr, DstDp, GBr, GDp) in *Bison* using mixed models with site as a random effect and *B. bison* as the comparison base for species. [1] = No linear effect of species on GL ($p > 0.05$).

Measure	Obs.	Sites	Intercept (± SE)	Slope (± SE)
GL[1]	743	53	-6.22 ± 2.48	0.68 ± 0.01
DstBr	645	48	46.69 ± 2.06 + 3.14 ± 1.04 (*B.a.*) + 2.37 ± 1.18 (*B.o.*)	1.34 ± 0.05
DstDp	662	47	40.38 ± 2.78 + 4.53 ± 1.52 (*B.a.*) + 2.45 ± 1.45 (*B.o.*)	1.36 ± 0.07
GBr	714	51	40.13 ± 4.57 + 6.00 ± 1.93 (*B.a.*) + 5.99 ± 2.00 (*B.o.*)	1.08 ± 0.07
GDp	723	52	29.49 ± 4.88 + 5.77 ± 2.29 (*B.a.*) + 6.30 ± 2.35 (*B.o.*)	1.11 ± 0.07

The greatest proportion of specimens (50%) were those of *B. antiquus* and *B. occidentalis* that were dated between 7,000 and 13,000 years ago, whereas 38% of the specimens were those of *B. bison* from 3,000 years ago, to present. Average annual temperatures varied over 25°C on the scale of Greenland temperature over the last 40,000 years, which was equivalent to a span of 6°C on the relative global scale (Figure 2.5).

2.4.1. Paleotemperature

The largest proportion of *Bison* specimens were associated with two large fluctuations from 15,000 years ago to present that included warming in the Bølling-Allerød period (15,000 years to 13,000 years ago), cooling in the Younger Dryas (13,000 to 12,000 years ago) and warming through the Holocene period to present with small undulations in temperature, such as the Medieval Climatic Anomaly (approximately

1000 to 700 years ago) and Little Ice Age (approximately 700 to 150 years ago; Figure 2.5).

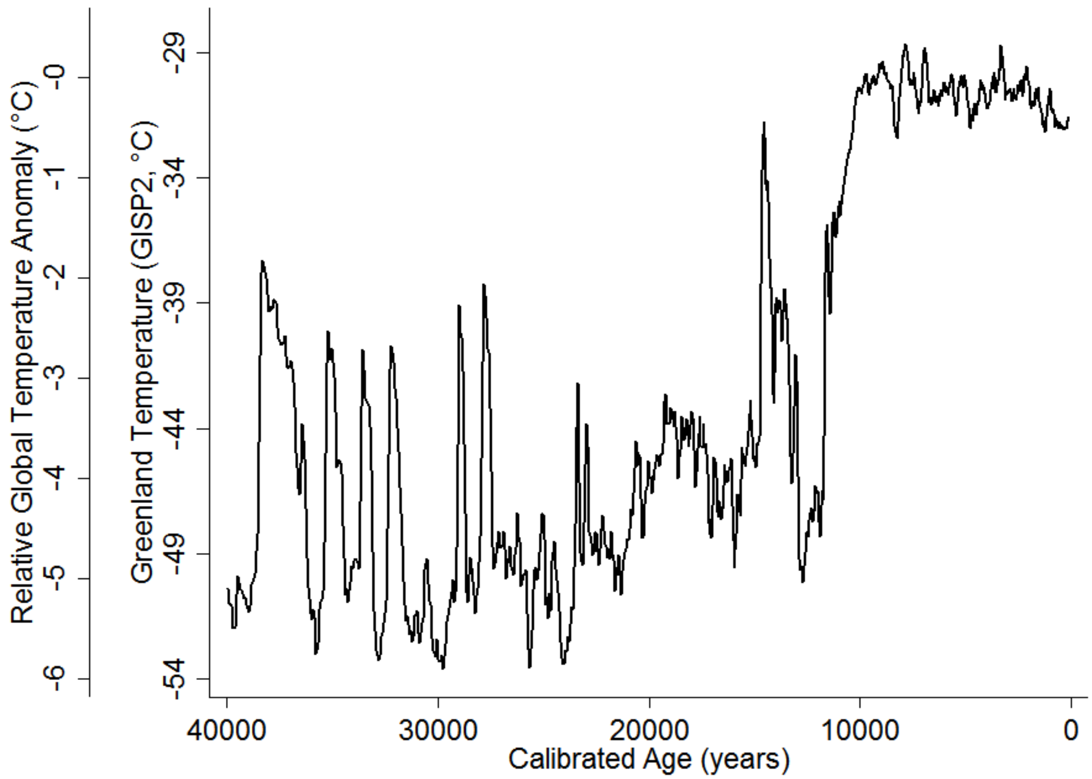

Figure 2.5. Sequence of Greenland mean annual temperature (°C derived from GISP2 δ^{18}O values (Alley & Ágústsdóttir, 2005)) and relative global temperature anomaly derived from modern Greenland temperatures (-29.9°C mean annual temperature) from 40,000 years ago (left) to today (right). Data are from Alley (2000) and: https://www1.ncdc.noaa.gov/pub/data/paleo/icecore/greenland/summit/gisp2/isotopes/gisp2_temp_accum_alley2000.txt. Figure reprinted from Martin et al. (2018).

2.4.2. Osteometrics and estimated body mass

Calcaneal distal tuber length (DstL) was negatively related to Greenland temperature (slope: -0.45 mm/°C ± 0.11; z = -3.95 P < 0.001) with intercepts at 78 ± 4 mm for *B. bison*, 90 ± 3 mm for *B. antiquus* and 87 ± 2 mm for *B. occidentalis*. The relationship between calcaneal distal tuber length (DstL) and relative global temperature was -1.77 mm/°C ± 0.45 (z = -3.95, P < 0.001) with intercepts at 92 ± 2 mm for *B. bison*, 103 ± 3 mm for *B. antiquus* and 101 ± 2 mm for *B. occidentalis*. Consequently, the slope of estimated body mass with global temperature was also negative at -41 kg/°C (± 10; z = -4.10 P < 0.001) with intercepts at 521 ± 36 kg for *B. bison*, 737 ± 45 kg for *B. antiquus* and 676 ± 36 kg for *B. occidentalis* (Figure 2.6). This relationship predicts that *B. bison* will decrease by 164 ± 40 kg to 357 ± 54 kg if global temperature rises from 0°C to +4°C (Figure 2.6).

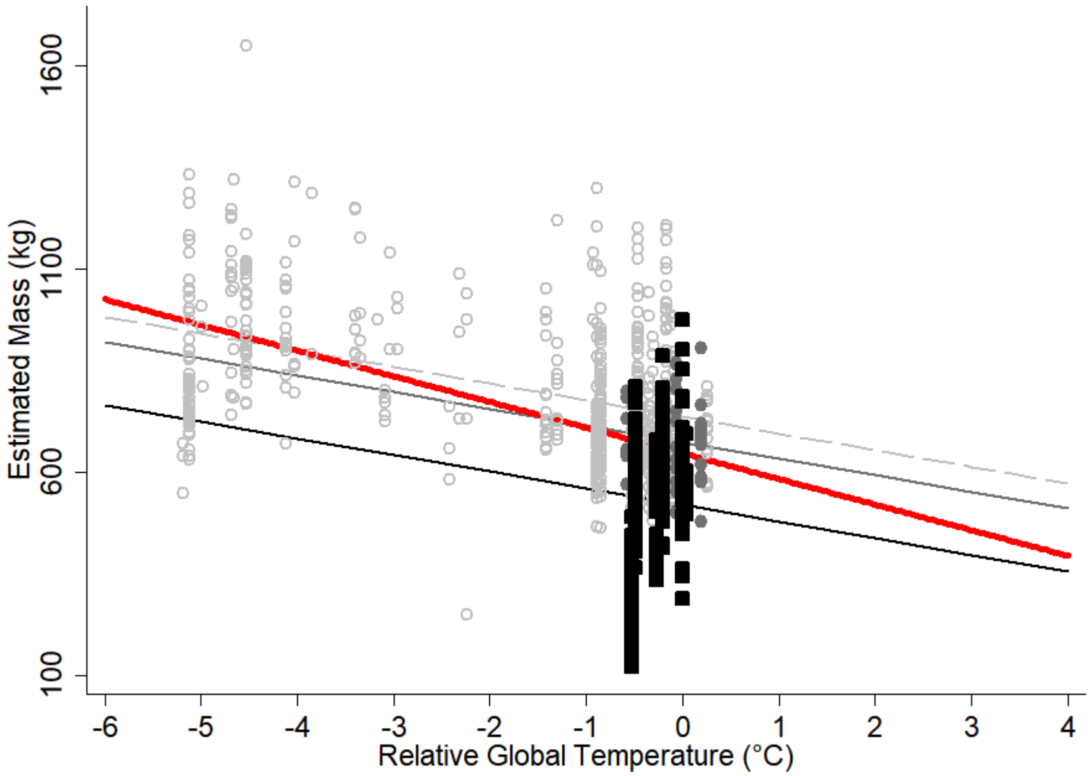

Figure 2.6. Relationship between estimated body mass (kg; ± *SE*) and the linear effect of relative global temperature (°C derived from GISP2 $\delta^{18}O$ values) from the mixed model regression with fixed effects of temperature, and the random effect of site. Regression line (y = -40.9kg/°C ± 10) with lines for specific regressions (intercepts for *B. bison* (black): 520.9 ± 36.1; *B. occidentalis* (dark gray): 675.6 ± 36.2; *B. antiquus* (light gray): 737.3 ± 44.7; *P* < 0.001, *n* = 849, *N* = 53). Regression line for the *Bison* clade (thick solid red line) is -63 kg/°C (± 10; *z* = -6.11 *P* < 0.001) with an intercept at 648 ± 26 kg. Reprinted from Martin et al. (2018).

Comparison of osteometric means and coefficient of variation by species is presented in Table 2.3. Values of CV at or greater than 10 suggest that variation is too high for one morphotype.

Table 2.3. Coefficient of variation summary table of *Bison* at the generic and specific level. Comparison of the genus, *Bison* sp., is comparable to *Bison bison*. Coefficient of variation equation is: $CV = \left(\frac{SD}{Mean}\right) \times 100$. Abbreviations: GL, greatest length; DstL, distal tuber length; GBr, greatest breadth; GDp, greatest depth; SD, standard deviation; CV, coefficient of variation.

Parameter	GL	DstL	GBr	GDp	Total
Bison sp. $\bar{X} \pm SD$ (mm)	153.9 ± 14.5	97.0 ± 13.6	52.3 ± 5.8	60.4 ± 6.0	67.7 ± 7.0
Bison sp. CV (%)	9.4	14.1	11.1	9.9	10.3
B. bison $\bar{X} \pm SD$ (mm)	142.0 ± 11.9	84.1 ± 11.3	47.9 ± 4.4	55.7 ± 4.4	62.4 ± 5.5
B. bison CV (%)	8.4	13.4	9.1	7.8	8.8

2.5. Discussion

Our data supported our hypothesis that global climate change drives body size of *Bison* spp., that is, as temperatures warmed, *Bison* became smaller. Generally, as described by Bergmann's rule (1847), endotherms increase in body size with increasing latitude (Huston & Wolverton, 2011). It is likely that negative correlation between temperature and latitude are driving Bergmann's Rule (i.e., body size) because even though we found that bison are larger at cooler temperatures, we were unable to correlate a significant effect of latitude over the geologic record ($P > 0.94$). The negative relationship between body mass and global temperature may reflect underlying relationships between body size and net primary production as well as heat loads (Speakman & Król, 2010; Huston & Wolverton, 2011; Figure 2.1).

Paleontologists have long used skeletal elements from extant animals to reconstruct body mass and body shape of fossils (Damuth & MacFadden, 1990; Gingerich, 1990; Christiansen, 2002). Data from some bones indicate body size more accurately than others. Indices of body size in mammals, including *Bison* are best indicated by bones of the hind foot (elements of the ankle, calcaneum and astragalus), and front foot (elements of the wrist, scaphoid and magnum), along with the toes (podial digits, distal and proximal phalanges; (Damuth & MacFadden, 1990)). The bulk of the foot bones precisely reflects body mass because they bear the weight of the animal, whereas the shape of the bones reflects the functional anatomy for locomotion through the attachment of tendons and muscle (Scott, 1990). Longer bones of limbs (femora and humeri) are also good proxies for reconstructing body size. Unfortunately, long bones in the fossil record are typically broken, whereas the calcanea, astragali, and phalanges are commonly well-preserved, likely because these dense elements resist degradation. Consequently, podial elements are well-studied within Bovinae, which includes cattle (*Bos taurus*, (Lawrence, 1951; Olsen, 1960; Balkwill & Cumbaa, 1992)), and Antilopinae, mountain goats (*Oreamnos* sp., (Carpenter, 2003)), bighorn sheep (*Ovis* sp., (Todd & Rapson, 1988; Rothschild & Martin, 2003), among others). However, it is difficult to distinguish taxa using podial elements. *Bison* and *Bos* can be resolved from traits of podial elements by the methods of Balkwill & Cumbaa (1992) but we cannot resolve *Bison* species based upon podial elements alone. Species designations in our dataset originated from whole collections of associated podial and cranial material that may not distinguish mixes of species at each location. For example, American Falls Reservoir in Idaho contains at least four co-existing species of *Bison* (Pinsof, 1991). If we ignore species designations, and analyze our data at the clade level, the slope of podial size with increasing temperatures becomes steeper; -63 kg/°C (± 10; $z = -6.11$ $P <$

0.001) with an intercept at 648 ± 26 kg for *Bison* spp., as compared to the -41 kg/°C for *Bison bison* (Figure 2.6). This slope may change regionally with latitudinal differences in body size of extant *Bison*.

Bison crania exhibit plastic morphology, likely due to a combination of environmental and sexual selection, whereas post-cranial elements – podial elements specifically – exhibit a more conservative and accurate reflection of body size due to functional anatomy of the appendicular skeleton (Clifford, 2009, 2010). Historically, it has been difficult to identify *Bison* fossil species (*Bison bison*, *B. occidentalis*, and *B. antiquus*) based on skeletal remains without skulls, especially those without horn cores (Skinner & Kaisen, 1947; McDonald, 1981). This issue continues today (McDonald & Lammers, 2002; Lyman, 2004; Grayson, 2006), with the exceptions of *B. latifrons* (Giant bison (Hopkins, 1951; Schultz & Hillerud, 1977; Pinsof, 1991)) and *B. priscus* (Steppe bison; (Gee, 1993; Zazula *et al.*, 2009; Boeskorov *et al.*, 2013)), which are distinct because of their massive size. Many of the above authors rely on cranial elements alone to specifically classify *Bison*, but recent studies suggest that the diagnostic *Bison* cranial characters vary-widely (Krasinska, 1988) and do not reflect conservative morphological variability in the skeleton. Cranial elements of *Bison* are now thought too variable to rely on for taxonomic classification (Prothero & Foss, 2007). Widga (2013) attempted to synthesize a large dataset of bison horn-core metrics and illustrates the noise inherent in these samples (Wilson, 1974; Hill *et al.*, 2014).

Some researchers suggest that the past several millennia of anthropogenic selection by Paleoindians, conservationists, and producers may have directly and indirectly selected traits that scale to body size (i.e., large heart girths, large heads, straight vertebral column; (Todd, 1983; Grayson, 2000, 2001)). Undoubtedly, early arrivals of modern humans were having impacts on the available bison through hunting some 14,000 years ago (Grayson, 2000; Barnosky *et al.*, 2014), however these effects were limited by small human populations dispersed over a large continent and were therefore local impacts (Hill *et al.*, 2008, 2014; Hawley *et al*., 2013). Others have acknowledged that any selection has not made significant changes to morphology (Hill *et al.*, 2008, 2014; Hawley *et al.*, 2013). Climate is the most parsimonious explanation for shaping *Bison* morphology (Shapiro *et al.*, 2004; Lewis *et al.*, 2007; Hill *et al.*, 2008). Changes in body size of *Bison* could be a result of migration or disease but those effects are geographically local and not likely to persist over the long-time-scale of the fossil record (Hamel *et al.*, 2016). Wilson *et al.*, (2008) postulate the decrease in body size of *Bison* is a consequence of dispersal theory, that is expansion of range, over the last 80,000 years (Wilson, 1996). A more cogent argument explaining decrease in body size is the rapidly warming global climate, characterizing the termination of the Younger Dryas period. This study demonstrates a strong inverse correlation between increasing global temperatures and body size of bison over the last 40,000 years. We hypothesize that increasing temperature alters both metabolic demands and available resources (Figure 2.1).

The IPCC (2014) predicts 4°C rise in global temperatures by year 2100. While the absolute increase of 4°C is not unprecedented in the evolutionary history of *Bison*, the rate of temperature change is 30 times faster than the Bølling-Allerød period, the transition from the Last Glacial Maximum to Holocene climate conditions. The Last Glacial Maximum corresponds with a global temperature 6°C cooler than the 20th century, when *Bison* mass was 910 kg. If global temperature warms to +4°C as predicted for the 21st century, *Bison* body mass will likely decline from 665 kg to 357 kg (Figure 2.6), if body size declines at the long-term average. The greatest decline in body size of *Bison* apparently occurred between 12,500 and 9,250 years ago, when mass declined by 26% (906 kg to 670 kg) in approximately 3,000 years. If generation time of *Bison* is 3–10 years (Gingerich, 1993; Evans *et al.*, 2012), the change in body size occurred in 325–1,080 generations producing an average rate of change of 0.2–0.7 kg per generation. It is unclear whether *Bison* can adapt body size to a 4°C warming within 10 generations by year 2100.

2.5.1. Summary of findings

Bison today express a 30% body mass gradient from North to South, that is, *Bison* in Saskatchewan (52°N) are at least 30% larger than those in Texas (30°N (Craine, 2013, p. 3)). This body size gradient is likely associated with latitudinal variation in timing of reproduction and parturition as well as windows for growth (Barboza *et al.*, 2009). Quantifying and comparing physiological thresholds and mechanisms driving body size change are imperative for managing *Bison* and other large herbivores (Figure 2.1). Conservation goals among latitudinally disparate *Bison* herds in North America should consider that resident *Bison* will likely grow smaller and more slowly in the South than in the North, which will impact management strategies at both regional and continental scales.

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3. HEAT AND DROUGHT DRIVE BODY SIZE OF NORTH AMERICAN BISON (*BISON BISON*) ALONG THE GREAT PLAINS†

3.1. Synopsis

Large grazers are visible and valuable indicators of the effects of projected changes in temperature and drought on grasslands. The grasslands of the Great Plains (GP) have supported the greatest number of bison (*Bison bison*; Linnaeus, 1758) since prehistoric times. We tested the hypothesis that body mass (BM; kg) and asymptotic body mass (ABM; kg) of *Bison* decline with rising temperature and increasing drought over both temporal and spatial scales along the GP. Spatially, we used photogrammetry to measure body height (H) of 773 *Bison* to estimate BM in 19 herds from Saskatchewan to Texas, including Wind Cave National Park (WICA), South Dakota. Temporally, we modeled the relationship of annual measures of BM and H of 5781 *Bison* at WICA from 1966 to 2015. We used Gompertz equations of BM against age to estimate ABM in decadal cohorts; both females and males decreased from 1960s to 2010s. Male ABM was variable but consistently larger (699 vs. 441 kg) than female ABM. We used mean decadal temperature and Palmer Drought Severity Index to model the effects of climate on ABM. Drought decreased ABM temporally at WICA (-16 kg) and spatially along the GP (-16 kg). Temperature decreased ABM temporally (-115 kg) and spatially along the GP (-1 kg). Our data suggest that growth of *Bison* is driven by temperature and drought. *Bison* body size is

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† Martin, J. M., and P. S. Barboza. 2020. Decadal heat and drought drive body size of North American bison (*Bison bison*) along the Great Plains. Ecology and Evolution 10(1): 336–349. DOI: 10.1002/ece3.5898. CC BY 4.0.

likely to decline over the next five decades throughout the GP due to projected increases in temperatures and both the frequency and intensity of drought.

3.2. Introduction

The relationship between temperature and body size of mammals has mainly been observed as a positive correlation with cold temperatures over large scales of space (e.g. subarctic vs. tropical latitudes) and time (e.g. fossil record) that lead to concepts such as Bergmann's rule (Bergmann 1847), which predicts that mammals increase body size as temperatures cool. Mammals may also decline in body size as temperatures warm (Gardner *et al.* 2011). The negative effects of hot temperatures on body size of animals have mainly been related to limitation of food and water for small desert mammals (Smith *et al.* 2014). Recent work on large mammals indicate that warming temperatures are also associated with a decrease in body size (Hoy *et al.* 2017). In North American bison (*Bison bison*: Artiodactyla, Bovidae, Bovini; Linnaeus, 1758), estimated body mass (BM; kg) declined 41 ± 10 kg over each 1 °C rise in global average temperature during the last 40,000 years through glacial stadials and interstadials (Martin *et al.* 2018). *Bison* body size also appears to decline as a result of low precipitation (Craine *et al.* 2009). The effects of environmental change on large animals, such as *Bison*, are difficult to study because they have long generation times (3 – 10 years) and use large areas that require measurements over large spatial and temporal scales. However, large grazers such as *Bison* are more visible and accessible than most small mammals, which facilitates measurement of functional traits such as growth rates and asymptotic body mass (ABM; kg) for studies of the response of the population to climate.

Body size has profound effects on both life history traits and physiological processes (Peters 1983, Hudson and White 1985, Barboza *et al.* 2009). Reduced body size is an outcome of slower growth that affects productivity (i.e. litter size or mass, litter number, frequency of reproduction) life span and sexual dimorphism. Moreover, large body sizes of mammals have been associated with greater rates of extinction in the last 100 million years and a greater vulnerability to climate change (Nogués-Bravo *et al.* 2010, Dietl and Flessa 2011, Barnosky *et al.* 2017). Large variations in body size within extant populations may also increase extinction probabilities (Isaac 2009, Bolnick *et al.* 2011). Additionally, climate–body size relationships reinforce feedbacks that can increase extinction risks (Isaac 2009). For example, both excessive heat (> 40 °C) and cold (< -30 °C) directly increase demands for energy, water, and nutrients in thermoregulation whereas indirect effects of temperature on the quantity and quality of plants ultimately affect the supply of energy, water, and nutrients to *Bison* (Martin *et al.* 2018; Figure 2.1). Droughts that decrease water availability compound the effect of hot temperatures on plants as well as *Bison*. Temperature and drought are increasing across North America, especially in the Great Plains (IPCC-AR5 2013, USGCRP 2018). We expect that body size and productivity of *Bison* and other large herbivores to decline with warming at large scales of space and time, but we require better local resolution to properly inform decisions for managing populations along the Great Plains (17, 18).

Across the contiguous United States, 95% of the land surface has warmed in mean annual temperature, including most of the Great Plains. The 4th National Climate Assessment (Wuebbles *et al.* 2017, USGCRP 2018) separates the Great Plains into northern and southern portions at the Nebraska-Kansas border. Since the beginning of the 21st Century, the northern Great Plains annual temperature has risen 0.8 °C whereas the southern Great Plains annual temperature has risen 0.4 °C (Wuebbles *et al.* 2017). Winters have warmed across both northern and southern Great Plains (~2.5 °C). However, annual summer temperatures are not consistently increasing across the Great Plains but daily record high temperatures have increased since the 1980s. Heatwaves that predispose droughts are frequent in the Great Plains and increasing in both frequency and intensity, even though precipitation has also increased across the Great Plains (Wuebbles *et al.* 2017).

Several models are used for predicting outcomes of climate change. Two prominent projection models are used to estimate warming: RCP4.5 and RCP8.5 correspond with lower and higher greenhouse gas emissions concentrations, respectively (IPCC-AR5 2013). Projection models of both near-term (1-3 decades; 2030-2050) and long-term (5-8 decades; 2070-2100) duration indicate rising annual average temperatures. Under the two emission scenarios, RCP4.5 and RCP8.5, annual average temperature of the northern Great Plains is projected to rise 2 – 3 °C in the near-term and 3 – 6 °C in the long-term (Wuebbles *et al.* 2017). In the southern Great Plains, annual average temperature is projected to rise 1 – 2 °C in the near-term and 2 – 5 °C in the long-term. Cook et al. (2015) evaluated the last 1,000 years of the Great Plains using the Palmer Drought Severity Index (PDSI). The record includes "megadroughts" that endured for approximately 35 years. Droughts projected for late 21st Century are likely to be more frequent and intense than 20th century averages with the probability of decadal droughts increasing from ~40% to >95%

and the probability of multi-decadal droughts increasing from ~10% to >80% under the RCP8.5 model (Cook *et al.* 2015). Droughts compound the effects of rising temperature on both plant and animal growth. We correlate climatic indicators, including temperature and drought, to measures of body size of *Bison*.

Bison provide an opportunity to evaluate the response of large herbivores to climate warming and drought. *Bison* in North America are monitored for production by census and by measures of BM and age (USDA 2016). The grasslands of the Great Plains have supported the greatest number of *Bison* since prehistoric times and currently supports ~75% of the extant population of 400,000 animals. Here we tested the hypothesis that *Bison* ABM declines with rising temperature and increasing drought, as a model for other large-bodied grazing ungulates, in the grasslands along the Great Plains using long-term and large-scale datasets.

3.3. Materials and Methods

3.3.1. *Bison* body size data assemblage

We assembled two independent datasets of *Bison* live BM and body size—one temporal and one spatial (Figure 3.1). Temporally, we modeled the relationship of annual measures of BM and body height (H; m) of 5773 *Bison* (3698 female; 2075 male) at Wind Cave National Park (WICA; site 8 in this study; Figure 3.2), Black Hills, South Dakota from 1966 to 2015. Spatially, we used photogrammetry to measure H of 773 *Bison* (579 female; 194 male) to estimate BM and population ABM from Gompertz equations in 19 herds from Saskatchewan (52.2 °N) to Texas (30.7 °N), including WICA (43.6 °N; Figure 1), during the summer of 2017 and following winter of 2017-2018. Studies were approved for animal use by the Agriculture Animal Care and Use Committee (Study #2017-015A, Texas A&M AgriLife Research) and for use of restricted imaging technology (#17-02-007, Texas A&M AgriLife Research; Appendix B). Data are available on Dryad Data Repository (Martin and Barboza, 2020), here: https://doi.org/10.5061/dryad.nvx0k6dnf.

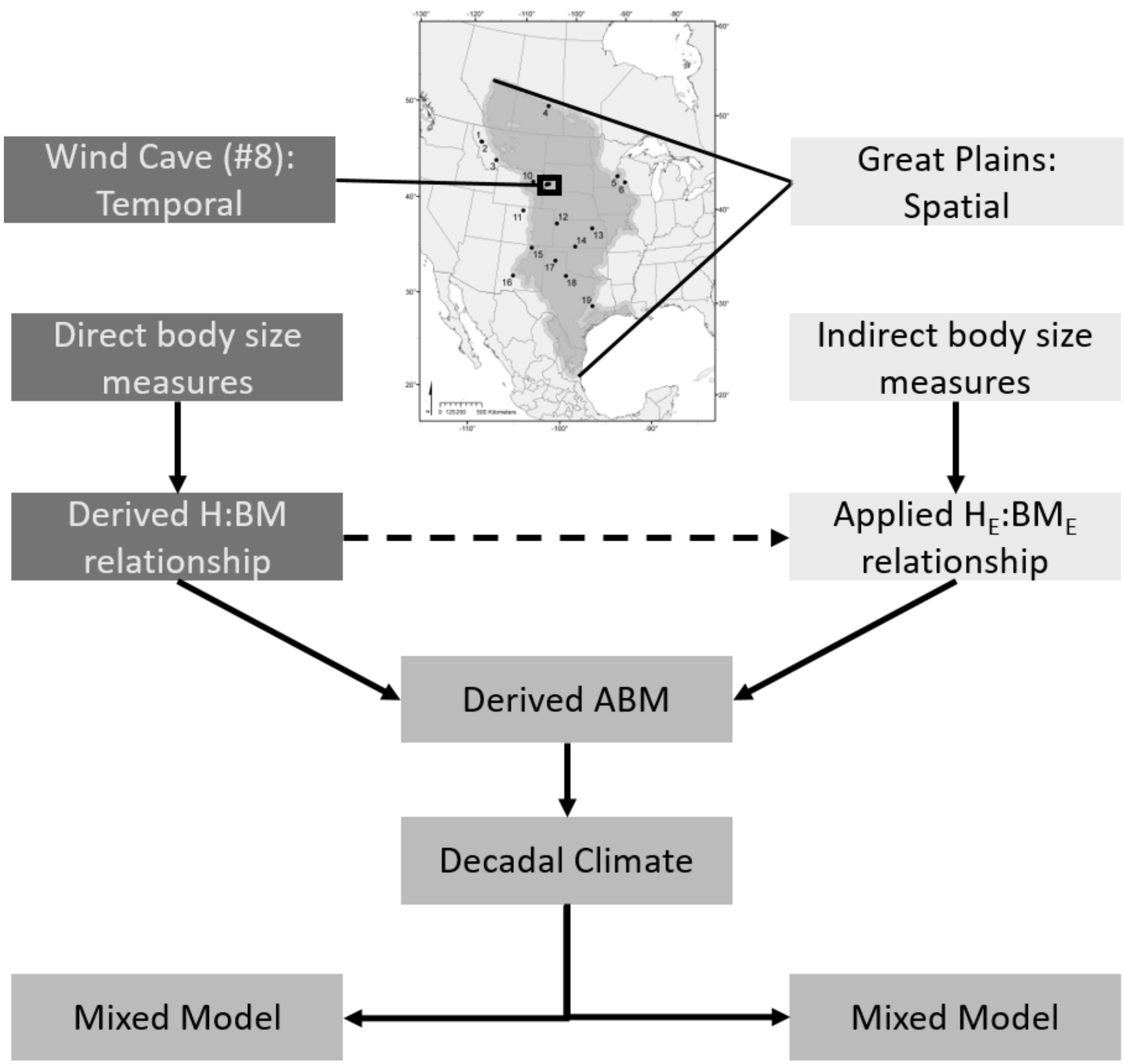

Figure 3.1. Conceptual chart of methodological design and hierarchical flow of data and analyses for the temporal dataset from Wind Cave National Park (1966–2015) and the spatial dataset from the Great Plains (summer 2017 and winter 2018). Reprinted from Martin and Barboza (2020a).

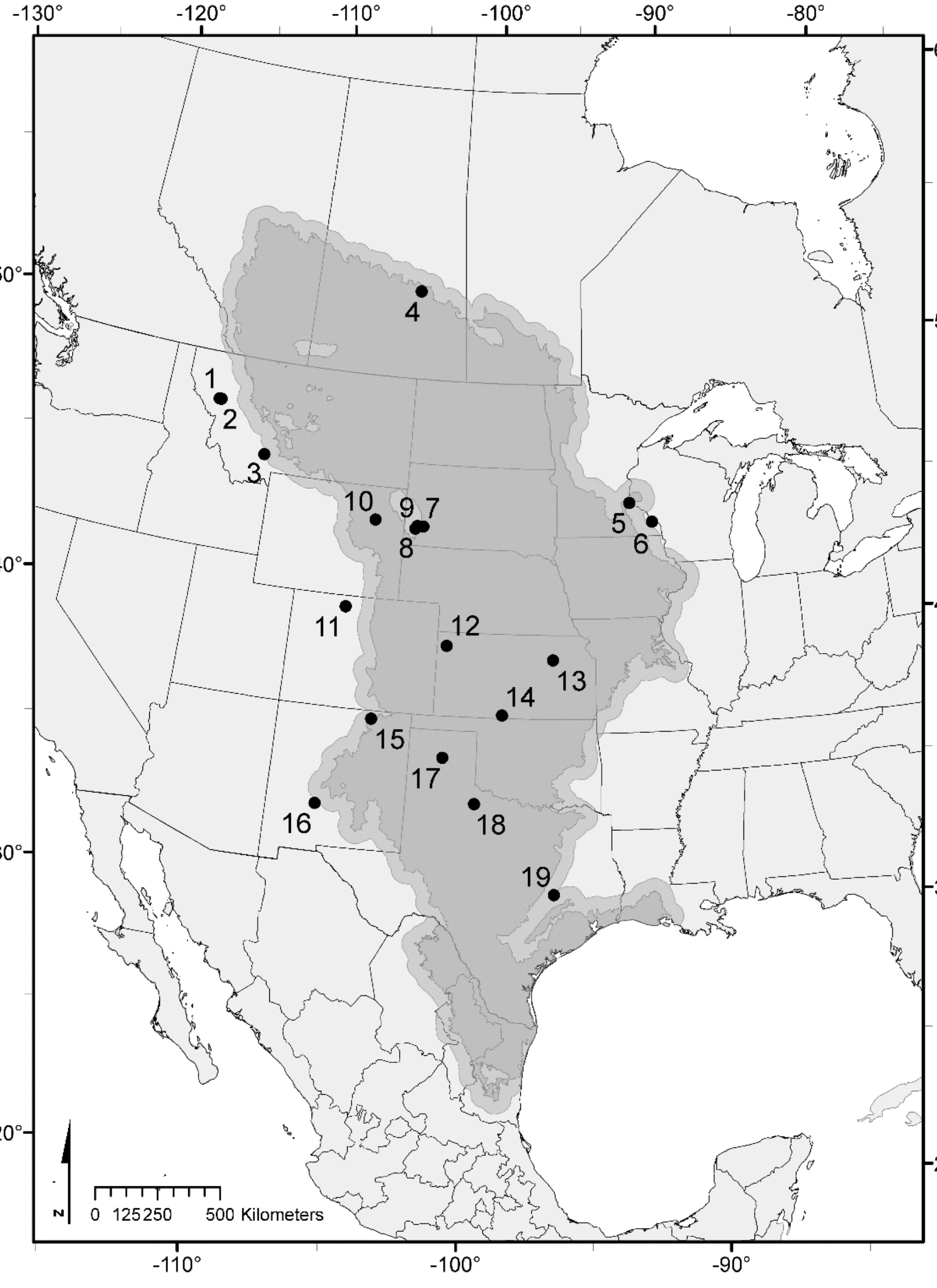

Figure 3.2. Spatial distribution of *Bison* study herds along the Great Plains of North America. Locality number corresponds to Appendix Table A1 and Appendix Table A2. Map geographic coordinate system is NAD83 and projection is USA Contiguous

Albers Equal Area Conic USGS. Note: Wind Cave National Park in the Black Hills, South Dakota is marked as location 8. Reprinted from Martin and Barboza (2020a).

The temporal dataset included 13,313 direct measures of BM and H over the last five decades from one location, WICA. *Bison* measures of BM (± 1 lb or ± 0.45 kg) and H (± 0.5 in or ± 1.27 cm) were collected annually starting from 6-months of age each autumn at WICA between 1966 and 1968 and again from 1983 through 2015. The spatial dataset included 1,995 photogrammetric images collected from 19 localities over the summer of 2017 and the following winter of 2017-2018 along the Great Plains, including WICA. *Bison* BM was predicted from H using the same Gompertz-Laird model (hereafter referred to as Gompertz; Tjørve & Tjørve, 2017) for both males and females (Equation 3.1). We chose the Gompertz model over the exponential curve because *Bison* growth is not indeterminate (Appendix C Figure 9.1 and Appendix C Figure 9.2). *Bison* BM was also predicted from age (years) using separate sex specific Gompertz models (Equation 3.2). We compared the outputs of the Gompertz growth models using 2010s-decade females from WICA with the WICA females from the spatial dataset (Appendix C Figure 9.3; Appendix C Table 9.1). Age determination of individuals in the spatial dataset were approximate and based on curvature and relative size of the horns. Ontogenetic horn size, shape, and topology is described in Skinner and Kaisen (1947, pp. 146–147 and plates 8-9), Fuller (1959), and Hornaday (1889).

Equation 3.1. $\boldsymbol{BM = b1 * exp\left(\text{-}exp\left(\text{-}b2 * (H - b3)\right)\right)}$

Equation 3.2. $\boldsymbol{BM = b1 * exp\left(-exp\left(-b2 * (age - b3)\right)\right)}$

3.3.2. Climatic data assemblage

We used mean decadal temperature (MDT), mean decadal precipitation (MDP), and mean decadal Palmer Drought Severity Index (dPDSI) to model the effects of climate on ABM. Corresponding measures of climate were obtained from United States National Oceanic and Atmospheric Administration (NOAA) Gridded Climate Divisional Dataset (CLIMDIV; version 1.0.0) database (Vose *et al.* 2014).

3.3.3. Photogrammetry

We used a forward looking infrared thermal camera (FLIR T1030sc; FLIR Systems, Wilsonville, OR, USA) with a 12° × 9° lens (f/1.2) to capture still images of *Bison* in the lateral view (Figure 3.3) to measure H (Shrader *et al.* 2006, Berger 2012). Infrared images had resolution of 1024 × 768 pixels. We captured 1,995 thermal images, of which 782 were suitable for photogrammetry. We validated photogrammetric estimated measures of height (Appendix C Figure 9.4) and measures of *Bison* body size in several postures, height was the most consistent measure of body size; likely related to the topology of head and neck movement (Appendix C Figure 9.5).

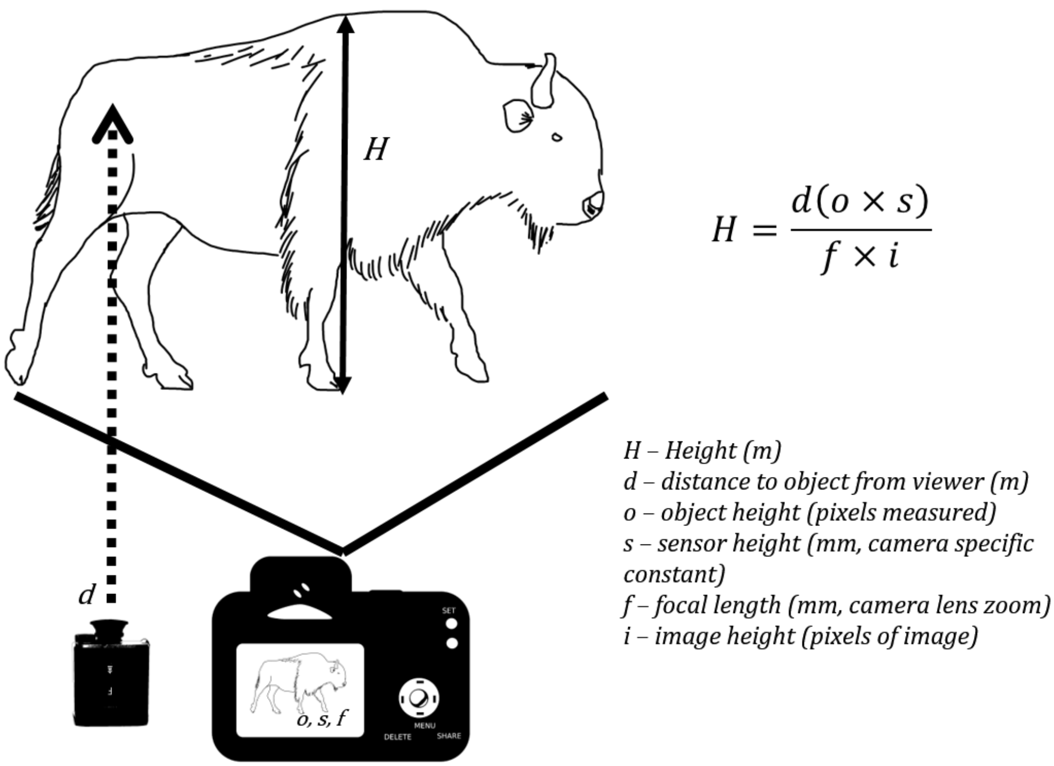

Figure 3.3. Photogrammetric technique for measuring body size dimensions (*H*) of *Bison* in lateral view using a laser rangefinder (lower left, *d*) and digital camera (lower center, *o,s,f*). The generalized photogrammetric equation for calculating the real-world measurement (*H*) of an object in a photograph (mm) is provided (upper right). Abbreviations: *d* is measured distance from camera to object (m) obtained by a laser rangefinder; *o* is relative digital length of the object of interest in the photograph (pixels); *s* is sensor height of the camera (mm); *f* is focal length of the lens (mm); *i* is total picture height (pixels); and *H* is height of the animal. Reprinted from Martin and Barboza (2020a).

Distance measures of *Bison* for photogrammetric techniques were determined using an RX-1200i TBR/W Leupold digital laser rangefinder (Leupold & Stevens, Inc., Beaverton, OR, USA) at 0.46 m accuracy. We used the upper rear leg of *Bison* as a standard target for distance measurement using the range finder, that is, we aimed for the center of the femur as our target for the distance measure. The hind-quarter was chosen because of the reduced variability in distance measures in comparison with the fore-quarters, likely due to the increasing refraction of the laser in the dense hair on the fore-quarters.

3.3.4. Computation and statistical analyses

Photogrammetric calibration on each image was performed in FLIR ResearchIR Max [version 4.40.1; 64-bit] software using the built-in focal length (83.2 mm) and spatial calibration tool (17 µm pixel pitch). All computations were performed in Stata/IC [v15.1, 2017, StataCorp, College Station, TX, USA]. We used 3-parameter Gompertz-Laird equations to estimate ABM and H against age (years). We binned the temporal dataset from WICA by decade of birth and used year of birth to relate individual data to annual climatic variables. Decadal measures of climate were used in the linear mixed model regressions as fixed effects, including MDT, MDP, dPDSI, and sex was also included to account for sexual dimorphism. Live BM and age were not included because these are already accounted for in the Gompertz curve to obtain ABM. Random effects were included in the models to account for repeated measures of individuals in the temporal dataset of WICA (i.e. decade of birth and individual identification) as well as the spatial dataset of the Great Plains (i.e. site and decade of birth). Environmental variable selection for each model were parsed using “best subsets variable selection” and “multi-model inference using information criteria” based upon Akaike information criterion values in “gvselect” and “miinc” packages for Stata, respectively (Guimaraes and Portugal 2010, Rabe-Hesketh and Skrondal 2012). We used the robust “sandwich estimator” to relax assumptions of normal distribution and homogeneity of variance for regressions (Bolker *et al.* 2009, Rabe-Hesketh and Skrondal 2012).

3.4. Results

3.4.1. Climatic context: spatial and temporal heterogeneity

Decadal temperatures (MDT) and index values for drought (dPDSI) increased at WICA in the Black Hills of South Dakota between 1895 and 2018, Figure 3.4 (Vose *et al.* 2014). A decrease in PDSI value refers to increasing drought—or decreasing water availability (Cook *et al.* 2015). In the 20th century, the Black Hills mean annual temperature was 6.2 ± 0.8 °C, mean annual precipitation was 509.8 ± 101.3 mm, and the average PDSI was 1.28 ± 2.97, whereas in the beginning of the 21st century, the Black Hills mean temperature was 7.1 ± 0.8 °C, mean annual precipitation was 517.2 ± 99.6 mm, and the average PDSI was 0.02 ± 3.02. In summary, the Black Hills have risen in temperature by 0.9 °C, increased annual precipitation by 7.4 mm, and increased in drought severity (Figure 3.4).

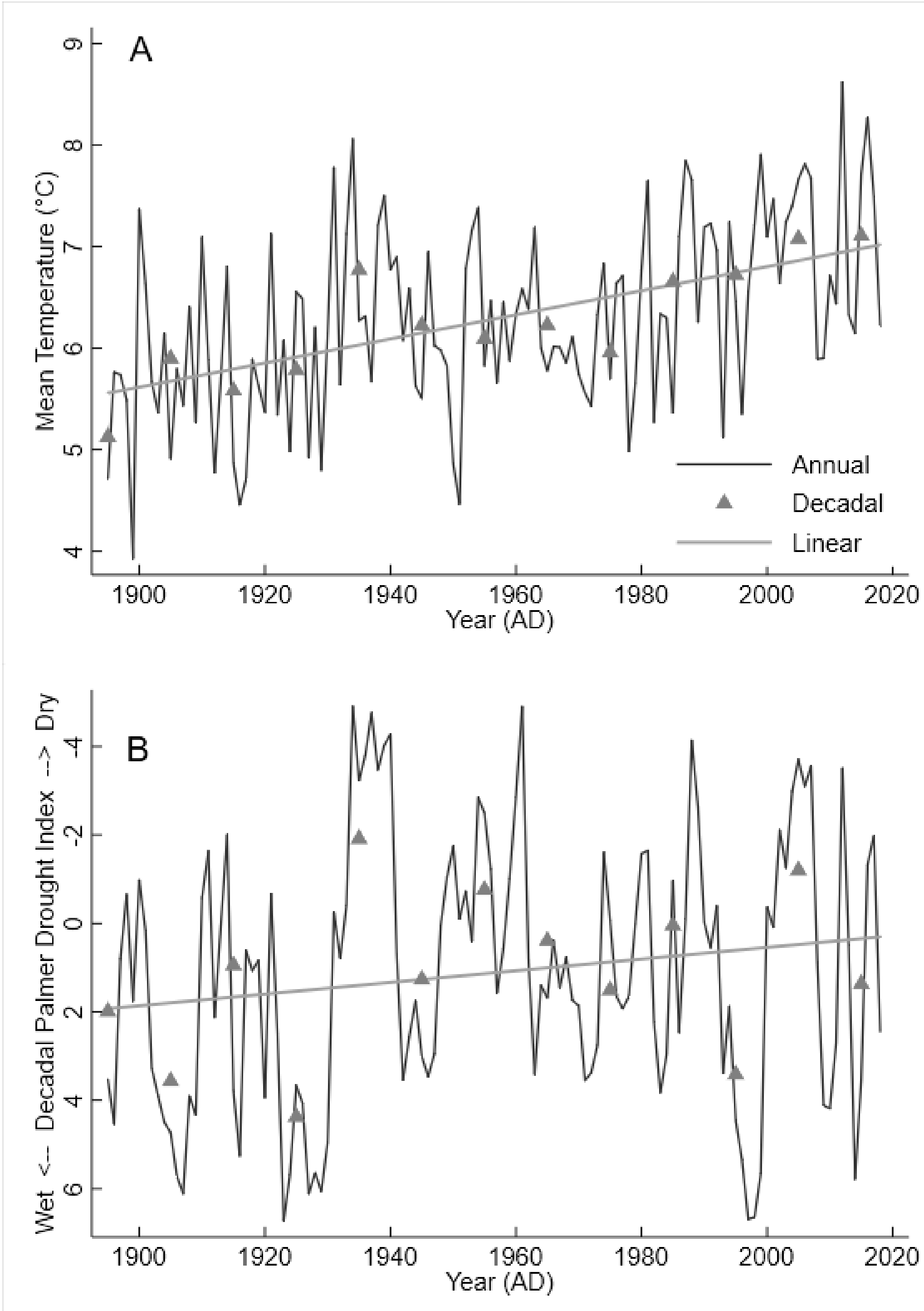

Figure 3.4. Wind Cave National Park in the Black Hills, South Dakota, (A) temperature and (B) drought profile from 1895 to 2018. Key: (A) mean annual

temperature (MAT, black line), mean decadal temperature (MDT, gray triangles), and linear trend (gray line); (B) mean annual Palmer Drought Severity Index (aPDSI, black line), mean decadal Palmer Drought Severity Index (dPDSI, gray triangle), and linear trends (gray line). Data are from Vose et al. (2014). Reprinted from Martin and Barboza (2020a).

The average conditions for our 19 study sites on the Great Plains in the 20th century, were: mean annual temperature was 9.3 ± 4.6 °C (range 1.7 °C – 20.0 °C), mean annual precipitation was 604.1 ± 240.5 mm, and the average PDSI was 0.48 ± 2.2. At the beginning of the 21st century, the Great Plains mean temperature was 10.2 ± 4.6 °C (range 3.4 °C – 20.1 °C), mean annual precipitation was 620.2 ± 260.2 mm, and the average PDSI was -0.04 ± 2.3. In summary, the means for study sites along the Great Plains have risen in temperature by 0.9 °C, increased annual precipitation by 16.1 mm, and increased in drought severity (Figure 3.5).

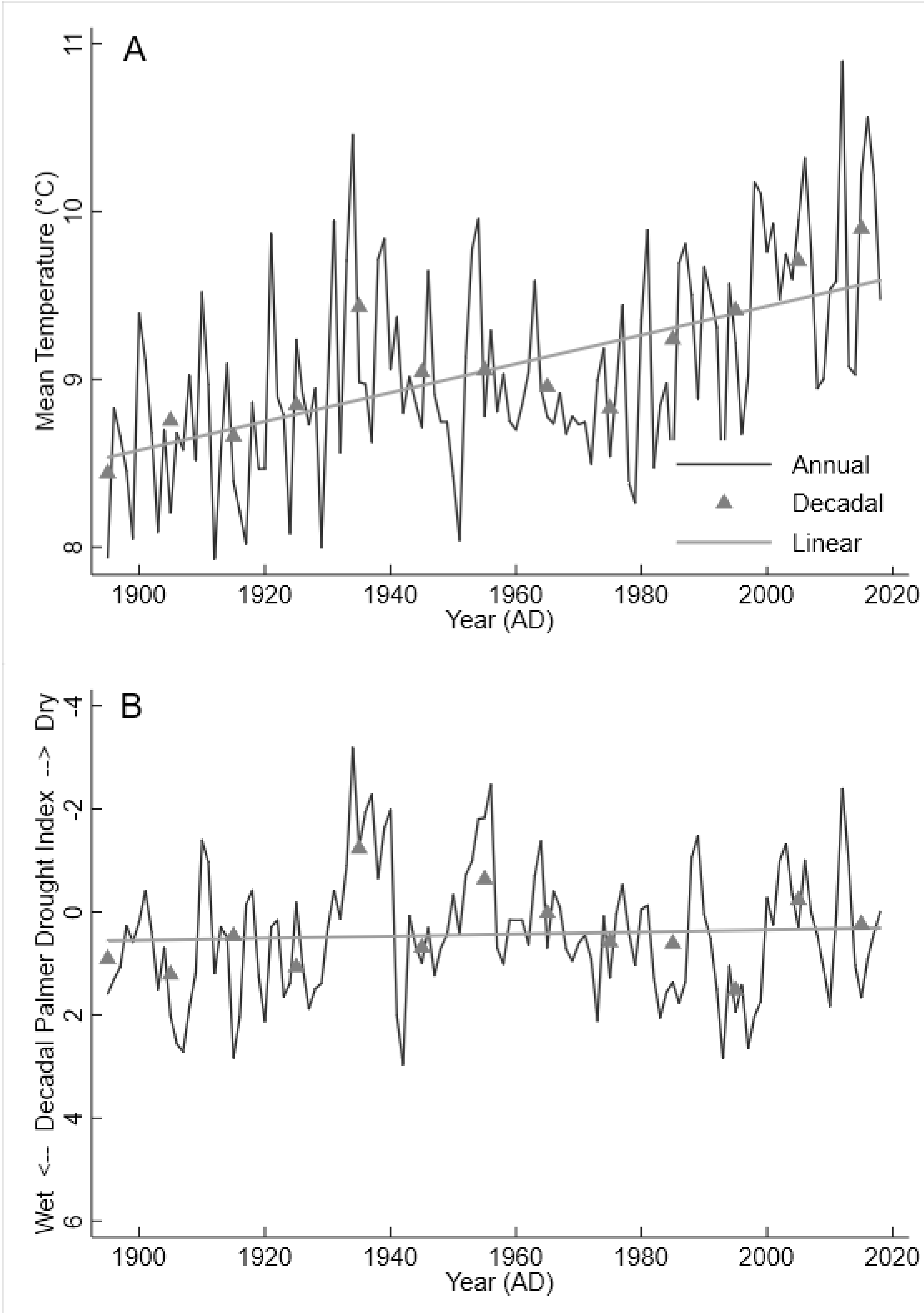

Figure 3.5. Average environmental conditions for 19 study sites along the Great Plains. Key: (A) temperature and (B) drought profile the from 1895 to 2018. Key: (A)

mean annual temperature (MAT, black line), mean decadal temperature (MDT, gray triangle), and linear trend (gray line) and (B) mean annual Palmer Drought Severity Index (aPDSI, black line), mean decadal Palmer Drought Severity Index (dPDSI, gray triangle), and linear trend (gray line). Data are from Vose et al. (2014). Reprinted from Martin and Barboza (2020a).

We used 13,313 records of BM (4,886 males; 8,427 females) with 13,062 corresponding records of age (4,871 males; 8,191 females) and 3,178 corresponding records of H (1,042 males; 2,136 females) for *Bison* at WICA. The dataset included 2,453 single observations of BM and 5,781 repeated observations of BM which included up to 18 measures from 36 individuals. Among females, average mass was 344.2 ± 104.8 kg (median 381.0 kg; range 27.6 – 646.4 kg; n = 3698) average age was 7.0 ± 5.4 years (median 5.5 y; range 0.5 – 23.5 y; Appendix C Table 9.3). Among males, average mass was 331.6 ± 146.7 kg (median 294.8 kg; range 21.8 – 936.7 kg; n = 2083) and average age 2.8 ± 1.6 years (median 2.5 y; range 0.5 – 17.5 years).

3.4.2. Photogrammetry

Variation in the position of the head and neck had a greater effect on estimates of body length than those of body height. Consequently, measures of H was more reproducible and thus more reliable than those of body length as a metric of body size (Appendix C Figure 9.4–9.5). We used 782 images (194 males; 579 females) to measure H of *Bison* from 19 localities across the Great Plains (Figure 3.2 and Appendix C Figure 9.6). Among females, average mass was 320.5 ± 89.8 kg (range 36.3 – 579.4 kg) and average age was 4.1 ± 3.2 years (median 4.0 y; range 0.2 – 15.0 years). Among males, average mass was 394.6 ± 139.4 kg (range 59.6 – 745.1 kg; n = 194) and average age was 2.8 ± 2.7 years (median 2.0 y; range 0.2 – 12.0 years).

3.4.3. Growth calculations: asymptotic body mass (ABM)

We modeled the relationship of H to BM for females (♀) and males (♂) in the temporal dataset of WICA (Equation 3.3 and Equation 3.4) and applied the output, presented in Appendix C Table 9.4, to the spatial dataset of the Great Plains to estimate BM from H. Note, that b3—the inflection point for BM—is negative because the model predicts the intercept at H = 0 m.

Equation 3.3. $\boldsymbol{BM♀ = 756.4 * exp\left(-exp(-2.6 * (H - 1.2))\right)}$

Equation 3.4. $\boldsymbol{BM♂ = 9573.9 * exp\left(-exp(-0.6 * (H - 3.2))\right)}$

We modeled the relationship of BM to age (years) in the temporal dataset of WICA (Equation 3.2; Appendix C Table 9.5; Figure 3.6). Estimated ABM of females was 428.2 ± 1.1 kg, whereas ABM was estimated at 742.0 ± 8.9 kg for males at WICA (Figure 3.5). We compared the decades of the 1960s with the 2010s at WICA, over which there was an increase in MDT of 0.9 °C. Females declined by 47.5 kg in ABM (Figure 3.7, Appendix C Table 9.1)—444.5 ± 8.6 kg (*n* = 338) to 397.0 ± 6.5 kg (*n* = 274)—whereas males declined by 186.1 kg in ABM—797.9 ± 41.9 kg (*n* = 252) to 611.8 ± 47.5 kg (*n* = 190). Along the Great Plains, females (*n* = 579) were estimated to achieve ABM of 362.2 ± 3.6 kg, whereas males (*n* = 194) were estimated to achieve ABM of 532.5 ± 12.3 kg (Appendix C Table 9.6 and Appendix C Table 9.1 for locality and sex specific outputs).

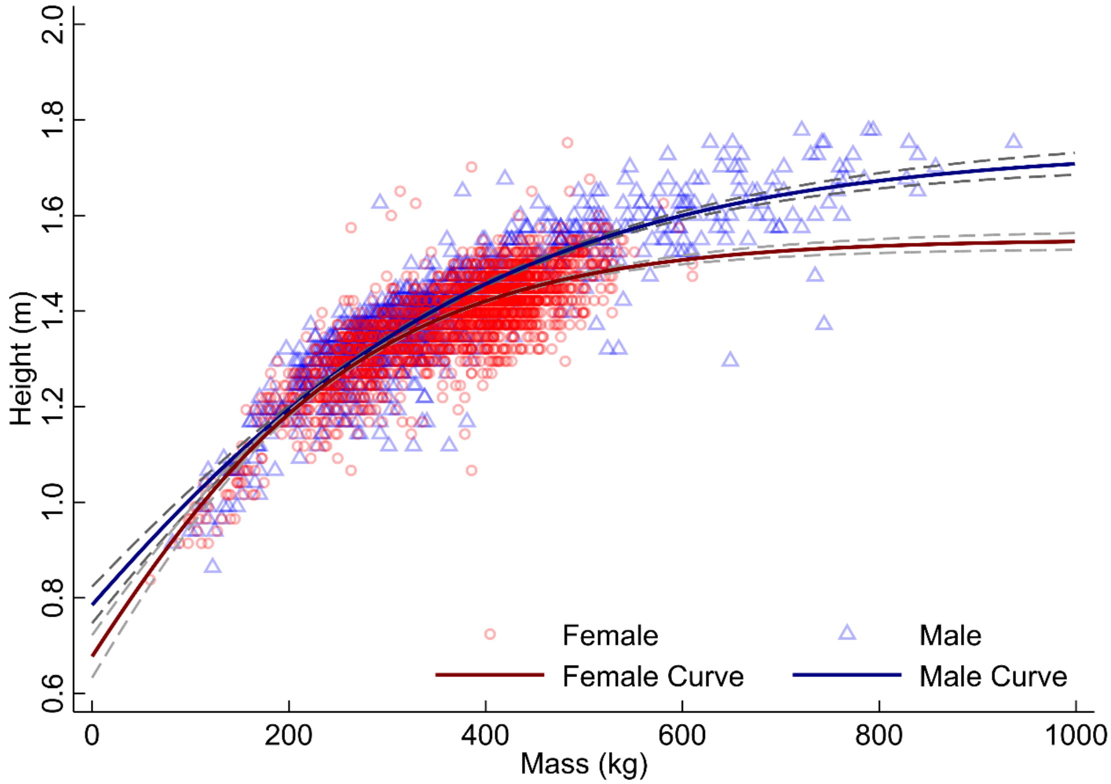

Figure 3.6. ***Bison*** **height (H m; log) and body mass (BM kg; log) over age (y) at WICA—1,042 males (blue open squares) and 2,136 females (red open circles). Reprinted from Martin and Barboza (2020a).**

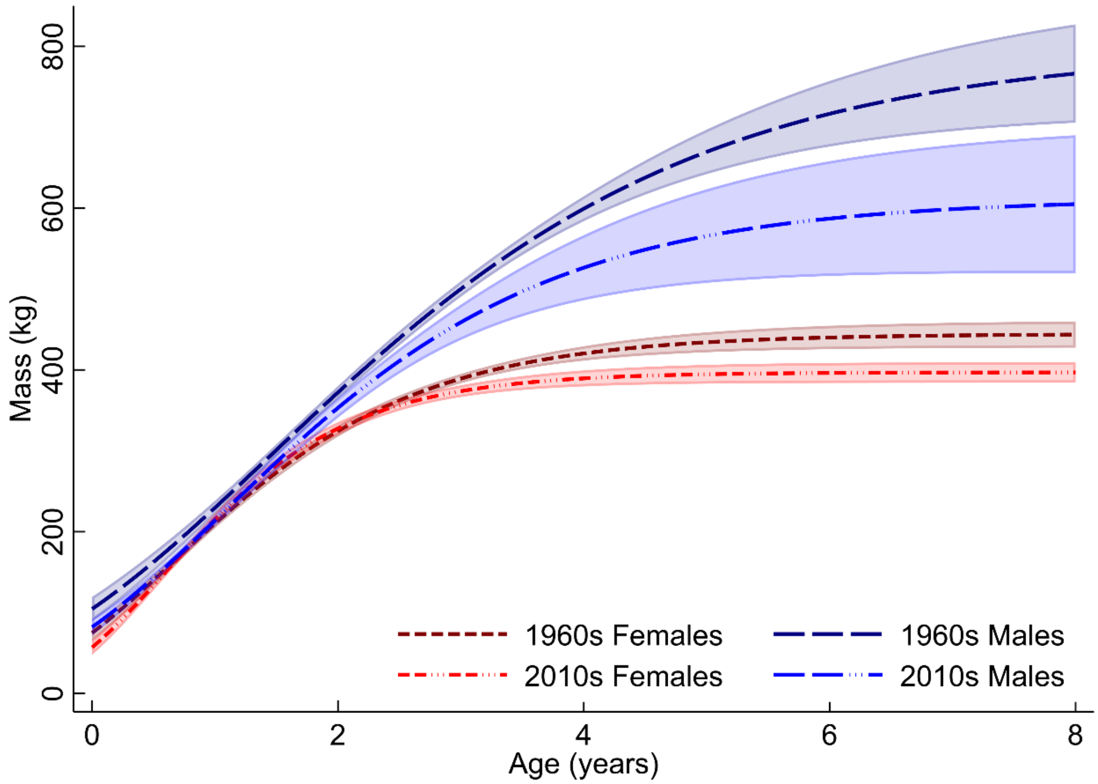

Figure 3.7. Decadal growth curves of *Bison* body mass over age at Wind Cave National Park, Black Hills, South Dakota between 1960s (dashed line) and 2010s (broken dashed line) when MDT increased by 1°C. Males (blue long dash) decreased in ABM by 186 kg and females (red short dash) decreased by 48 kg. Reprinted from Martin and Barboza (2020a).

3.4.4. Climatic drivers of ABM

At WICA, male ABM declined with increasing MDT and decreased with drought severity (dPDSI; a positive PDSI value indicates increasing wetness) in the temporal model for growth (Table 3.1; Figure 3.8a,b). In the spatial model for growth, *Bison* ABM decreased with increasing MDT and ABM decreased with drought severity (dPDSI; Table 3.1; Figure 3.8c,d).

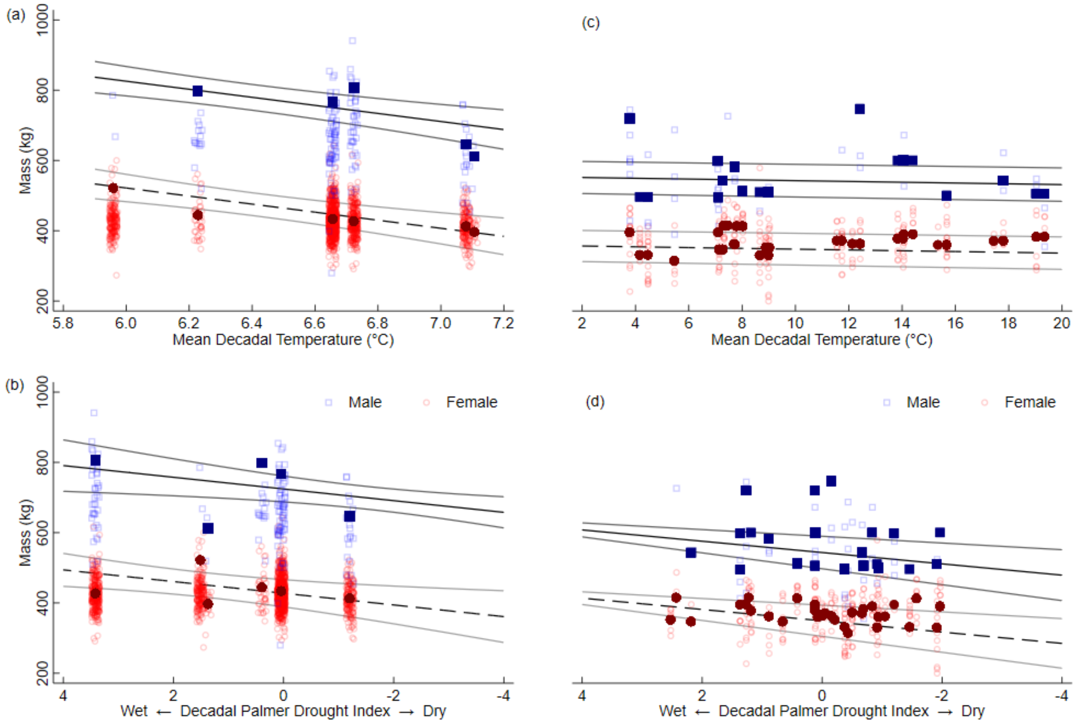

Figure 3.8. (a) Asymptotic body mass (ABM, kg) of male (solid blue squares) and female (solid red circles) *Bison* at Wind Cave National Park, South Dakota, in relationship to mean decadal temperature and (b) decadal Palmer Drought Index for the 1960s–2010s. Analyzed using multilevel mixed-effects model (Table 1). Observed body mass (BM, kg) of males (open blue squares) and females (open red circles) of four years of age and above plotted for reference. ABM was estimated with the Gompertz–Laird models using observed age and BM measures (males: 0.5–17.5 years, n = 2,075; females: 0.5–23.5 years, n = 3,698). (c) ABM of male (solid blue squares) and female (solid red circles) *Bison* along the Great Plains in relationship to mean decadal temperature and (d) decadal Palmer Drought Severity Index. Analyzed using multilevel mixed-effects model (Table 1). Observed BM of males (open blue squares) and females (open red circles) ≥4 years is plotted for reference. ABM was estimated with the Gompertz–Laird models using observed age and BM measures (males: 0.1–12 years, n = 194; females: 0.1– 15.0 years, *n* = 579). Reprinted from Martin and Barboza (2020a).

Table 3.1. Summary table of temporal (WICA) and spatial multilevel mixed effects general linear models of ABM with fixed effects of sex, and decadal measures of drought and temperature. Abbreviations: β, beta coefficient; FE, fixed effect; RE, random effect; LB, lower bound; UB, upper bound; SD, standard deviation; SE standard error; DoB, decade of birth; id, animal identification; dPDSI, mean decadal Palmer Drought Severity Index; and MDT, mean decadal temperature.

Parameter	β	SE	*z*	*p*	LB	UB
			Temporal Model			
FE: Female (x_1)	-304.9	0.8	-367.1	< 0.001	-306.5	-303.3
FE: dPDSI (x_2)	16.6	7.0	2.4	0.017	2.9	30.4
FE: MDT (x_3)	-114.9	24.1	-4.8	< 0.001	-162.0	-67.4
β_0 (constant)	1501.4	161.5	9.3	< 0.001	1184.8	1818.0
RE: DoB:id (ϵ)	0.0	0.0	--	--	0.0	0.0
SD of model	27.2	5.2	--	--	18.7	39.6
			Spatial Model			
FE: Female (x_1)	-193.6	1.0	-186.8	< 0.001	-195.6	-191.5
FE: dPDSI (x_2)	16.2	3.2	5.0	< 0.001	9.8	22.7
FE: MDT (x_3)	-1.1	0.0	-28.2	< 0.001	-1.2	-1.1
β_0 (constant)	554.1	22.8	24.27	< 0.001	509.4	598.9
RE: DoB:Site (ϵ)	2.4	131.0	--	--	0.8	7.2
SD of model	39.7	1.4	--	--	38.6	40.8

3.5. Discussion

Our data indicate that temperature and its combination with water restrictions in drought drive growth of *Bison*. Mean decadal temperatures had a greater effect on *Bison* ABM at one location—WICA—than across the multiple study sites along the Great Plains. Drought decreased ABM of *Bison* likely because of declines in plant productivity and water availability across the landscape. Temporal variation in primary productivity, water availability, and heat stress likely cause declines in ABM of *Bison* within sites at single locations such as WICA. *Bison* body size and ABM is likely to decline over the next five decades throughout the Great Plains where increases in annual and decadal temperatures and both the frequency and intensity of droughts are projected.

3.5.1. Model application and validation

Our estimates of ABM of *Bison* on the Great Plains can be compared with observations of *Bison* in other populations to evaluate the model. Table 3.2 includes the climatic variables of decadal drought and temperature for four comparisons. We include a population of *Bison* oustide the Great Plains in southwestern California (Division 6 of California, NOAA Gridded Climate Divisional Dataset (Vose *et al.* 2014)) on Santa Catalina Island (SCI) in two decadal periods (1970s and 2000s). We also include a forecast for the Southern Great Plains by year 2100 and a backcast for the Great Plains to the Last Glacial Maximum (~22,000 years ago). Our model is conservative because predicted ABMs are below the body masses observed in each comparison. The model may be better suited to predicting ABM under hot and dry conditions because predicted ABM of fossil *Bison* are 38% below the estimated mass whereas comparisons for hot and dry conditions result in predictions of ABM that are less than 6% of the observed mass. *Bison* on SCI are outside of the study area in which we developed our model. SCI *Bison* have been on the island since 1924, well adapted to the local environment today, thriving in fact, requiring contraceptives to manage the population (Duncan *et al.* 2013). The *Bison* at SCI are described as diminutive—321 kg for females and 524 kg for males (Derr *et al.* 2012) whereas continental female *Bison* are 441 kg and 699 kg for males (this study). Although genetic effects may be involved, it is likely that the small body size of this isolated population is also due to life on a shrinking, warming, drying island.

Large *Bison* may be better represented in the fossil record because large bones are more detectable and more likely to survive taphonomy. Large *Bison* may be under represented in long term data sets such as those collected at WICA because mature bulls are dangerous to handle and destructive to handling systems and scales (Licht and Johnson 2018). Reduction in observations of large, mature bulls at WICA since the 2000s may have reduced the expected ABM and age due to artificial selection bias. Additional photogrammetric studies may aid in generating observations for mature bulls and otherwise un-weighed *Bison* populations across North America.

Table 3.2. Comparison of *Bison* asymptotic body mass (ABM; kg) case studies across space and time. *Bison* ABM were calculated using the following equation from the spatial dataset (this study): ABM (± 39.7 kg) = 554.1 - 193.6 × Sex [1: Female (F), 0: Male (M)] - 1.1 × MDT + 16.2 × dPDSI. Observed climate data from NOAA's Gridded Climate Divisional Dataset (Vose *et al.* 2014) and predicted temperature data are from Wuebbles et al. (2017) for southern Great Plains (South GP) and projected drought data from Cook et al. (2015). Both population average and sex-specific ABM are provided for comparison with modern and fossil datasets.

Locality	Decade (AD)	MDT (°C)	dPDSI	Sex	Predicted ABM	Population average	Recorded ABM	Difference (%)
SCI, CA[1]	1970s	15.0	-0.2	F	341	438	362	-5.9
				M	534		--	--
SCI, CA[2]	2000s	16.0	-1.5	F	319	416	321	-0.7
				M	512		524	-2.3
South GP[3] (RCP8.5)	2100s	25.0	-5.0	F	252	349	357[3]	-2.3
				M	446			
Last Glacial Maximum[4]	22,000 years ago	-20.0	5.0	F	469	566	910[3]	-37.8
				M	663			

[1] Santa Catalina Island body mass from Lott and Galland (1987).

[2] Santa Catalina Island body mass from Derr et al. (2012).

[3] Southern Great Plains, Projection from RCP8.5 for long-term and high emission scenarios (IPCC-AR5 2013, USGCRP 2018).

[4] Reconstructed and projected climate data and modeled population body mass from Martin et al. (2018).

3.5.2. Additional drivers of body size

Body size of *Bison* has been related to genetics (Derr *et al.* 2012), and changes in foraging condition (Tieszen *et al.* 1998) due to timing and variability of precipitation

(Craine *et al.* 2013, Licht and Johnson 2018). Derr et al., (2012) present that *Bos taurus* introgression with *Bison* appears geographically widespread throughout North America, yet at low levels of detection (~10%)—citing early conservationists cross-breeding tactics to save the species from extinction. However, various authors (White and Wallen 2012, Licht 2017) genetic introgression only accounts for 2–9% of body mass variation in plains *Bison*. It remains unclear if changes in forage composition have affected body size change of *Bison* even though diet selection varies between males and females (Post *et al.* 2001, Mooring *et al.* 2005). Precipitation was not included in our spatial and temporal models for ABM even though the significant effect of drought implies that water availability and its interaction with temperature drives body size of *Bison*. Drought indicators—dPDSI and PDSI—may be useful to determine sub-decadal to annual cohort body sizes of *Bison* and other wildlife (Pigeon *et al.* 2017, Licht and Johnson 2018). Climate change and land use/land cover change are of a growing concern and threat to sustained and improving conservation for *Bison* and their grassland habitats.

An additional explanation for body size diminution, unmeasured in this dataset, is the unintentional consequence of selecting against larger more aggressive individuals when gate-cutting animals to be culled. That is, larger more brazen individuals are typically the first and in the front in a group of bison to go through a gate of a sorting pen. If a quota is set to cull animals, often it is easiest and most efficient to select using the first-come first-culled method. The result being an unintentional selection against the largest within each cohort. Repeating this technique for 5 decades may explain some of the results observed at

Wind Cave National Park. The preponderance of all 19 examined bison herds sharing a shrinking trend between the 2000s and 2010s, suggests climate change is the likely driver.

3.5.3. Life history consequences of body size change

We would expect that changes in body size of *Bison* would be associated with changes in life history (Peters 1983). Korec et al. (2019) reported median lifespan of North American *Bison* for females at 6.6 years (n = 1612) and males at 2.1 years (n = 1300). We estimate median lifespan for females was 5.5 years (n = 714; average 7.0 ± 5.4 years) and males was 2.5 years (n = 307; average 2.8 ± 1.6 years) in the WICA dataset based on the last observed record of each individual. Longevity of *Bison* may be shifting with declining body size at WICA because the 90th percentile of maximum age has declined from 21.5 years in 1970s to 17.5 years in the 1980s and 16.5 years in the 1990s. Reproductive strategies may also shift as female *Bison* decline in body size. Famoso et al. (2018) derived a threshold of 300 kg for mammals below which strategies for reproduction tended to *r*-selection. The SCI female population (ABM = 321 kg) is approaching this threshold and we predict that body size may decline further to 252 kg if temperatures and droughts rise as projected (MDT = 25 °C; dPDSI = -5.0). The combined effects of reproductive shifts under diminished forage production (desertification) and water availability may cause local extinction of *Bison* on SCI as well as in the Southern Great Plains (Nogués-Bravo *et al.* 2010, Rozzi 2018).

3.5.4. The upshot

We posit that being able to monitor both vast metapopulations and local subpopulations across spatial and temporal scales are paramount to monitor ecological changes throughout the Great Plains and prairies of North America (Kearney and Porter 2006, McGill *et al.* 2006a, 2006b, Barnosky *et al.* 2017). Photogrammetric methods has proven to be a useful technique for determining and monitoring relative and absolute changes in ABM for *Bison* sub-populations that are not often weighed on a scale (Berger 2012, Zein 2013, Weisgerber *et al.* 2015). Shifts in life history traits lacking proper adaptive management strategies may challenge sustainable conservation for wildlife species at large (Glick *et al.* 2011). Shifts in *Bison* growth across the Great Plains, ranging from Saskatchewan to Texas, may indicate physiological adaptation to local climate, however are more likely the result of persistent, chronic effects of warming and drying climates (Martin *et al.* 2018). Local adaptation of management may be needed to complement the adaptation of wildlife to the heterogeneity of plant growth and environmental demand along the Great Plains.

If *Bison* body size is declining in response to increasing temperature and drought, then projected climate change will further challenge growth and management of these animals and other large mammals (Elayadeth-Meethal *et al.* 2018). The North American *Bison* may be sentinels of global climate change impacts on the Great Plains and prairies of North America. Adaptive management of *Bison* to sustain populations in both harsh and lush environments without major human-induced changes to local food and water availability may provide a solution to sustainably managing wild and domestic herbivores in a variable climate.

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4. THERMAL BIOLOGY AND GROWTH OF BISON (*BISON BISON*) ALONG THE GREAT PLAINS‡

4.1. Synopsis

Body size of bison (*Bison bison*) declines with rising global temperature across the fossil record and rising annual temperatures across the Great Plains, but what are the underlying drivers? Body size depends on growth, which depends on maximizing net energy and nutrient flows for the production of tissues at seasonal scales across the range of the species. We measured thermoregulation costs of body surface temperature (°C) and heat exchanges (W and $W \bullet m^{-2}$) of 350 adult and 345 adolescent *Bison* from 19 herds in summer and winter along the Great Plains from Saskatchewan (52 °N) to Texas (30 °N). At the smallest scale, daily body surface temperature increased with solar radiation and decreased with relative humidity and wind speed, which is consistent with Kooijman's dynamic energy budget theory. Total surface heat transfer (W) increased with body mass (kg) at an exponent of 0.63 ± 0.03, which is consistent with Schmidt-Nielsen's principle of surface-area-to-volume ratios (b=0.67). On an annual scale, growth ($kg \bullet y^{-1}$) of adolescent *Bison* decreased with increasing total surface heat transfer (W) during summer, which supports Speakman and Król's heat dissipation limit theory. On the largest scale, heat flux was weakly related to latitude in summer and winter for adolescent *Bison*, which provides

‡ Martin, J. M., and P. S. Barboza. 2020b. Thermal biology and growth of bison (*Bison bison*) along the Great Plains: testing four theories of endotherm body size. Ecosphere. *In press.*

support for Bergmann’s rule and suggests a role for local primary production along the Great Plains. Cooler summers are more optimal for *Bison* growth because of reduced heat loads during the growing season. Rising temperatures are likely to constrain body size and productivity of *Bison* and other large endotherms in North America.

4.2. Introduction

Body size of bison (*Bison bison*) has shrunk by 31% (Martin et al. 2018) with rising mean global temperature since the last Ice Age and over the last 5 decades, body size of *Bison* has declined by 11–23% (Martin and Barboza 2020) with rising mean annual temperature along the Great Plains of North America, but what are the mechanisms driving temperature response? Maximum body size of endotherms depends on optimal growth of individuals and thus populations. Optimal growth depends on low costs of maintenance for the efficient production of tissues, especially in seasonal environments when food availability and environmental demands constrain the annual window for growth. High thermal loads increases costs of body maintenance to balance internal and external heat loads through thermoregulation, which ultimately reduces the energy available for growth. Heat loads are measured by heat flux ($W \cdot m^{-2}$) which measures the exchange of thermal energy between an animal and their environment. Here, we describe heat flux ($W \cdot m^{-2}$) and total surface heat transfer (W) of *Bison* as measures of thermal energy balance at small time scales and growth at seasonal and annual scales of time. Thermal balance is central to four theories that attempt to explain the change in body size of animals with warming from small to large scales of organization, space, and time:

1. Kooijman’s dynamic energy budget hypothesis (Kooijman 2000, Kearney 2012),

2. Schmidt-Nielsen’s body surface area to volume ratio (Schmidt-Nielsen 1970),
3. Speakman and Król’s heat dissipation limit hypothesis (Speakman and Król 2010, 2011), and
4. Bergmann’s rule (Bergmann 1847, Clauss et al. 2013).

Kooijman’s dynamic energy budget theorized that energy balances and thus micro-climates and weather affected heat transfer and energy use of animals on the landscape to ultimately affect life history. Schmidt-Nielsen theorized that allometric scaling of surface-area-to-volume ratio (b = 0.67) increased heat retention as animals increased body size, which would favor survival in cold environments for larger animals. Speakman and Król theorized that heat dissipation limits to thermoregulatory costs under rising heat loads limited reproduction and growth and affects life history and body size of animals. Bergmann’s rule predicts thermal conservatism of animals for cooler climates at higher latitudes will produce larger individuals within and across species than warmer climates at lower latitudes.

The theories of Bergmann and Schmidt-Nielsen emphasize selection for survival by reducing heat flux that results in a net loss of energy from the body during extreme cold and prolonged winters. The theories of Kooijman, Speakman and Król emphasize selection for growth and reproduction by controlling excessive heat flux during a short summer window of food availability with heat waves and drought. Bergmann and others predict that environmental selection is driven from north to south by winter bottlenecks in survival whereas Kooijman and others predict that environmental selection is driven from south to north by summer bottlenecks in production and reproduction. All the above theories ultimately are related to thermoregulation and heat exchange. While the above theories are not mutually exclusive, the integration of each may help understand and better predict endotherm response to a changing climate.

Thermoregulation is the cost of achieving heat balance. Thermoregulatory processes usually increase energy use by increasing heart rate and blood flow (e.g., vasodilation and metabolism). In hot weather, thermoregulation increases the flux of body water because water is used for evaporative cooling (e.g., panting and, to a lesser extent for *Bison*, perspiration). In cold weather, thermoregulation generates body heat (e.g., shivering, increasing metabolic heat production, and muscular activity) and conserves core body heat through control of blood flow to the periphery. Thermoregulation affects the use of energy, water, and nutrients such as electrolytes and organic nitrogen, which ultimately affects resting and foraging behaviors (Clarke 2017). High costs of energy are associated with high levels of heat transfer (e.g., thermal windows, Figure 4.1) and are quantified as heat flux ($W \bullet m^{-2}$). Thermography uses long-wave infrared radiation at 7.5–14 µm to record thermal windows (FLIR Systems 2017). We used a combination of photogrammetry and thermography, known as thermogrammetry, to quantify heat flux of *Bison* during both summer and winter seasons along the Great Plains (Figure 4.2) from central Saskatchewan to southeast Texas.

Figure 4.1. Side by side comparison of Left) a longwave forward looking infrared (FLIR) thermal spectrum image (pseudo color, lighter hues are hotter (i.e., thermal windows) and darker hues are cooler) and Right) a visible wavelength spectrum photograph of the same adult male *Bison* in western Montana, summer of 2017. Reprinted from Martin and Barboza (2020b).

The Great Plains (Figure 4.2) are predicted to warm (IPCC-AR5 2013, Wuebbles et al. 2017)—winters are more likely to shorten but the longer summers are likely to be hotter with more severe droughts (Fawcett et al. 2011, Cook et al. 2015, Cowan et al. 2017). *Bison* are resilient to short duration extreme weather events such as blizzards, dry spells, heat waves, or wildfires; however, chronic droughts and warming may affect long-term life history traits (Martin and Barboza 2020). Moreover, anticipated warming and drying along the Great Plains will shift the distribution of vegetation types by mid- and late-century to alter the supply of digestible energy and digestible nitrogen available to *Bison*, native wildlife, and domestic livestock (Tieszen et al. 1998, Craine et al. 2015, Briske 2017).

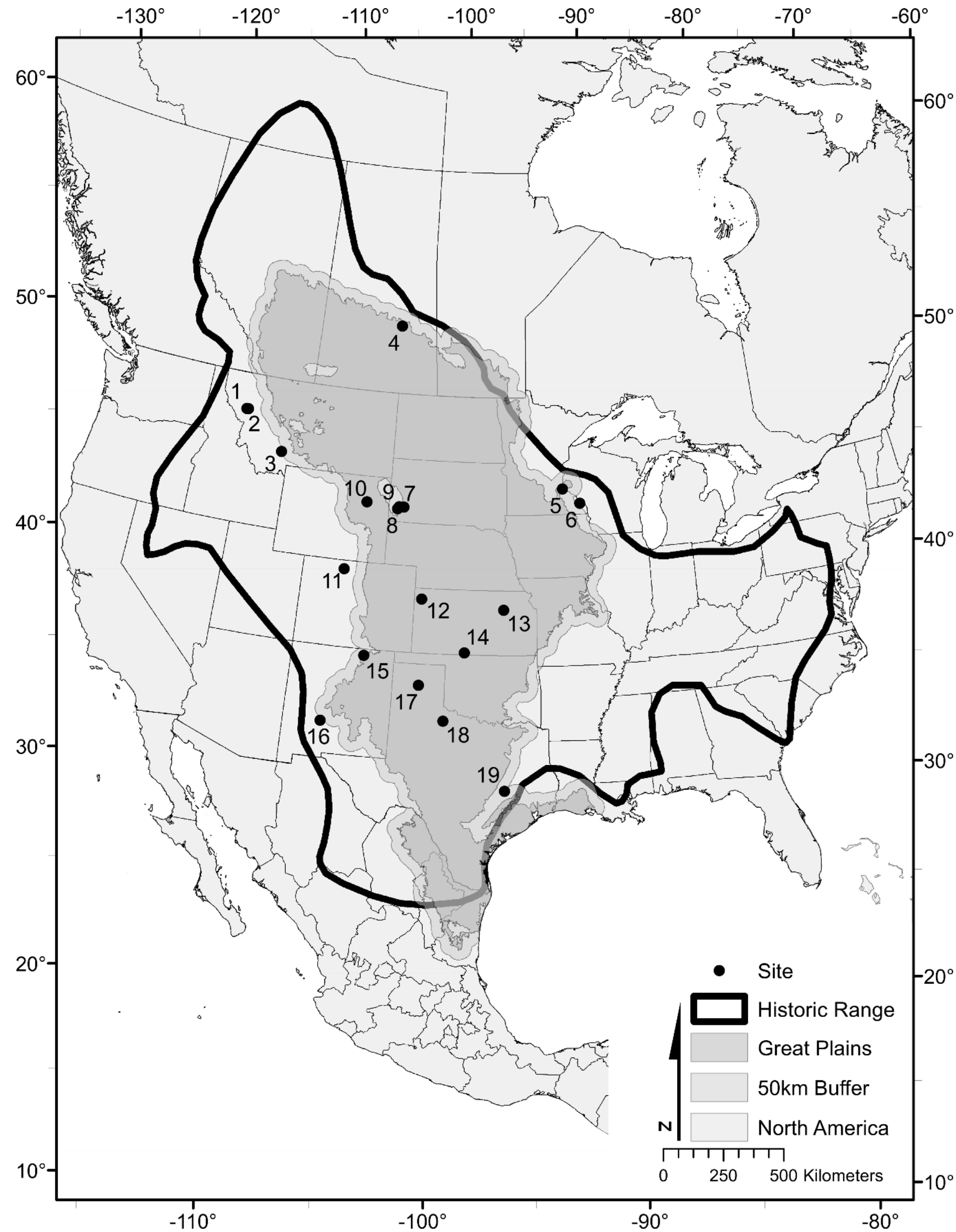

Figure 4.2. Map of the Great Plains and study sites in North America. Individual site numbers correspond with Table 4.1. Shaded area is the Great Plains ecoregion from EPA ecoregions level I (https://www.epa.gov/eco-research/ecoregions-north-america)

and the 50-km buffer is to demarcate transitional zones between other neighboring ecoregions. Historical bison range (thick solid black outline) is the pre-1870s distribution of *Bison* traced and georeferenced from Hornaday (1889). Reprinted from Martin and Barboza (2020b).

We use heat flux as an indicator of thermoregulatory effort to independently examine predictions from four complementary theories concerning body size and heat loads:

1. Kooijman (daily dynamic energy budget): total body surface temperature (°C) is driven by local weather conditions,
2. Schmidt-Nielsen (surface-area-to-volume ratio): total surface heat transfer (W) should increase over body mass (kg) and that logarithmic scaling of heat transfer and body size is allometric, predicting that b=0.67,
3. Speakman and Król (heat dissipation limit affects growth): growth rate ($kg•y^{-1}$) should increase with decreasing total surface heat transfer (W), and
4. Bergmann (latitudinal thermal conservatism): heat flux ($W•m^{-2}$) should increase from winter to summer and from north to south.

Finally, we test the general hypothesis that body size of endotherms is an outcome of reinforcing thermoregulatory effects on growth from immediate heat transfers to the body size eventually attained by the animal over several growing seasons in the population, that is, if all theories are supported, heat transfer processes spanning temporal and organizational scale to consistently drive body size.

4.3. Materials and Methods

4.3.1. Study design

We measured thermal exchange and heat loads of female *Bison* in adolescent (< 3 years) and adult (≥ 3 years) age classes that were growing along the Great Plains. In addition to thermal information, we also estimated body surface area (SA; m^2) and body mass (BM_E; kg) from body height (H_E; m) using photogrammetric techniques (Martin and Barboza 2020). We observed *Bison* in 19 herds during the summer of 2017 from North to South to measure *Bison* at the hottest time of the year over 46 days from 26 June through 11 August, spending 1 day for observations at each location from Saskatchewan, Canada (52.2 °N) to Texas, United States (30.7 °N). We returned to 16 herds in the winter of 2017-2018 by traveling from North to South to measure *Bison* at the coldest time of the year over 38 days from 26 December through 2 February. Each of our locality visits represented the typical seasonal conditions (Appendix D Figure 10.1). The three missed sites were excluded from follow-up observations because two were inaccessible due to blizzards (sites 1 and 2) and all the *Bison* from a third site had been removed from the range to enclosures because natural forage had been lost to an autumn wildfire (site 9). Collectively, the sites represent a mix of management by privately owned and non-governmental organizations as well as state and federal government agencies; the sites and their respective annual climate measures are presented in Table 4.1. Data are available on Figshare Data Repository (Martin and Barboza, 2020). DOI: 10.6084/m9.figshare.12084645.

Table 4.1 ***Bison*** **site number, name, sector, state/province, mean annual temperature (MAT; °C), and mean annual precipitation (MAP; mm). Abbreviations: USFWS, United States Fish and Wildlife Service-Department of the Interior; NPS, United States National Park Service-Department of the Interior; SDGFP, South Dakota Department of Game, Fish, and Parks; and TNC, The Nature Conservancy. Climate data are from NOAA (Vose et al. 2014, NOAA 2018).**

Site #	Site Name	Sector	State	MAT	MAP
1*	National Bison Range, USFWS	Federal	MT	5.5	807.5
2*	Montana Buffalo Gals	Private	MT	5.5	807.5
3	Flying D	Private	MT	4.5	547.2
4	Quill Creek	Private	SK	4.8	449.9
5	Long Ago Ranch	Private	WI	7.3	942.9
6	Rockie Hill Buffalo	Private	MN	7.5	958.2
7	777 Ranch	Private	SD	8.9	482.0
8	Wind Cave National Park, NPS	Federal	SD	7.1	554.0
9**	Custer State Park, SDGFP	State	SD	7.1	554.0
10	Durham Ranch	Private	WY	7.7	391.9
11	Eagles Wing	Private	CO	8.0	463.0
12	Beaver Creek	Private	KS	11.7	521.3

Table 4.1 Continued

Site #	Site Name	Sector	State	MAT	MAP
13	Konza Prairie Biological Station, TNC	NGO	KS	12.4	855.3
14	Z Bar Ranch	Private	KS	14.0	720.3
15	Vermejo Park	Private	NM	9.0	405.3
16	Armendaris Ranch	Private	NM	14.4	250.6
17	Herring Ranch	Private	TX	15.7	465.6
18	Y Ranch	Private	TX	17.8	600.2
19	Lucky B Bison	Private	TX	19.3	1230.1

*National Bison Range and adjacent private ranch, blizzard/snow storm prevented second visit in winter.

**Custer State Park had a fire in late 2017 (Legion Lake Wildfire), no repeat visit in winter.

4.3.1.1. Animal use and selection

Studies were approved for use of animals by the Agriculture Animal Care and Use Committee (AACUC study #2017-015A, Texas A&M AgriLife Research) and for use of restricted imaging technology under Technology Control Plan (TCP #17-02-007, Texas A&M AgriLife Research; Appendix B). *Bison* grow over several years to achieve asymptotic body size—typically by 3 years of age for females and by 5 years of age for males (Martin and Barboza 2020). Environmental demands during growth of *Bison* affect asymptotic body size. Although genetic variation among bison herds exists, merely 1-2% of height variation derives from genetic variation (Musani et al. 2006, White and Wallen 2012, Licht 2017). Moreover, height and body mass are tightly related and have little variation (Martin and Barboza 2020), with 80-96% variation of body mass explained by temperature and drought, that is, large phenotypic variation is not likely due to the existing small variations in genetic makeup. Here, we focused primarily on adolescent female *Bison*, between their birth and their third year, because they shape the foundation for subsequent generations and cohorts of the population; but, when explicitly stated, adults are included as a comparison group for analyses. We categorized adolescent *Bison* into the following age classes at each site: calves (1 y > x), yearlings (1 y ≤ x < 2 y), and twolings (2 y ≤ x < 3 y).

4.3.2. Thermography and photogrammetry techniques

4.3.2.1. Thermography: measure of heat exchange

We used a forward looking infrared (FLIR) thermal imaging camera [FLIR T1030sc; FLIR Systems, Wilsonville, OR, USA] with a 12° × 9° lens (f/1.2) for long distance thermography. Infrared images (Figure 4.1) had a fixed resolution of 1024 × 768 pixels. Camera and image calibrations were necessary for accurate and precise measures of heat exchange between each *Bison* and their environment. Seasonally, *Bison* molt their winter coats, therefore there was a fundamental difference in the insulation factor, emissivity (ε), and reflectance (ρ) between bare skin of summer and woolly fur undercoat of winter (see Appendix C, section “Emissivity calibration”). Emissivity values for each image were seasonally calibrated to 0.94 for *Bison* skin in summer and 0.90 for their woolly fur undercoat in winter. All measures, calculations, and model assumptions are presented in Appendix D Table 10.5. Methods for calibrating emissivity are presented in Appendix D Table 10.6.

4.3.2.2. Photogrammetry: measure of body size

We estimated body size of *Bison* using photogrammetric methods (Berger 2012, Martin and Barboza 2020). Calculating heat flux ($W \bullet m^{-2}$) requires heat exchange over surface area (SA; m^2; Figure 4.3). We calculated surface area and body height using standardized linear and area measures (Figure 4.3) of *Bison* in lateral view (Martin and Barboza 2020). Optimal distance between animal and camera for most accurate height representation of the animal was determined at and around 40 m (Martin and Barboza 2020), but distance at or near 20 m was optimal for pixel coverage and density of body surfaces. We estimated body mass from body height by applying known relationships of direct measures of *Bison* body height to body mass (Martin and Barboza 2020). Similarly, calculating growth rate ($kg \bullet y^{-1}$) requires a measure of body mass (BM; kg) over age (y). To estimate rate of growth per year ($kg \bullet y^{-1}$), we averaged body mass of twolings and calves for each locality, took the difference, and divided by 2 for the two-year age gap.

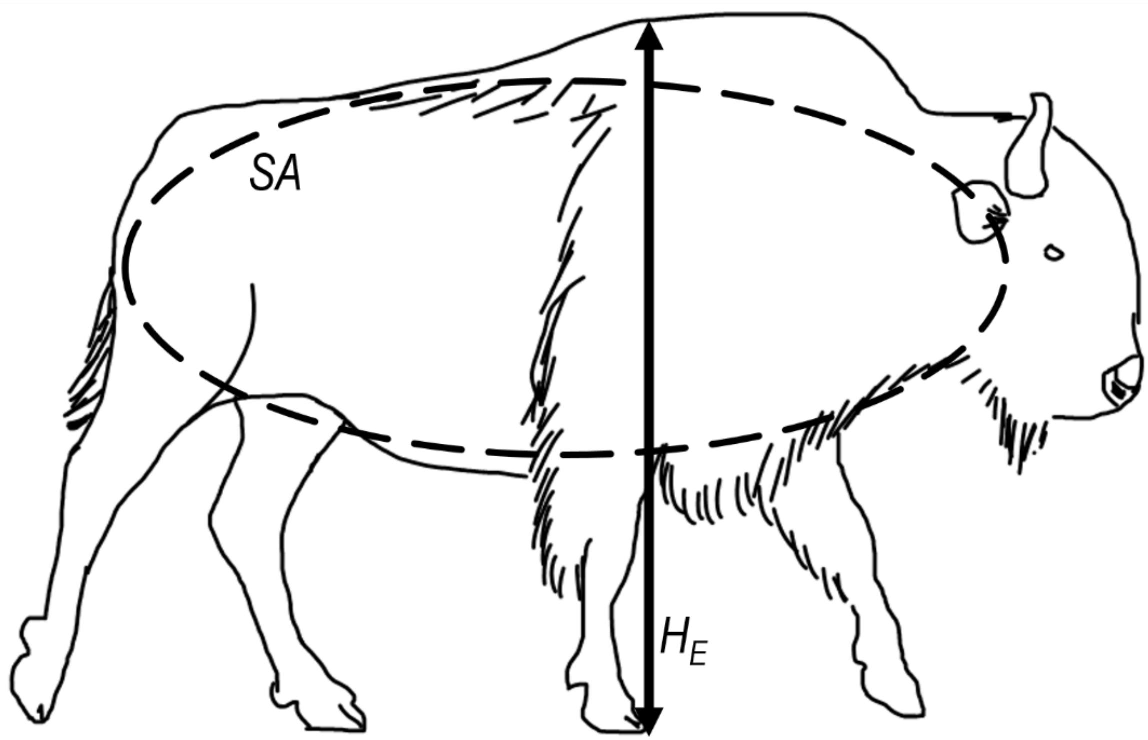

Figure 4.3. Schematic of estimating size and heat flux of photographed *Bison* standing at rest in a perpendicular plane to the camera. Double black arrows indicate the estimated height (H_E; m) from the highest point on the curvature of the spine along the length of the forelimb to the ground. The ellipse indicates the effective body surface area (SA; m^2) from the ischial tuberosity to the base of the skull (posterior to the external auditory canal, clearly demarcated in thermal images) and from the dorsal plane to the ventral plane. Reprinted from Martin and Barboza (2020b).

4.3.2.3. Thermogrammetry: measure of heat exchange and body size of *Bison*

We estimated heat flux (W•m^{-2}) between *Bison* and their environment by integrating thermographic and photogrammetric data—thermogrammetry. We extracted thermal information (e.g. temperature averages, standard deviations, minima, and maxima) of body surface area using FLIR ResearchIR Max software. Thermal data were exported for subsequent analyses to calculate net heat flux (W•m^{-2}). We calculated total surface heat transfer (convective and radiative) using the ‘heat calc’ functions as part of the

‘Thermimage’ package in R [Thermimage, version 3.2.1 (Tattersall et al. 2009, Tattersall 2016, 2019); R version 3.6.1, 64-bit (R Core Team 2019)]. However, sensible heat flux was not included in ‘Thermimage’, we thus added this term to the calculations because *Bison* are highly insulated. Sensible heat is the non-evaporative latent heat of the boundary and insulating layers related total depth of fat cover, skin thickness, and hair depth, as well as insulating characteristics of the hair (i.e., not all hair is equal for insulating; see Appendix section of “composition of torso mass and insulation depth” for more details). All heat flux calculations were exported as a CSV file for subsequent analyses in Stata. All parameters and assumptions for calculations in ‘heat calc’ and ‘Thermimage’ are presented in Appendix D Table 10.5 and data are available at the following DOI: 10.6084/m9.figshare.12084645.

We focus on the torso of *Bison* in this study for two primary reasons, 1) it is the effective thermal window that is responsible for most of the heat transfer of the heat produced from rumination and metabolism, and 2) efficient use of time. 1) The torso is also the site where the dense cape of hair is not present, enabling the large thermal window, that is the forequarters and head are draped in a dense coat of long guard hairs that is not shed seasonally and limits thermal exchange. Although, heat transfer from appendages and horns should not be discounted (Nienaber 2009, O’Brien 2020), which leads to the next point. 2) Previous studies have captured full-body heat transfers of animals such as muskoxen (Munn et al. 2009) and sums of compartmentalized body parts (Tattersall and Cadena 2010, Tattersall et al. 2018) but we had captured 1,995 thermal images from the field, of those 779 were usable after manual digitization. Computer automation of certain BioImage informatics tasks including digitizing whole body images or body parts would increase efficiency of image processing but were not developed for this study. We acknowledge that proportional limb lengths to body height and length are important for determining heat displacement but were beyond the scope of this study.

Heat flux is a negative value when energy is emitted (i.e., heat transfer loss) from the animal to the environment. Heat transfer increases with surface temperature and solar radiant heat gain, and decreases with wind, convective, and radiative heat loss. Heat flux indicates that the animal was expending energy on thermoregulation. Heat transfer was calculated by converting mean surface temperature (T_s; °C) of *Bison* to Watts of thermal energy exchanged with their environments, including measures of ambient air temperature (dry bulb; °C), body surface reflectance (0-1), daily cloud cover (0-1), ground temperature (T_g; °C), incoming solar radiation (SE; $W \cdot m^{-2}$), wind speed (V; $m \cdot s^{-1}$), and convection coefficients (c, n, a, b, m) for forced and free convection flow. Conductive thermal energy is ignored because we only collected images of *Bison* in a standing posture with the soles of their hooves as the only contact with the ground. All heat flux comparison is based on black body absorbers (i.e., a perfect absorber of electromagnetic radiation), in this case a black globe temperature (T_{BG}; °C). The surface of the animal was the skin or the fur, which was always above ambient temperature and thus emitting radiant heat to the environment when compared with an inert black globe. Moving air convects heat from the animal to the environment. To estimate isometric surface-area-to-volume ratio, we fitted a regression of total surface heat transfer (W) over estimated body mass (BM_E). To test allometric scaling, we fit a log:log regression of the $\log_{10}$ of the absolute value of total surface heat transfer ($\log_{10}|W|$) and $\log_{10}$ of estimated body mass ($\log_{10}BM_E$).

4.3.3. Computation and statistical analyses

All thermogrammetric information, locality metadata, weather, and climate data were related and analyzed in Stata/IC [version 16.0; 64-bit, Stata Corp., College Station, Texas, USA]. We used daily measures of weather and climate as variables for converting body surface temperatures to thermal heat flux, as well as independent terms in multilevel mixed effects models. For mixed effects models, random effects were included in the models as locality to account for repeated measures of each site. Environmental variable selection for each model were parsed using the ‘least absolute shrinkage and selection operator’ (or lasso) package for Stata (Tibshirani 1996). Where appropriate, model fit was assessed using either adjusted-R^2 and root square mean error of residuals (RMSE) for ordinary linear regressions or *k*-fold cross-validation to report the square of the correlation (pseudo-R^2) and RMSE for mixed effects models to describe model fit and strength.

4.4. Results

South of 43°N (e.g., South Dakota-Nebraska border), adolescent *Bison* between the ages of 3 months and 3 years (n = 214) have a smaller surface area (7.8 ± 2.1 m^2), lower total surface heat transfer (-221 ± 78 W), lower body mass (271 ± 94 kg), and more heat loss (-286 ± 76 $W \bullet m^{-2}$) than their northern (n = 131) counterparts (8.9 ± 2.1 m^2; -224 ± 72 W; 324 ± 105 kg; -254 ± 67 $W \bullet m^{-2}$, respectively). Distance between animal and camera averaged 22 ± 11 m (n = 374; ranging from 8 to 68 m). Average pixel size represented 0.034 ± 0.038 m^2 (ranging from 0.003 to 0.331 m^2) of real-world size.

4.4.1. Body surface temperature

Body surface temperature of *Bison* averaged 38.4 ± 4.5 °C in summer (*n* = 351) and 17.1 ± 16.6 °C in winter (*n* = 428). Highest mean body surface temperature in summer was 48.3 °C for two yearlings on a cloud free day (0%), air temperature 34 °C, relative humidity of 35%, black globe temperature 46 °C, and calm wind speeds of 3.2 m/s. Lowest mean body surface temperature in winter was -55.3 °C for one calf on a mostly cloudy day (63%), air temperature of -28.5 °C, relative humidity of 100%, black globe temperature -14.1 °C, and mild wind speed of 1.2 m/s. Body surface temperature was above or equal to average *Bison* body temperature (T_b) of 38.4 °C (Christopherson et al. 1979) in summer in 98 instances (or 67.1% of observations) and in winter in 20 instances (or 8.8% of observations). The upper limit threshold (ULT) likely ranges between 30 °C and 35 °C, based on ULT values for black *Bos taurus* and black *Bos indicus*, respectively (Nielsen-Kellerman 2009). Body surface temperature increased with black globe temperature (°C; i.e., solar energy) and with wet bulb globe temperature (°C; i.e., effective temperature) more quickly in winter than in summer (Figure 4.4; Appendix D Table 10.1).

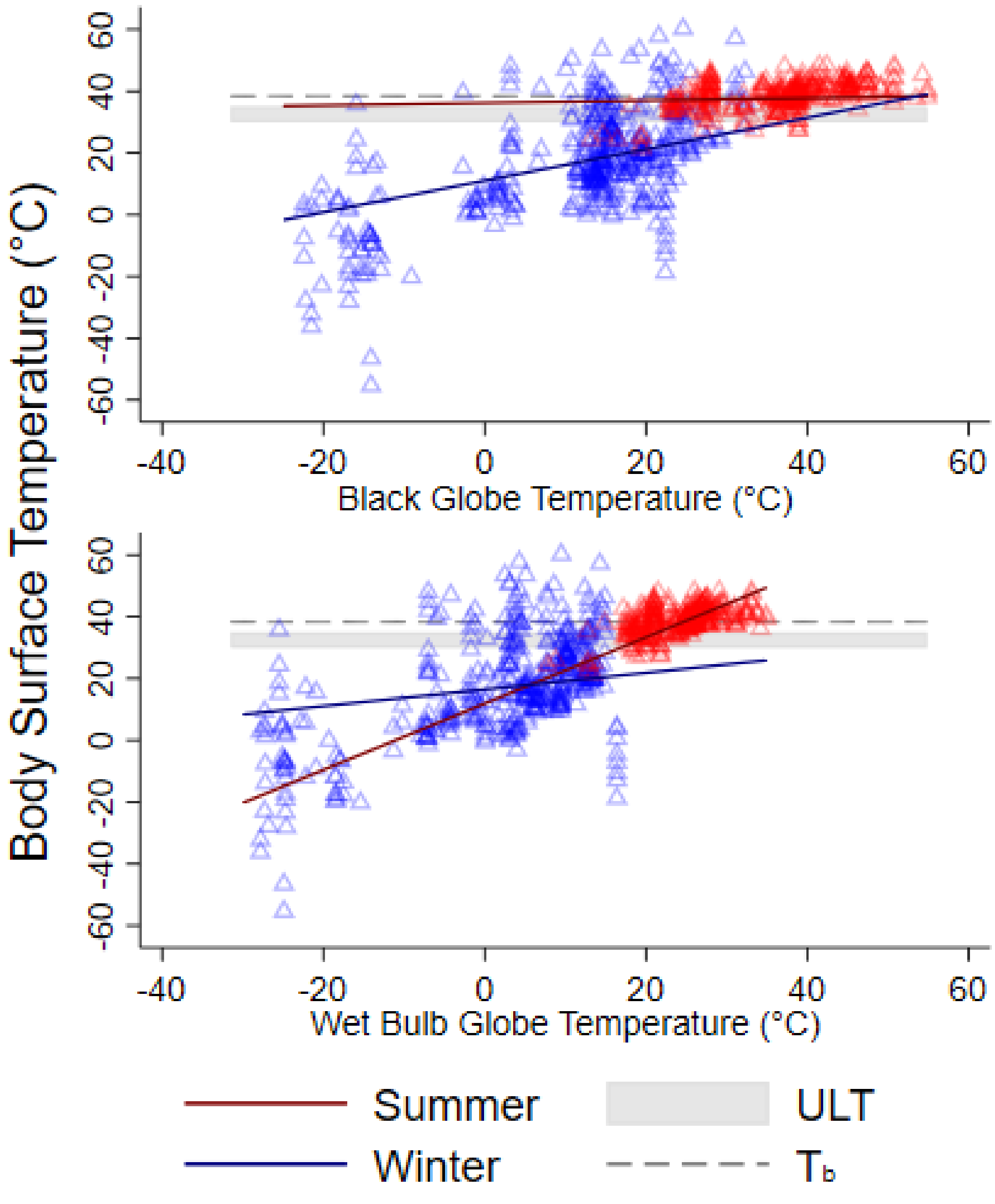

Figure 4.4. Body surface temperature (°C) of *Bison* in summer (red) and winter (blue) in relation to air temperature measured as black globe temperature (°C; upper) and wet bulb globe temperature (°C; lower). Horizontal gray box indicates upper limit threshold (ULT) for black *Bos taurus* (30 °C) and black *Bos indicus* (35 °C). Horizontal dashed gray line represents core body temperature for *Bison bison* (38.4 °C). Cross-validation support metrics using $k_{(10)}$-fold: pseudo-R^2 = 0.61, RMSE =

10.3, *N* = 779 individuals, *n* = 19 groups by site. Random effects (site) explained 0.26% of variance. Reprinted from Martin and Barboza (2020b).

4.4.2. Components of heat exchange

Seasonal body surface temperature was related to heat flux (Figure 4.5A). Heat flux was comprised of radiative thermal energy (difference between incoming solar gain and outgoing radiating loss; Figure 4.5B), convective thermal energy (Figure 4.5C), and sensible thermal energy (non-evaporative insulation; Figure 4.5D). Total surface heat transfer was negatively affected by radiative heat in summer when the body surface was exposed to high radiant loads from the environment. In winter, total surface heat transfer was positively related to radiative heat, that is radiant heat from the environment reduced total surface heat loss from the animal (Figure 4.5B). Total surface heat transfer was similarly affected by movement of air on the body surface albeit with a greater effect in winter than in summer (Figure 4.5C). The greatest range of heat fluxes ($W \bullet m^{-2}$) occurred in winter amongst the youngest and smallest age class. The greatest heat flux was estimated for a calf in winter at -620.8 $W \bullet m^{-2}$ when windy condition provided the highest convective loss and high cloud cover reduced radiative heat from the environment. The smallest heat flux was estimated from a calf in winter at -141.2 $W \bullet m^{-2}$ when radiative heat from the environment was low because of cloud cover and when convective losses were high due to wind.

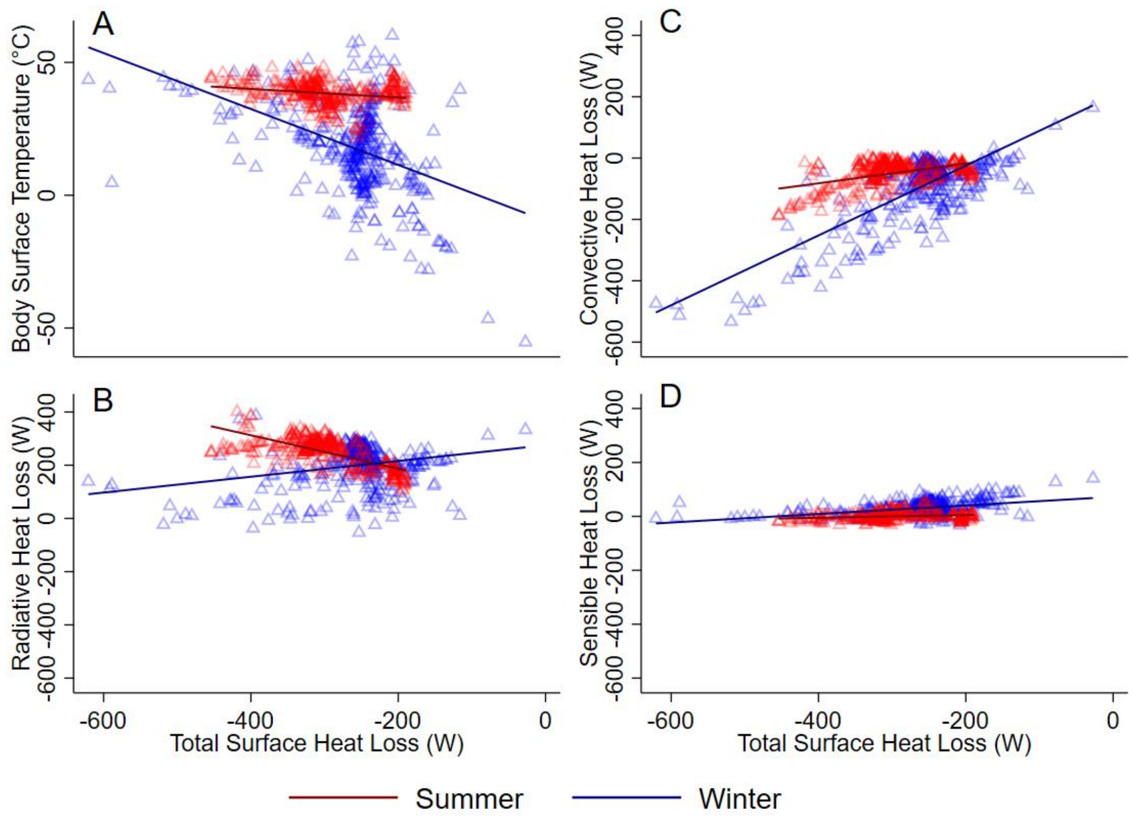

Figure 4.5. Components of total surface heat loss (W) in *Bison*. A; body surface temperature (°C), B; radiative heat loss (W; difference between incoming solar radiation and outgoing radiation), C; convective heat loss (W), and D; sensible heat loss (W). Reprinted from Martin and Barboza (2020b).

4.4.3. Heat transfer

Total surface heat transfer (W) from the effective thermal window surface of the torso of *Bison* averaged -270 ± 95 W (n = 694) across both seasons; the most heat transfer was -589 W, and the least was -21 W. Total surface heat transfer (W) was linearly related to body mass of *Bison* from 44 to 745 kg (mean 335 ± 103 kg; Figure 4.6, upper). The relationship between total surface heat transfer (W) and body mass (kg) was linearly related after transformation to logarithms for the allometric relationship. The slope of the log:log relationship between $\log_{10}|W|$ and $\log_{10}BM_E$ was 0.63 ± 0.03 $\log_{10}|W|\bullet\log_{10}kg^{-1}$

(95% CI: 0.57–0.69; Figure 4.6, lower), which was significantly less than an isometric slope of 1.0 but consistent with the expected slope of 0.67. Results and supporting statistics for both isometric and allometric models are presented in Appendix D Table 10.2.

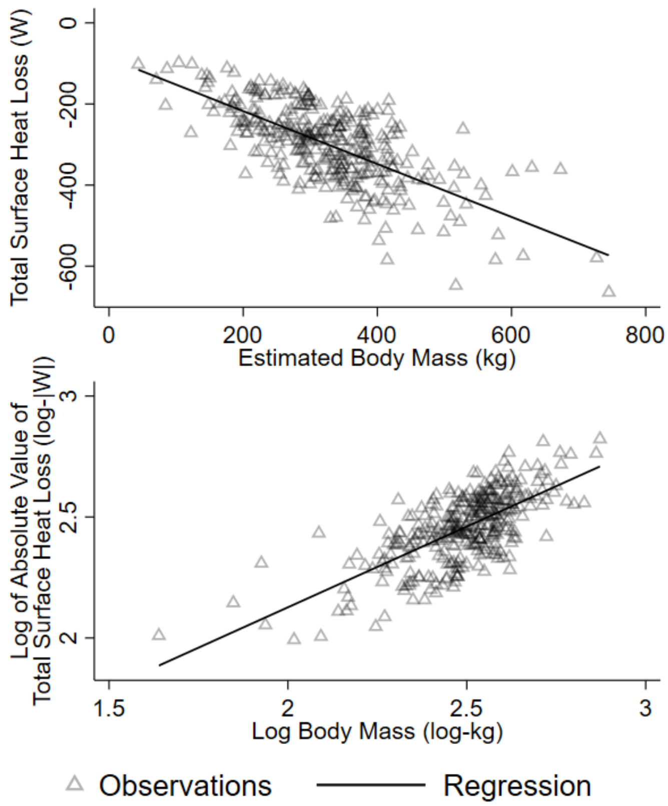

Figure 4.6. Relationship between heat transfer (W) and body mass (kg) of *Bison*. Upper panel: total surface heat transfer (W) against body mass (kg) in an isometric model (Ordinary Least Squares Regression $W = ß_0 + ß\ x_1$; Adj. $R^2 = 0.31$, RMSE = 79, $ß = -0.52 \pm 0.03$; $n = 694$ individuals). Lower panel: log_{10} absolute value of total surface heat transfer ($log_{10}|W|$) against log body mass ($log_{10}kg$) in an allometric model ($log_{10}kg$; $n = 694$) ($W = ß_0 \bullet x_1{}^{ß} \rightarrow log_{10}|W| = log_{10}\ ß_0 + ß \bullet log_{10}\ x_1$; $ß = 0.63 \pm 0.03$; Adj. $R^2 = 0.36$, RMSE = 0.13, $n = 694$ individuals). Reprinted from Martin and Barboza (2020b).

Total surface heat transfer varied with annual growth rates of calves and twolings (Figure 4.7, Appendix D Table 10.3). Observed total surface heat transfer decreased from -340 to -207 W as annual growth increased from 41 to 126 kg•y^{-1} in adolescent *Bison*.

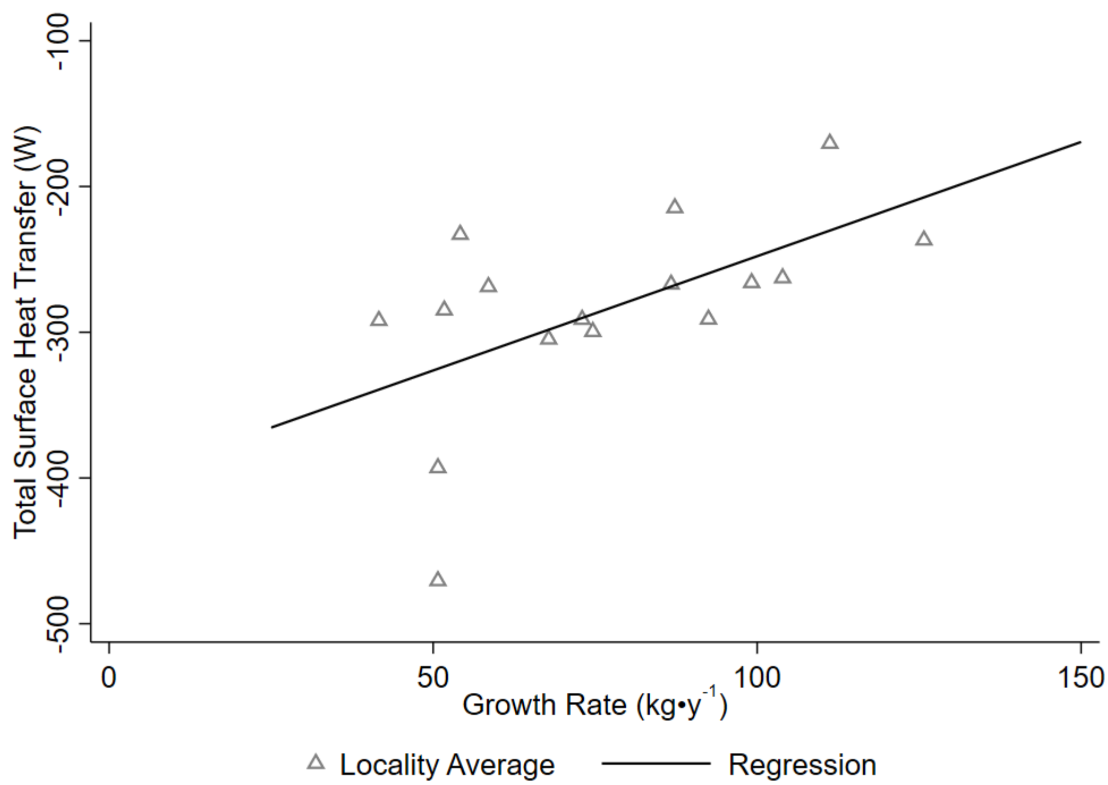

Figure 4.7. Average total surface heat transfer (W) of *Bison* in relation to average growth rate (kg•y^{-1}; n = 16) at each site (pseudo-R^2 = 0.28, RMSE = 58.6, n = 16 sites). Figure 8. Heat flux (W•m^{-2}) of *Bison* in summer (red) and winter (blue) against latitude (°N). Cross-validation support metrics using $k_{(10)}$-fold: pseudo-R^2 = 0.12, RMSE = 64.6, N = 345 individuals, n = 19 groups by site. Random effects (site) explained 0.61% of variance. Reprinted from Martin and Barboza (2020b).

Heat flux also declined with increasing latitude in summer from -331.2 W•m^{-2} at 30 °N in Texas to -263.5 W•m^{-2} at 52 °N in Saskatchewan (Figure 4.8). Latitudinal declines in heat flux were more pronounced in winter than in summer (Appendix D Table 10.4), that is heat flux decreased by 3.85 ± 1.64 W•m^{-2} in winter and by 3.08 ± 1.66 W•m^{-2} in summer with each degree of latitude gained.

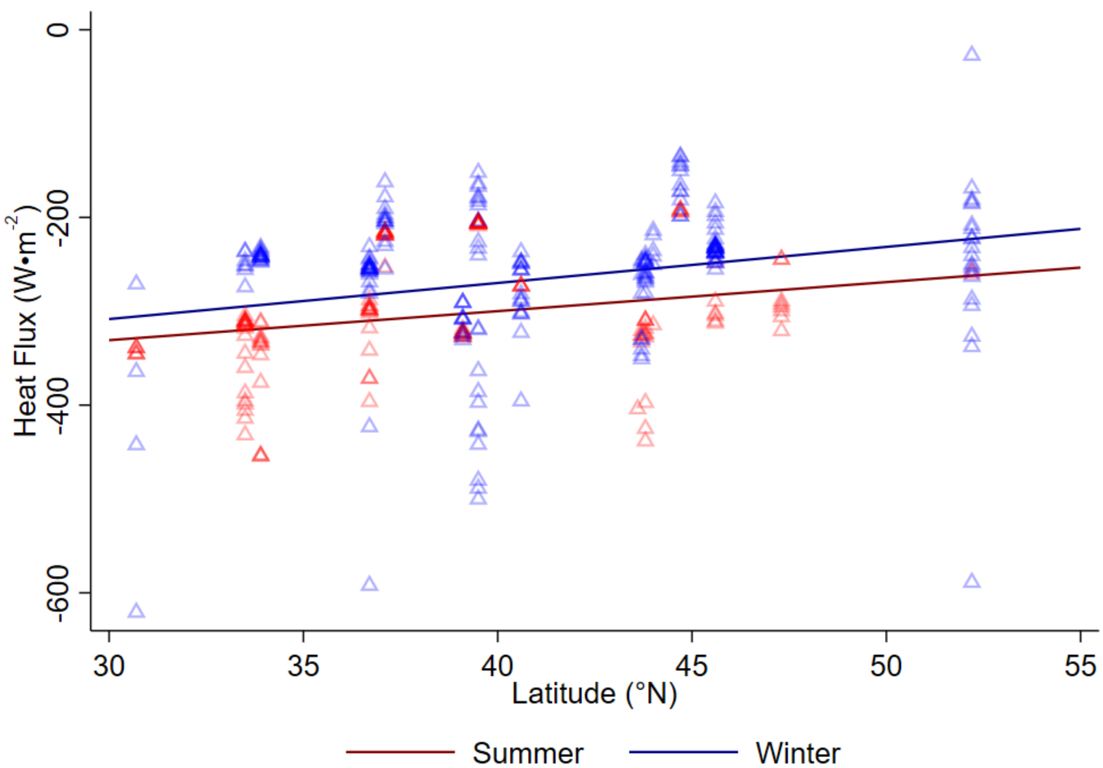

Figure 4.8. Heat flux (W•m^{-2}) of *Bison* in summer (red) and winter (blue) against latitude (°N). Cross-validation support metrics using $k_{(10)}$-fold: pseudo-R^2 = 0.12, RMSE = 64.6, *N* = 345 individuals, *n* = 19 groups by site. Random effects (site) explained 0.61% of variance. Reprinted from Martin and Barboza (2020b).

4.5. Discussion

We used heat flux (W•m^{-2}) and total surface heat transfer (W) as measures of thermal exchange between *Bison* and their environment along a ~2,500 km transect, from Saskatchewan (52 °N) to Texas (30 °N) in summer and in winter. We compared four body size theories using heat flux as a common currency: Kooijman's dynamic energy budget, Schmidt-Nielsen's surface area to volume rule, Speakman and Król's heat dissipation limit, and Bergmann's rule.

Unseasonably warm winter days appear to raise surface temperatures of *Bison* (Figure 4.4). The frequency of these warmer winter scenarios are expected to increase in the coming decades (Wuebbles et al. 2017), which may be stressful for large animals that are well insulated with a woolly underfur and a layer of subcutaneous fat.

Kooijman's dynamic energy budget theory predicts animals to have greater thermal loss in short-term (daily) extreme weather conditions such as high winds and extreme heat. Black globe temperature represents the effect of incoming solar radiation with ambient temperature, whereas wet blub globe temperature represents the effect of relative humidity and wind speed as ambient temperature. Our data supports Kooijman's dynamic energy budget theory (Figure 4.4 and Figure 4.5) because body surface temperatures were directly related to radiative loads and convective losses of energy. Schmidt-Nielsen's rule predicts that surface-area-to-volume ratio decrease with increasing body size to slow heat transfer from large animals. We found that increasing body mass increased total surface heat transfer in both an isometric and an allometric fashion (Figure 4.6). The isometric model predicted greater heat transfer than was observed for the smallest 5% of *Bison* (≤164 kg; -162 W vs. -138 W) whereas estimates from the allometric model were not significantly different; this was tested by using a paired t-test of the observed and predicted heat transfer values of the smallest and the largest 5% (≥511 kg) of *Bison*. Speakman and Król's heat dissipation limit theory predicts that production is suppressed when heat loads from the environment and metabolism divert energy to thermoregulation. Our data demonstrates that growth of *Bison* is limited by heat loads because the slowest annual growth rates were associated with the greatest heat transfer (Figure 4.7). However, we acknowledge that the temporal resolution of growth data is too large to resolve the relationship of growth and excessive heat loads within a growing season. Bergmann's rule predicts that selection favors large animals at higher latitudes. The ability to retain heat in cold winters (*sensu* Schmidt Nielsen; Figure 4.6) has been invoked as an explanation for Bergmann's rule. Our data provides some support for thermal conservatism, because heat flux from the smallest 5% of *Bison* (≤164 kg; -248 + 58 W•m^{-2}) was greater than that of the largest 5% of *Bison* (≥511 kg; -230 ± 30 W•m^{-2}). However, Bergmann's rule is also explained by summer growth and the net primary production of food (Huston and Wolverton 2011). Asymptotic size of *Bison* on the Great Plains declines with high decadal temperatures and droughts that suppress growth of both the animal and the forages they consume (Martin and Barboza 2020). In this study, high annual growth rates were observed at high and low latitudes at sites with mean annual precipitation above 450 mm (Appendix D Table 10.1; Figure 4.7), which suggests that growth is dependent on thermal exchanges as well as forage supplies.

Our study of heat transfers in bison provided support for all four theories of body size, which suggests that body size is an outcome of consistent effects across temporal and organizational scales from instantaneous heat balance through seasonal growth of this long-lived animal. Reinforcement between levels of organization multiplies the effect of body size of individuals in a population on other ecological processes especially for large keystone species such as bison that influence the composition of plant and animal communities in their ecosystem (White 1983, Knapp et al. 1999, Beschta et al. 2020).

4.5.1. Conservation implications

Annual and seasonal mean temperatures are expected to rise over the next eight decades, this will increase heat loads and thus increase negative heat transfer. Increasing negative heat transfer will further decrease growth rates and likely alter life history traits (Martin and Barboza 2020) including reproduction rates. Special conservation and management considerations by organizations like the IUCN-SSC Bison Specialist Group will need to be given to the southern Great Plains where the number of extremely hot days (> 32 °C) are expected to rise to 87 days per year from 32 days per year (Weatherly and Rosenbaum 2017). Marginal habitats will also challenge conservation plans in places like the arid desert regions of the American southwest where drought is expected to be persistent, lengthening, and intensifying (Cook et al. 2015).

4.5.2. Summary of findings

Cooler summers are more optimal for *Bison* growth because of reduced heat loads during the growing season. Rising temperatures constrain body size and productivity of *Bison*. We report five key findings:

1. Daily measures of weather—wind speed, heat index, solar radiation, relative humidity—affect heat flux of endotherms seasonally; our study supports Kooijman's dynamic energy budget hypothesis (Figure 4.4).

2. Heat transfer is allometric with body size (*b*=0.63) and thus consistent with Schmidt-Nielsen prediction of *b*=0.67 (or the two-thirds rule) that mass specific heat transfer declines with increasing body size (Figure 4.6).
3. Annual growth declined with increasing heat flux, which supports Speakman and Król's heat dissipation limit hypothesis (Figure 4.7).
4. Winter and summer seasons appear to conform to Bergmann's rule, where *Bison* conserve heat in cooler-northern locations (Figure 4.8).
5. The confirmation of the above four theories, using heat flux as a common currency, suggests that an integrated general theory of thermoregulation could be developed with additional studies of other taxa following the framework put forth in this study.

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5. VULNERABILITY AND ADAPTIVE CAPACITY OF THE NORTH AMERICAN *BISON* COALITION TO CLIMATE CHANGE[§]

5.1. Synopsis

Climate change throughout the North American Great Plains may challenge conservation strategies for the iconic bison (*Bison bison*) which was threatened with extinction in the late 19th century. The bison population of 373,000 animals is maintained by the bison coalition, which is a self-assembled group of organizations focused on bison conservation and production. The coalition is comprised of public, private and not-for-profit non-governmental organizations (NGO), with complementary goals, practices, and values that contribute to a robust conservation footprint for the species. We assessed vulnerability of the bison coalition to 21st century climate change with a scoping diagram that focuses on dimensions of exposure, sensitivity, and adaptive capacity. We surveyed 132 bison managers from North America, from both the private and public/NGO sectors. Respondents were predominantly educated white males, in the northern and central mixed grass prairies, that typically manage bison herds of 51-100 animals. The public/NGO and private sectors differ on dimensions of adaptive capacity, specifically in measures of information exchange, external revenue, use of management plans, and access to grazing leases but both appear moderately adaptation savvy. Some adaptation areas that require improvement include monitoring environmental variation, age and gender, grazing leases,

[§] Martin, J.M., J. Zarestky, D.D. Briske, and P.S. Barboza. Vulnerability and adaptive capacity of the North American *Bison* coalition to climate change. (Expected 2020). People and Nature. *In prep.*

bison population, and harvest. These low-score traits increase vulnerability to the effects of climatic change. Across the coalition, higher education and long personal experience with managing bison appears to increase adaptive capacity and thus increases preparedness to the accruing effects of climate change. Experience increases institutional memory for dealing with droughts, and high information sharing improves the response to droughts for all managers. Values and attitudes of ecology and economy are shared among bison managers, suggesting that integration and collaboration between sectors is likely. Trust among other bison managers is high compared to other sources of bison-related information. Further integration of bison sectors into a more inclusive coalition would likely initiate creation of novel adaptive solutions to the effects of changing climate and culture.

5.2. Introduction

North American bison (*Bison bison*) are a keystone species of the Great Plains. The bison population was estimated at 30 million circa 1868 (Hornaday 1889, Knapp et al. 1999, Allred et al. 2013, Martin and Barboza 2020*a*) but less than 1,000 animals remained by 1884 (Stoneberg Holt 2018); bison populations have since rebounded to approximately 373,000 animals. Ironically, accelerating climate change throughout the Great Plains in the 21st century (Wuebbles et al. 2017) may represent the next challenge to the survival and persistence of bison. Climate change, particularly warming and drought, has a greater potential effect on the remaining grasslands and shrublands of the Great Plains than human land use, human population, pollution, and invasive species (Knapp et al. 1999, Allred et al. 2013, Bowler et al. 2020). One-third of the 2100 terrestrial vertebrate species of the

United States inhabit grasslands of the United States (Johnsgard 2003, International Union for Conservation of Nature 2020). Today, grasslands are the largest biome in North America and cover nearly 40% of global terrestrial landmass. Historically, the Great Plains had an extent of 2.8 million km^2 (14% the landmass across US and Canada (Licht 1997, Johnsgard 2003)). These Great Plains-prairie biomes are now 70% privately owned (Holechek et al. 2011) and the bison population is 80% privately owned.

As a keystone species, bison provide many ecosystem services: iconic symbolism for cultural ecosystem services; providing meat, bone, leather, skin, dung compost, and fiber products for provisional ecosystem services; attributes of soil building, erosion control, carbon sequestration, and nutrient cycling are regulating ecosystem services; and prairie restoration, biodiversity conservation are supporting ecosystem services. *Bison* are unique because they are both a native wildlife species that can be used for commercial production of meat and skins, recreational services (i.e. watching or hunting), and reinforcing ecological services such as restoration of native prairies and grasslands (Gates et al. 2010). The bison coalition is a conglomeration of public, non-governmental, and private organizations focused on bison conservation and production that self-assembled over the last 100 years. The bison coalition is at the nexus of two shifting paradigms: changing climate and changing cultural values.

Climate change directly affects bison, and other mammals and birds, by increasing heat loads and decreasing available water, thereby reducing body size and reproduction (Martin et al. 2018, Martin and Barboza 2020*b*); Martin and colleagues estimate that body size of bison will halve by the end of the 21st century if global temperature warms by 4°C.

Indirect consequences of climate change that will affect managers include: increasingly variable weather and seasons, spreading and increasing internal and external parasites (Patz et al. 2000, Kutz et al. 2005, Morgan and Wall 2009), increasing occurrence of disease exchange and distribution (Janardhan et al. 2010), reduced rangeland productivity due to hotter, drier summers (Eastman et al. 2001, Briske et al. 2015), phenological mismatches between grassland green-up, grass senescence, and animal life histories (McCain and King 2014, Kharouba et al. 2018), reduced calf survival due to reduced grassland productivity (Loison et al. 1999), reduced pregnancy rates due to reduced grassland productivity (Fuller et al. 2007), increased droughts due to increased temperature (Fawcett et al. 2011, Nairn and Fawcett 2014, Cook et al. 2015).

Animals' body size changes affect mass-specific rates of energy, nutrient, and water exchange between animals and their environments (Peters 1983, Barboza et al. 2009, Martin and Barboza 2020*a*). Ultimately, decreased body size affects ecosystem services that come from bison because smaller body sizes diminish rates of ecological interactions, exchanges, and thus productivity (Martin and Barboza 2020*a*). Public lands are warming and drying at an accelerated rate compared to the rest of North America (Gonzalez et al. 2018). In effect, shrinking ecological boundaries, transitioning grasslands to more xeric-shrubland biomes, and pressuring the existing 700 terrestrial vertebrate species of the Great Plains to change their distributions, migration paths, and ecological interactions. Consequently, private working lands are becoming more important as habitat for wildlife that may be displaced by the combined effects of changing climate and land use. Disruptions in ecosystem services will likely have cascading negative consequences for market supply and prices for *Bison* meat. Markets for bison have been strong, nearly 3-4 times that of beef with growing demand (Carter 2019). Supply chains for bison meat and products to consumers are vulnerable to changes in the environment.

Since the turn of the 20th century, Americans have culturally shifted from a nation of traditionalists to mutualists (Manfredo et al. 2020). However, while most Americans value nature, they are growing disconnected from nature (Kellert et al. 2017). These two scenarios pose issues of consumer acceptance and perceptions of various traditional livestock husbandry and wildlife management practices. For example, in the public wildlife management system, citizen acceptance for harvest has declined, urging translocation as an alternative strategy but with limited success. Conflicts with abundant terrestrial wildlife are largely managed through harvest and by relocation or culling but such removals may be insufficient to manage long term risks to habitat, other species, and people (Simard et al. 2013, Boulanger and Curtis 2016, Nunez et al. 2016). The North American system for wildlife conservation also largely underrepresents private working lands, especially in the grasslands of the Great Plains. In the private livestock system, citizens perceive meat production as unsustainable (D'Silva and Webster 2017). The culmination of these shifting and growing cultural values will continue to negatively affect implementation of evidence-based animal conservation and production systems world-wide.

We examined the vulnerability of the bison coalition to projected environmental and cultural changes by conducting a survey of bison managers. We used exposure, sensitivity, and adaptive capacity as the dimensions of vulnerability, as described by Adger

(2006) and Polsky et al. (2007). Exposure characterizes the community assets that may be threatened: natural resources such as wildlife; human resources such as skilled workers, and weather conditions that directly and indirectly affect people. In the bison coalition, bison and bison managers are disproportionately exposed to stressors from climate change including extreme weather events and variable rates of temperature and precipitation change across regions and ecosystems. Sensitivity characterizes the speed and impact of a projected change in the environment, assets, and the human community. Bison managers respond to annual variation in rangeland production, bison herd health and production, markets, and the ability to recruit the next generation of bison managers. Adaptive capacity characterizes social responses to change that include the availability of relevant information, physical assets (e.g., grazing leases), and social institutions. High adaptive capacity reduces vulnerability by reducing sensitivity to exposure of environmental and social change. Adaptive capacity of geographically isolated bison ranchers can be improved by access and exchange of information on management practices (e.g., drought plans) and assets (e.g. drinking water, grazing leases). Values, attitudes, and practices drive differences in individual and group decisions regarding adaptive capacity (Heberlein 1988, 2013, Heberlein and Ericsson 2005). Future management decisions and strategies will need to accommodate the consequences of environmental change, climate change, and land-use change, all of which are influenced by individual and collective values, attitudes, and practices of bison managers.

To measure these dimensions of vulnerability, we implemented the vulnerability scoping diagram (VSD) to integrate questions about exposure, sensitivity, and adaptive capacity (Figure 5.1) in our survey (Turner et al. 2003, Polsky et al. 2007, Stafford Smith et al. 2009, Clark 2010). Resilience is loosely considered the antonym of vulnerability (Adger 2000). Resilience increases the capacity of a community to cope with stress (Adger 2000, 2006, Janssen and Ostrom 2006).

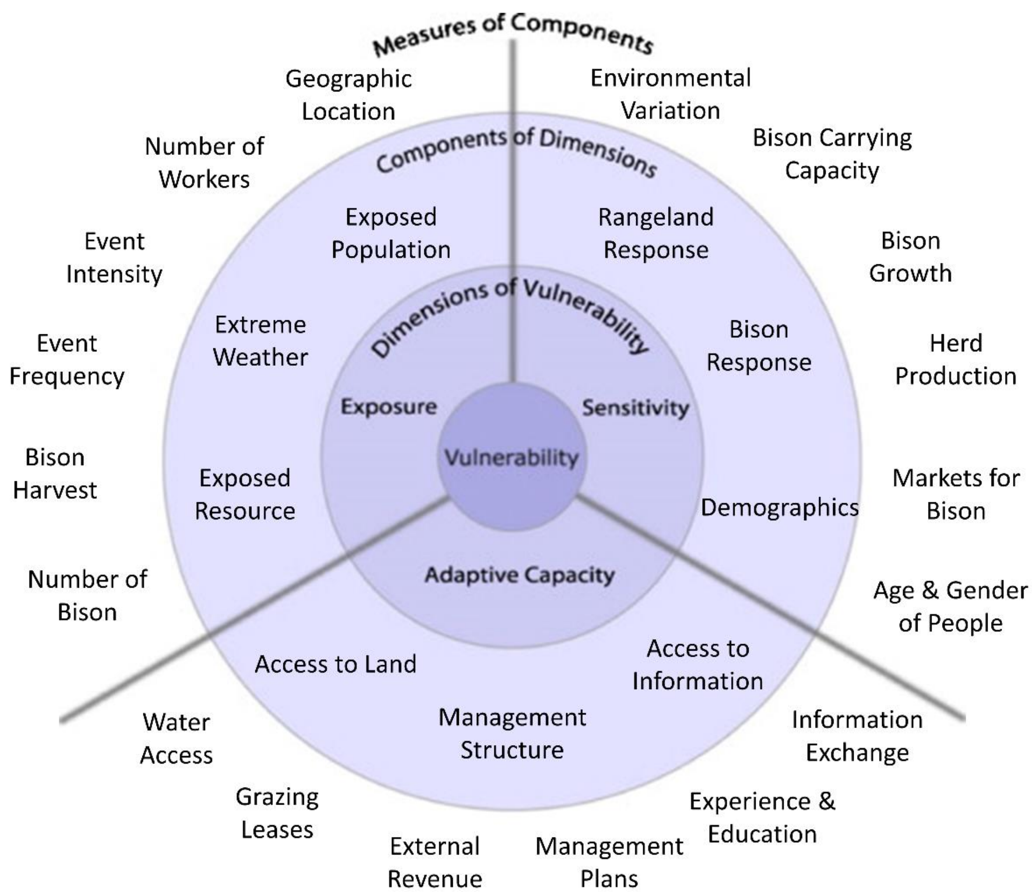

Figure 5.1. Vulnerability Scoping Diagram of Coupled Natural-Human system of *Bison* management and culture. The vulnerability hazard at the center is anthropogenic climate change. The next ring are the dimensions—exposure, sensitivity, and adaptive capacity. The next two rings are the components and measures. The components and measures are modified from Polsky and colleagues (2007) to fit our system.

We sought to identify feedbacks that indicate disparities between public and private management that reduced overall vulnerability of the coalition. We predicted public and private sectors of bison management differ in measures of adaptive capacity, exposure, and sensitivity. We also hypothesize that differences among measures of adaptive capacity, exposure, and sensitivity are driven by differences in core values, attitudes, and practices. We discuss measures and approaches to reduce vulnerability for each sector and of the entire coalition to environmental change by comparing values, attitudes and practices.

5.3. Materials and Methods

The study was approved by the Institutional Review Board at Texas A&M University (TAMU IRB: 2018-1654). Participation in the survey was restricted to managers of bison herds who were 18 years or older, spoke English, resided in North America and provided informed consent. The survey was delivered online and open for one month (from February 11, 2019 to March 14, 2019). Participants were recruited through listserv emails and social media posts of the National Bison Association and herd managers.

5.3.1. Survey instrument

We asked 43 questions (five questions had various sub-components, summing to 68 total questions), divided into 18 measures, two measures for each of the nine components that represent three dimensions of vulnerability—exposure, sensitivity, and adaptive capacity (Figure 5.1 and Table 5.1). Total resiliency scores are derived from the 11 questions measuring exposure, 23 questions measuring sensitivity, and 15 questions measuring adaptive capacity (49 total questions; Table 5.1). To test whether survey participants could understand the scale items (i.e., face validity), a pretest was conducted with a 10-person focus group comprised of private and public bison herd management officials (Miles et al. 2020). We used an established VSD structure (Turner et al. 2003, Polsky et al. 2007, Stafford Smith et al. 2009, Clark 2010) with questions specific to the bison coalition.

Survey responses were recorded on a Likert scale from 0 to 5 or on a scale of agreement with three points (agree-neutral-disagree) or two points (positive or negative). Focal topics included elements of management philosophy, diversity of income, land and animal health monitoring, management practices, value of economic and ecological factors, quality of life and career experiences, and personal characteristics. We also asked about attitudes towards various ecological or economic practices, such as using prescribed burning or diversifying livestock species on their operations. We asked respondents about their perceptions and/or observations about climate from the last 10 years, such as warming mean summer temperature or shifting calf survival rates on their operations.

Responses from the VSD indicating greater resilience were valued higher (e.g. "Do you provide water to your animals?" — Yes or no; where yes is scored as 1 and no as 0). In this study, we developed a new means to interpret and visualize the results of the VSD. All non-personal trait questions were standardized to a 10-point scale for subsequent analyses; high scores to each question indicating greater resilience. For each measure of the VSD, we took the median of the corresponding questions. For each dimension of the VSD, we took the median of the corresponding measures. The overall vulnerability score is inverted, where low scores indicate large vulnerabilities but high scores indicate low vulnerability because the visualization of the 10-point radar plot seeks to fill the circle (presented in results). A full circle also indicates a robust system; henceforth, scores will be termed resiliency scores because resiliency is the antonym to vulnerability (Adger 2000, 2006). The resiliency score is calculated as the mean of the three median scores of exposure, sensitivity, and adaptive capacity.

Table 5.1. Vulnerability scoping diagram dimensions, components and measures mapped to survey questions. Supplemental Information presents the survey questionnaire. Abbreviations: C, cultural ecosystem services; P, provisional ecosystem services; R, regulating ecosystem services; S, supporting ecosystem services.

Dimension	Component	Measure	Survey question number(s)[1]	Ecosystem Services
Exposure				
	Exposed resource	Number of bison	19	P, R, S
		Bison harvest	20	P
	Extreme weather	Event frequency	31, 34i	S
		Climate velocity	34e, 34f, 34g, 34h	S
	Exposed population	Number of workers	17	C, P
		Geographic extent	16, 28d	S
Sensitivity				
	Rangeland response	Environmental variation	34i, 34j, 34k	R
		Bison carrying capacity	27b, 29, 35a	P, R, S
	Bison response	Bison health	27c, 27d, 27f, 27e, 34c, 34d	C, P, R, S
		Herd production	27g, 34a, 34b	C, P
	Demographics	Markets for bison	9, 11a, 11b, 27a, 28a, 28c	P
		Age and gender of managers	2, 7	C
Adaptive Capacity				
	Access to information	Information exchange	35b, 35c, 35d	R
		Experience & education	5, 37	C
	Management structure	Management plans	15, 39, 42	R, S
		External revenue	10, 11c, 11d, 28b	P
	Access to land	Grazing leases	38	P
		Water access	40, 41	R

[1] See Appendix E Table 11.1: Survey Questionnaire.

5.3.2. Respondents

We collected 156 responses from an estimated pool of 1,049 bison managers (National Agricultural Statistics Service 2019) for a response rate of almost 15%. We removed 24 incomplete or unqualified responses for an analytical set of 132 responses. The median time spent by each respondent on the survey was 10.4 minutes.

We classified respondents by sector, region, ecosystem, operation size, and education level. Respondents were asked if they represent private, public, or non-governmental organization bison herds. Non-profit non-governmental organizations (NGOs) have similar goals as public agencies, therefore we combined the two groups as one, public/NGO. Most responses were from the private sector (121 or 92%) with 5 (4%) responses from NGO, and 6 (5%) from managers of public herds—for a combined public/NGO sector of 11 (9%) responses, which reflects the proportional ownership of bison in North America: 81% private, 5% NGO, 8% public, and 5% tribal. Respondents were predominantly male in both the public/NGO (91%) and private sectors (82%).

Regions of North America were separated into northern, central, southern, and eastern sections (Figure 5.2). Ecosystems of tallgrass, mixed-grass, shortgrass grasslands—and one 'other' category (Omernik and Griffith 2014, U.S. Environmental Protection Agency 2014). The 'other' category refers to ecosystems that are characterized as a non-prairie type; most often in regions other than the Great Plains. When the regions and ecosystems of the Great Plains are overlaid, nine distinct sections become apparent—northern tallgrass, southern shortgrass, and so on. Most public/NGO bison herds were located in northern and central regions (82%) on shortgrass and mixed grass prairies

(64%). Private bison herds were also located in northern and central regions (81%) on shortgrass and mixed grass prairies (79%; Appendix E Table 11.1). Demographic attributes of respondents are presented in Table 5.2.

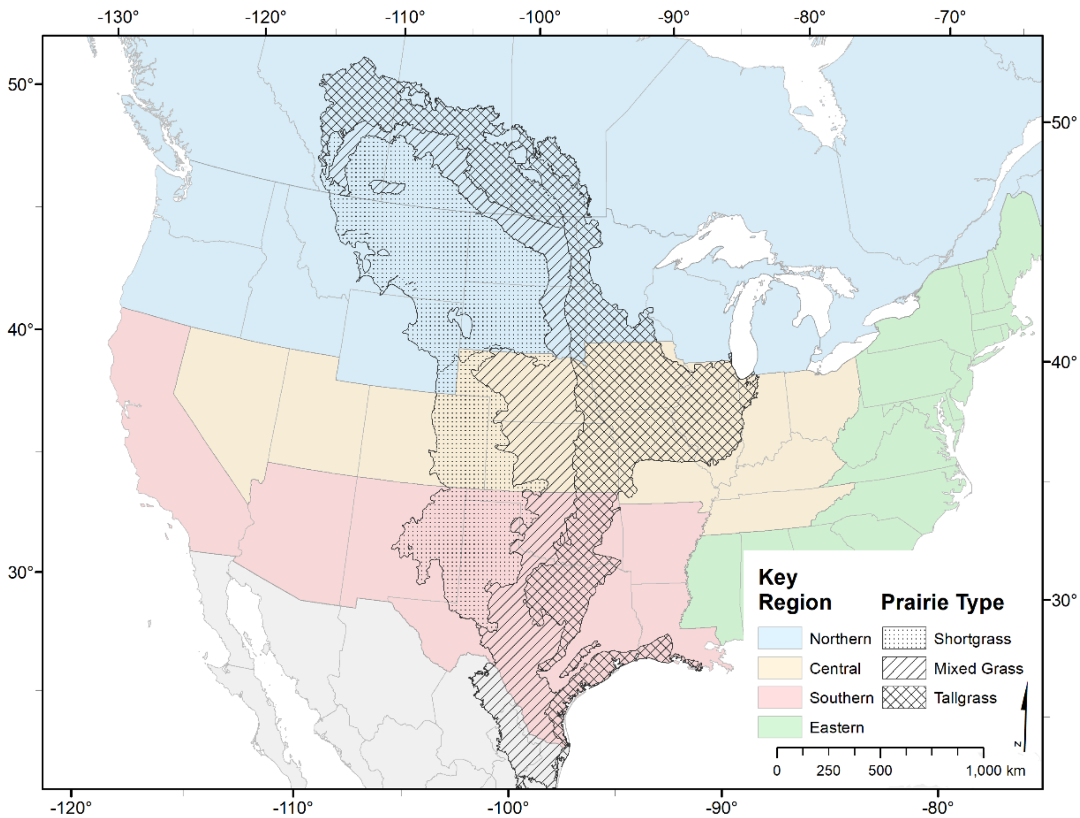

Figure 5.2. Map of North America divided into regions and prairie types; regions: northern (blue), central (orange), southern (red), and eastern (green), and prairie types: shortgrass prairie (stippled), mixed-grass prairie (diagonal hatch), and tallgrass prairie (cross hatch). Note that lack of prairie type indicates "other" ecosystems.

Table 5.2. Summary of demographic attributes of bison manager respondents by sector.

	Bison coalition sectors (n = 132)	
Attributes	**Private (n = 121)**	**Public/NGO (n = 11)**
Gender		
Male	99	10
Female	19	1
Preferred not to answer	3	--
Region		
Northern	56	2
Central	42	7
Southern	17	2
Eastern	6	--
Ecosystem		
Shortgrass	21	3
Mixed grass	75	4
Tallgrass	10	4
Other	15	--
Education level		
Without college experience	20	1
With college experience	68	7
Graduate degrees	33	3
Management experience with bison		
Less than 4 years	16	4
4-10 years	34	--
11-20 years	36	2
More than 20 years	35	5
Operation Size		
Preferred not to answer	8	1
Small (<100 animals)	60	6
Medium (101-999 animals)	39	4
Large (>1000 animals)	14	--
Acreage		
Preferred not to answer	5	1
Small (<100 acres)	25	--
Medium (101-999 acres)	44	1
Large (>1000 acres)	47	9

We separated bison herds by size. The respondents represent up to 132 separate operations ranging from <15 to >3,000 bison with an average of 51-100 bison in each herd.

In the public/NGO sector, 10 herds varied widely from <15 to 1,000 bison on large land holdings of 401 to >5,000 acres including seven without leasing grazing land. Three of 11 indicated that they had privately owned bison at the time or prior to taking the survey, indicating some level of integration between public and private sectors. In the private sector, 14 large operations with more than 1000 bison accounted for 12% of the 121 responses. Thirteen of those 14 large operations used more than 5,000 acres, and one used 2,000–5,000 acres, with six leasing grazing land and eight without leasing grazing land. Thirty-nine medium sized operations in the private sector with 101–1,000 bison used 100 acres to over 5,000 acres, with 11 managers leasing grazing land and 27 without leasing grazing land. Sixty private sector managers held less than 100 bison on 11–5,000 acres, with 12 managers leasing grazing land and 44 without leasing grazing land. A comprehensive table of responses is presented in Appendix E Table 11.3.

We ask for educational levels and binned them into three major classifications, including no high school diploma, high school diploma/GED into the class of ‘without college experience,’ some college experience, 2-year degree, 4-year degree into the class of ‘with college experience,’ and finally master’s degree, professional degree (including MAg, MBA, MEng, etc.), and doctoral degrees (Ph.D., Sc.D./D.Sc., DVM, EdD, MD, JD) into the class of ‘graduate degree.’ Predominantly, bison managers have college degrees, accounting for 91% of public/NGO managers and 84% of private managers. Managers with over 11 years of bison experience were 64% of the public/NGO sector and 59% in the private sector. Income from managing bison accounted for less than 33% of annual income in 56% of public/NGO managers and 50% of private sector managers.

5.3.3. Statistical analyses

All data visualizations and computations were performed in Stata/IC (v16.0, 2019, StataCorp, College Station, TX, USA). Slideplots (Stata Statistical Software Components package “slideplot”), similar to Likert graphs without neutral illustrated, were used to show relative leanings of respondents’ values, attitudes, practices, and observations of various economic and ecological perspectives and techniques by sector. Predictive ordinary least squares linear regressions were based on ordinal educational levels and categorical educational disciplines and results were adjusted according to survey sampling. Default method for variance estimation is Taylor linearization. Finite population correction is 0.95 because we sampled from an estimated 15% of the bison manger population without replacement (Valliant and Dever 2018). We used t-tests to compare means between private and public/NGO sectors with α at $p < 0.05$.

5.4. Results

Total resiliency was 6.0 out of 10 for the entire bison coalition; individual managers ranged from 0.5 to 10, the public/NGO sector averaged 5.8, and the private sector averaged 6.0 (Figure 5.3). We now call attention to measures at or below the midpoint on the resiliency scale of 0–10. Low scores on these measures reduce the system’s overall resiliency to environmental change. Low resiliency scores in the public/NGO sector were associated with one primary measure of exposure (bison herd size), three primary measures of sensitivity (herd production, other markets, age and gender) and two primary measures of adaptive capacity (external revenue, grazing leases). Low resiliency scores in the private sector were associated with two primary measures of exposure (bison population, and harvest), three primary measures of sensitivity (environmental variation, herd production, age and gender) and one primary measure of adaptive capacity (grazing leases; Figure 5.3).

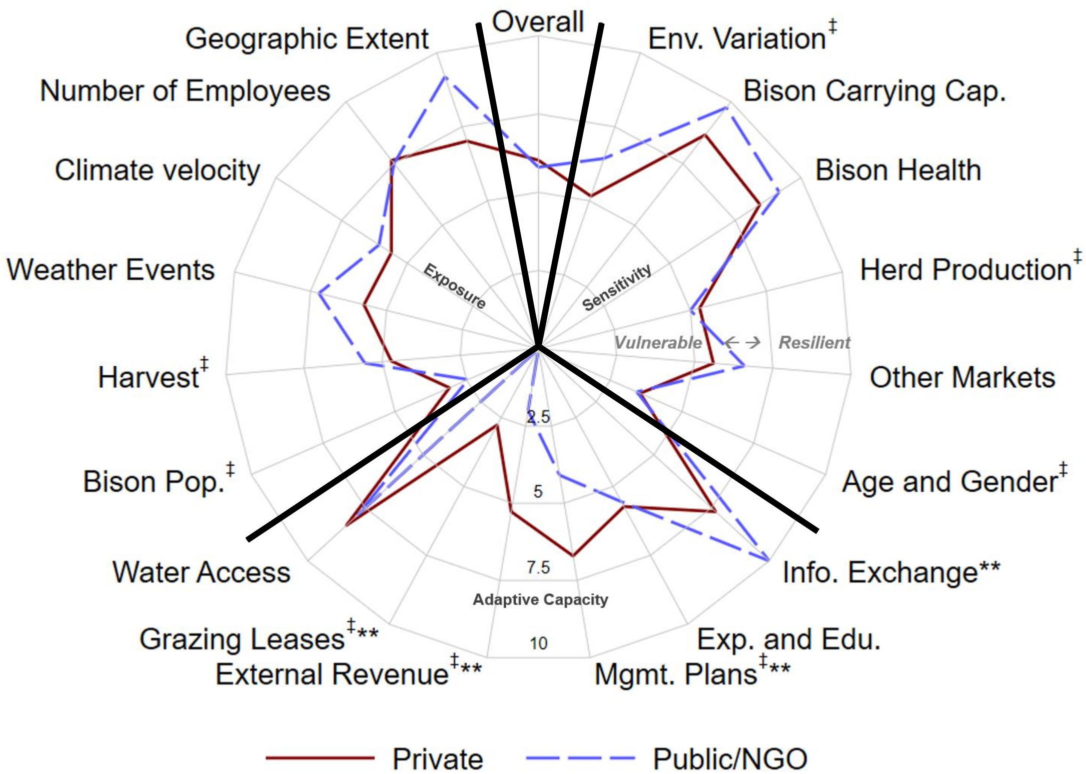

Figure 5.3. Radar plot of vulnerability scoping diagram median measures of private (*n* = 121) and public/NGO (*n* = 11) bison mangers. Symbols: ‡ = near or below the acceptable resilience midpoint of 5, and ** = significantly different between sectors.

5.4.1. Exposure, sensitivity, and adaptive capacity

Adaptive capacity was the only dimension of vulnerability that varied significantly (Figure 5.4). Public/NGO respondents averaged 4.1 ± 1.8 and ranged from 0.7 to 7.5, and private respondents averaged 5.7 ± 2.1 and ranged from 1.4 to 10 (Table 5.3). Exposure did not vary significantly between sectors but averaged 6.1 ± 1.4 and ranged from 4.7 to 8.8 for public/NGO respondents; private respondents averaged 5.8 ± 1.2 and ranged from 2.8 to 8.8 (Table 5.3). Sensitivity did not vary significantly. Public/NGO respondents averaged 7.5 ± 1.9 and ranged from 2.8 to 10 while private respondents averaged 6.3 ± 1.5 and ranged from 0.3 to 10 (Table 5.3). Comparison of means of exposure, sensitivity, or adaptive capacity across regions and across ecosystems did not vary significantly (Appendix E Table 11.2). Three of 11 public/NGO sector respondents indicated that they privately owned bison at the time or prior to taking the survey, indicating some level of integration between public and private sectors.

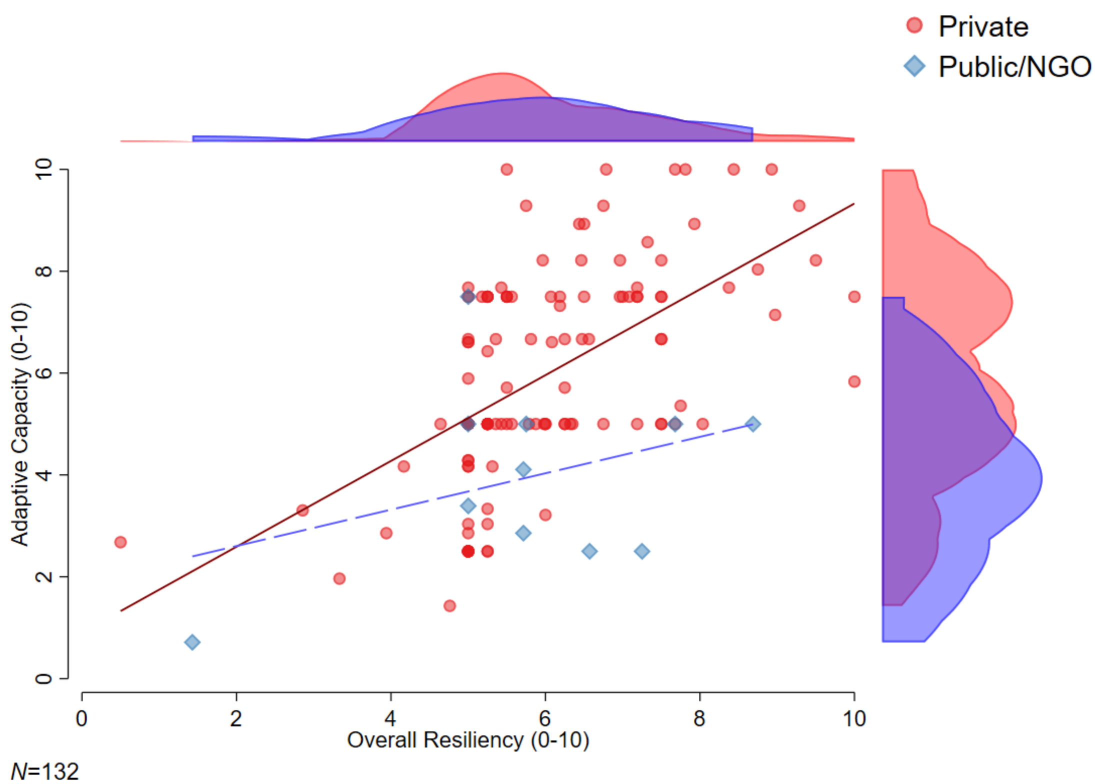

Figure 5.4. Correlation of adaptive capacity scores by sector over overall resiliency score by private (*n* = 121) and public/NGO (*n* = 11) sectors with kernel density plots

illustrating overlapping distribution. Adaptive capacity resiliency scores differ significantly ($p \leq 0.005$), where private sector averages 5.7 and private/NGO sector averages 4.1 (Table 5.2).

Table 5.3. Overall resiliency scores and composition of dimension resiliency scores by sector.

Sector	Resiliency Score	N	Median	SD	Min	Max
Private	Overall resiliency	121	5.6	1.4	0.5	10.0
	Exposure	117	5.8	1.2	2.8	8.8
	Sensitivity	121	6.3	1.5	0.3	10.0
	Adaptive Capacity	121	5.7	2.1	1.4	10.0
Public/NGO	Overall resiliency	11	5.7	1.9	1.4	8.7
	Exposure	10	6.1	1.4	4.7	8.8
	Sensitivity	11	7.5	1.9	2.8	10.0
	Adaptive Capacity	11	4.1	1.8	0.7	7.5

Four measures indicated the largest differences in adaptive capacity between public/NGO and private sectors (Figure 5.3): information exchange, leasing grazing lands, management plans, and external revenue. In particular, information exchange—monitoring diversity of pasture plants and wildlife was more prevalent in public/NGO sector ($p \leq 0.001$), external revenue—investment income for sustaining bison production was more prevalent in the private sector ($p \leq 0.05$), and leasing grazing lands was more prevalent in the private sector ($p \leq 0.001$). Some measures indicated exceptionally high or low scores, including the highly scored water access and lowly scored grazing leases within adaptive capacity. A comprehensive description of the responses from bison managers that comprise measures of resiliency is presented in Appendix E Table 11.2. A summary cross-tabulation of overall resiliency, exposure, sensitivity, adaptive capacity scores over region, ecosystem, and sector is provided in Appendix E Table 11.3.

5.4.1.1. Education level

An increase in education corresponded to an increase in an individual's resiliency score from an estimated score of 5.3 for those without college experience, to 6.1 for those with college experience (some college experience or have attained a 2-year or 4-yr degree), to 6.3 for those with a graduate degree and up to 7.3 for respondents with a doctoral degree (Figure 5.5). Resiliency scores were linearly related to gender and management experience and education level (n = 129, R^2 = 0.08, $p \leq 0.001$).

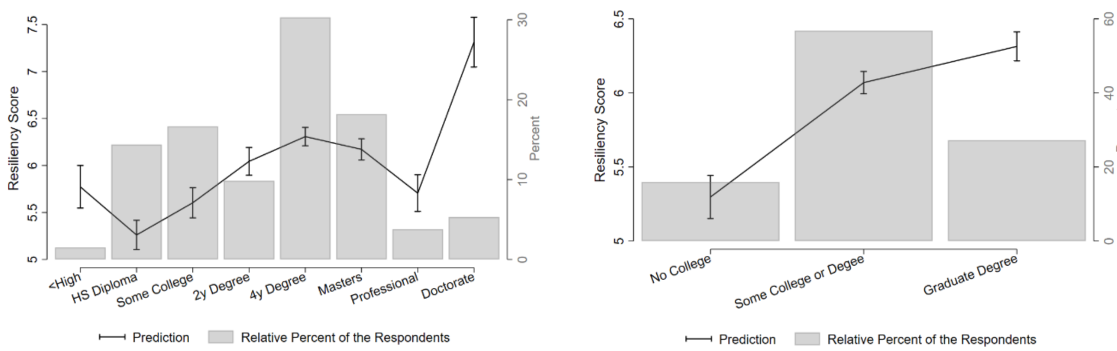

Figure 5.5. Average resiliency score by educational level (left, specific levels and right) binned educational levels). Education levels range from not having a high school diploma to a doctoral degree.

5.4.2. Values, attitudes, and practices

Private and public/NGO bison managers share similar values and attitudes towards ecological and economic balance (Figure 5.6 and Figure 5.7). Ecological balance was endorsed by 90% of public/NGO and 86% of private managers but only 60% of public/NGO managers valued economic balance, which was endorsed by 81% of private managers. However, when presented with various attitudes and practices for ecological and economic management techniques, affirmation declined within and between the sectors.

Ecological attitudes were consistently affirmative in both sectors for hunting (70% positive), prescribed burning (72% positive), fecal analyses for diet and disease (84% positive), vaccinations (81% positive) and necropsies (83% positive; Figure 5.6). Treatment for intestinal parasites was more acceptable in the private sector (89% positive) than the public/NGO sector (66% positive). Both sectors were ambivalent about the use of genotypic and pedigree tools for breeding (53% positive). Private sector managers were more likely than public/NGO managers to practice treating parasites (91% vs. 36% affirmative), treating diseases (89% vs. 45% affirmative) and monitoring spring green-up (93% vs. 64% affirmative).

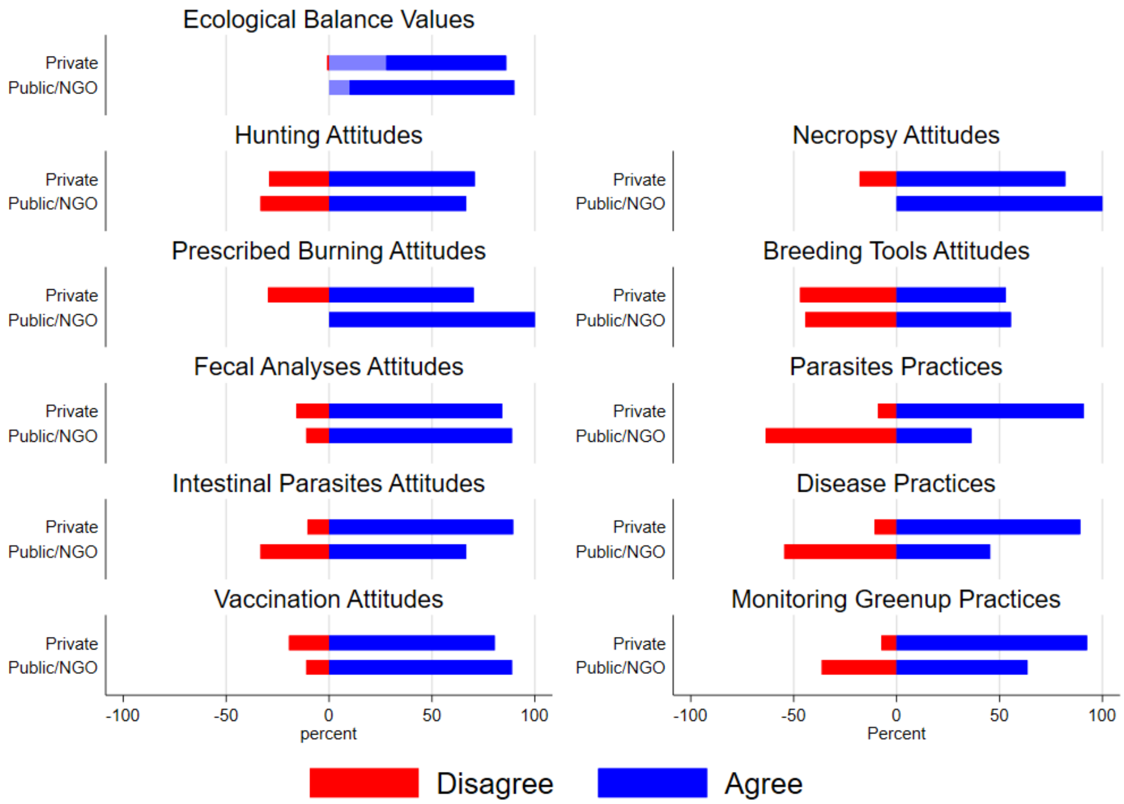

Figure 5.6. Bison manager values, attitudes, and practices towards various ecological tools by sector.

Economic attitudes were less consistent than ecological attitudes in both sectors (Figure 5.7). Public/NGO sector managers viewed agricultural subsidies negatively, such as tax credits (33% positive), but were open to cost sharing programs (78% positive), diverse livestock (78% positive), and diverse land use (100% positive). Private sector managers were split on attitudes towards cost sharing (51% positive), agricultural subsidies (61% positive) and diverse livestock use (58% positive), but largely agreed with diverse land use (90% positive) and hunting on property (71% positive). Over 75% of private managers pumped drinking water and prepared drought management plans while also monitoring pastures, bison pregnancy, and survival of bison calves whereas only 50% of public/NGO managers used these practices.

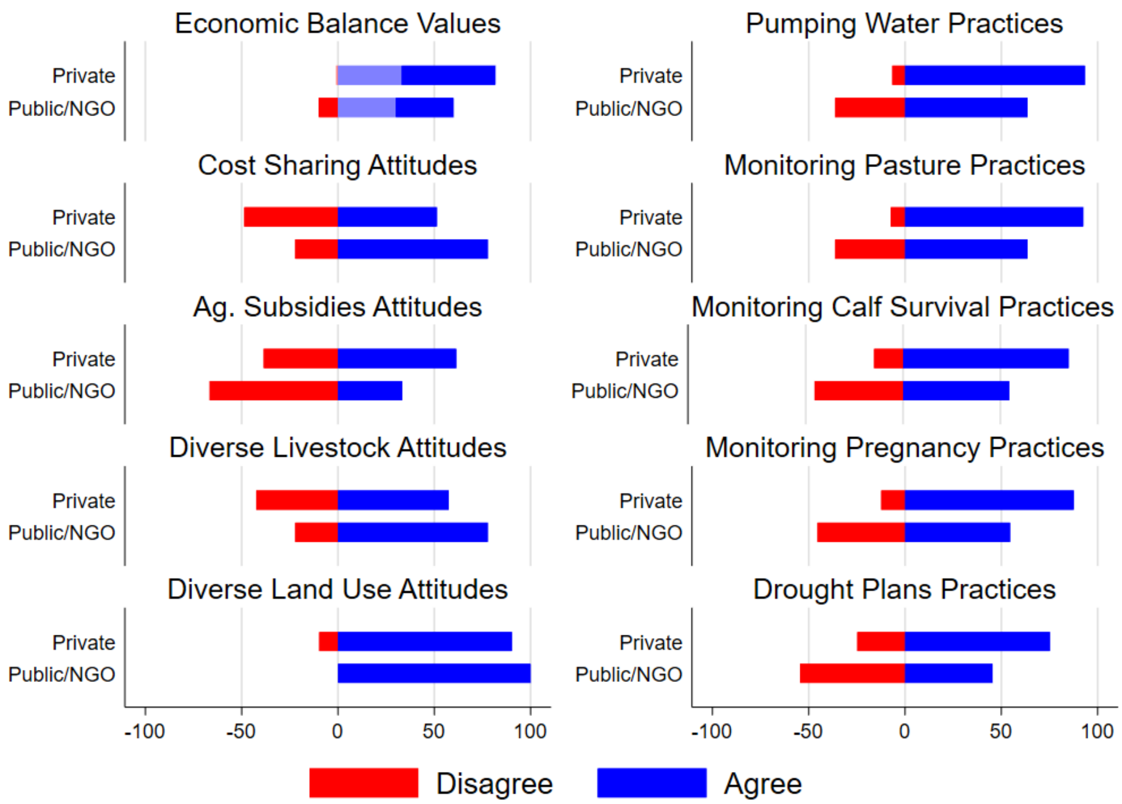

Figure 5.7. Bison manager values, attitudes, and practices towards various economic tools by sector.

5.4.3. Dietary supplementation management practices

Majority of bison diet supplementation was reported as minerals (75%) and hay (70%), whereas the next highest supplementations, but a minority of managers indicated, were protein boosted roughage cubes (30%) and grain (23%; Table 5.3). The predominant combination of supplements was to use roughage cubes, minerals, and hay (16%); the next two most common combinations were minerals and hay, and grain, minerals and hay

(~14% each); followed by minerals only (10%) and hay only (7%). In sum, the use of either hay or minerals in combination with either roughage cubes or grain are the predominant supplementation practices by bison managers (62%). Of the 11 NGO/public managers, three (27%) indicated that they supplied minerals and hay, one (9%) indicated “none”, and the remaining 7 (64%) preferred not to answer. By comparison to the private sector to the NGO/public managers that responded, hay and minerals are consistent management practices (≥70%).

Table 5.4. Bison managers’ responses about supplementation used to sustain bison.

Supplementation Type	Count	Percent
Minerals	99	75%
Hay	93	70%
Roughage cubes	40	30%
Grain	31	23%
Haylage/Silage	14	11%
Other	10	8%
Prefer not to answer	9	7%
None	6	5%

Only 10 (less than 8%) of responses indicated using ‘other’ supplementations and were also only in the private sector. Of the ‘other’ responses, only four prompted re-coding to existing categories, as an example; “protein cubes”—re-coded that individual’s response to include roughage cubes as a supplement (Table 5.4).

Table 5.5. Respondents typed answers to Q30: “What supplement(s) do you use with your herd(s)?” under the option of ‘other.’ Abbreviation: ID, response identification number.

ID	Other (<8% of respondents)	Recode?	Reason
25	“alfalfa pellets for crude protein when winter feeding hay”	Yes	Included “roughage cube” as response, hay was already indicated
51	“Pellets and hay for Alberta winter”	Yes	Included “roughage cube” as response, hay was already indicated
59	“protein cubes”	Yes	Included “roughage cube” as response
74	“Hay only from thier [*sic*] grazing fields”	No	Already indicated “hay” in their response
87	“Potatoes”	No	Already indicated “grain” in their response
92	“Protein Cubes”	Yes	Included “roughage cube” as response
94	“lick tubs”	No	Already indicated “minerals” in their response
102	“Salt”	No	Already indicated “minerals” in their response
118	“grass screenings”	No	Already indicated “hay” in their response
136	“Acv = Apple cider vinegar”	No	No good fit to existing categories

5.4.4. Source of bison information that bison managers use

Majority of bison managers seek information from their own bison network of bison associations and other bison managers (83% and 80%, respectively; Table 5.5). Thirty-six percent indicated that they seek information from university professors or research scientists. Only 12-15% seek information from public officials such as extension agents or wildlife biologists. Of the managers that seek bison-related information, they reach out at least 2-3 times per year and many reach out more than 4 times per year

(Appendix E Table 11.3). This suggests that bison managers trust information they receive from their closest circles (i.e., other bison managers).

Table 5.6. Bison managers seek bison-related information from various sources (out of 132 respondents).

Supplementation Type	Count	Percent
Bison associations	109	83%
Bison producers (not neighbors)	106	80%
University professors and research scientists	47	36%
Family members	22	17%
Extension agent	20	15%
Public agents (wildlife officers, state park bison herd managers, etc.)	16	12%
None	12	9%
Neighbors	10	8%
Other	9	8%
Prefer not to answer	0	0%

5.5. Discussion

Our hypothesis that public and private sectors of bison managers would score differently for vulnerability was not supported by comparisons of exposure and sensitivity. Both sectors encounter the same environmental conditions (e.g., weather events, climate velocity; Figure 5.3). Moreover, vulnerability did not differ across regions and ecosystems (Figure 5.2) for either private or public sectors. Private sector operations were much more variable than those of the public sector in attributes of bison production (number of bison, carrying capacity) but attributes of managers were similar among sectors, which resulted in similar scores for sensitivity to environmental change. Therefore, the vulnerability of the bison coalition collectively scores moderately to effects of environmental change.

Strong values for ecological balance (Figure 5.6) in both private and public sector are consistent with the high variability of weather on the Great Plains and the nature of bison that, unlike domestic livestock, are non-amenable to intensive use but tolerant of extreme weather (Martin 2014). Bison managers in both sectors minimize their vulnerability to drought by emphasizing water supplies (Figure 5.3), which is consistent with the high drought frequency of the Great Plains (Cook et al. 2015). A wide diversity of operations exists within the bison coalition, but managers appear to possess similar characteristics. Most bison managers were male (85%) and 67% have attained higher educations and 62% have over a decade of experience with bison. The managers of the bison coalition appear to match Californian cattlemen who are also predominantly male (83%) and highly educated (63% having an associate's degree or higher (Roche et al. 2015)) and 72% of rangeland managers have a 4-year degree (U.S. Bureau of Labor Statistics 2018), whereas only 36% rural Americans of have attained a 4-year education (United States Census Bureau 2017, USDA Economic Research Service 2018). Higher education of bison managers may be key to reducing vulnerability in two ways: 1) education increases the ability to seek, sort, and apply new information from multiple sources (Appendix E Table 11.3), and 2) education also increases the ability to generate external income that diversifies revenue streams (Figure 5.3). Education facilitates information exchange through social networks and associations outside the bison coalition, which may be critical to recruitment of new managers in the private sector and thus building the adaptive capacity of the bison coalition (Table 5.1).

The use of drought plans, grazing management plans, insurance policies, and external revenue among the private sector managers is consistent with high scores for information exchange (Appendix E Table 11.2). As an example, 70% of cattlemen of the southern Great Plains (Kansas, Oklahoma, and Texas), of whom 57% agree that climate is changing and that climate variability is increasing, believe that win-win approaches for conservation and production are possible, education will help demonstrate long-term ecological benefits of conservation, and mitigation of economic trade-offs for environmental conservation and adaptation is necessary. Cattle ranchers also identified governmental regulations and policies to be the largest threats to their operations, not environmental change. Cattle ranchers place their trust in other cattle ranchers and cattlemen's associations. Similarly, in this survey, bison managers appear to place more trust in other bison managers and bison associations over other sources for bison-related information, that is, 80% of bison managers seek bison-related information from bison associations or other bison managers, followed by academic scientists at 36% (Table 5.6); public officials were contacted less than 15% of the time. Whereas cattlemen have been classified as "adaptation deficient" (Williamson et al. 2012, Joyce et al. 2013), in this study, bison managers appear to be moderately adaptation savvy. Although, levels of adaptive capacity will decline proportionally with accruing effects of climate change into the remainder of the 21st century if improvements are not enacted.

Experience may be an important factor for managing the complexity of grazing systems; managing bison in either public or private sectors appears to favor long personal experience with the animals and the environment that may be achieved through apprenticeships with experienced managers (Sorice et al. 2014). Similarly, in Kenya, Tanzania, and Australia, having long personal experience is desirable because of the frequent cycles of drought. Such experiential knowledge was critical for appropriate and timely responses to altering stocking rates, catalyzing a quicker rebound for grassland and animal productivity than inexperienced managers (Fratkin 1991, Stafford Smith et al. 2007, Mlekwa 2018). Roughly 20% of bison managers had more than 20 years of experience. High years of experience also indicates an aging population of bison managers that mirrors the aging demographic of farm operators in the US nationwide (United States Department of Agriculture 2019). It raises the question, unanswered by our data, of how bison managers are practically prepared for their work, beyond formal education. Apprenticeships are common in all agricultural livelihoods, bison included, but it is unknown the extent to which apprenticeship requirements (formal or ad hoc) drive the exclusion of women or people of color in the bison industry. Future studies should investigate the professional training and development of bison managers outside of the formal education system, including the influence of family businesses, professional organizations, and youth programs such as FFA and 4H. Possible future interventions might draw from the lessons learned in traditional STEM disciplines' to diversify membership.

Values for economic balance were also similar between private and public sector despite large differences in their source of revenues (Figures 5.3 and 5.7). Private and public managers probably experience and share similar economic risks on the Great Plains where droughts, fires, heatwaves, and blizzards impact all rural communities. Managers in both sectors had experienced 2–5 extreme environmental events in the last decade (Appendix E Table 11.2). Up to 27% of public sector managers also had experience of bison as private producers, which suggests a familiarity with the economic risks to the bison coalition. Consistent scores for economic elements of exposure (e.g. number of employees) and sensitivity (e.g. herd production, bison health, other markets) provide consistent experiences that reinforce values for managers in the system.

Public and private sector managers held similar attitudes: seven attitudes related to ecological balance and four attitudes related to economic balance. Shared ecological values of private and public managers indicate private managers are aware of the ecological importance of bison (Figure 5.6). However, sectors differed in their decisions about management practices, which indicates a diversity in solutions to common environmental and economic constraints. Private management emphasized practices focused on animal production, including parasites, disease, and forage growth (green-up) and availability more than the managers in the public sector. Privately owned bison may have greater exposure to transmission of parasites and diseases, if animals are held at high densities (Huntington et al. 2019). Furthermore, private managers may need to comply with animal health regulations to maintain consistency and quality of meat for markets and to reduce the costs of supplemental feed as soon as possible in the spring (National Bison

Association 2015). Private managers recognize the genetic value of public herds of bison as a “seed bank” that should be preserved (Sanderson et al. 2008). Public managers were less likely than private managers to monitor pastures, calf production, and pregnancy because bison are managed as part of an ecosystem with minimal handling and observation. The lower use of drought and grazing plans in the public sector is consistent with the management of bison for cultural and supporting ecosystem services rather than as provisioning services of the ecosystem (Figure 5.7). “Wild” phenotypes of public bison have an economic value to private owners of bison (Sanderson et al. 2008), for example, management practices for public herds of bison may also foster valuable phenotypes for expansion and persistence of bison as climate changes. Public managers are less likely to provide supplemental food and water or to treat parasite and disease loads of bison (Figure 5.6), which passively selects for phenotypes that can tolerate extreme weather and outbreaks of disease. Modern bison are the survivors of an outbreak of Texas tick fever that is estimated to have caused 81% mortality of bison in the 1880s (Stoneberg Holt 2018). Differences between public and private practices may be complementary and thus provide resilience for the bison coalition across both sectors.

As example of progressive conservation economics within the private sector in the initiative to strive for smaller carcasses because larger carcasses were less efficient in meat processing facilities and counter to consumer preferences (Conley et al. 2018, Gehring 2018). Bison carcasses are longer than those of beef carcasses, so an increase in carcass size would potentially contact the floor, requiring premature partitioning of the carcass, taking more time to process each carcass—a considerable delay in production efficiency.

In addition, consumers are accustomed to smaller cuts of steaks associated with beef cattle. This is counter to the trends of the beef industry, where size of beef carcasses has increased over the last 30 years and is incentivized by market premiums from beef processors and meat packers (Klemm and Briske 2020). The bison industry could prepare producers for climate change by using market premiums for high quality, high efficiency to offset smaller carcass sizes. Short-term gains in body size may occur in some isolated locations along the Great Plains into the next 5-10 years if increasing atmospheric carbon dioxide improves forage quality (i.e. CO_2 fertilization (Mack et al. 2004, Griffith et al. 2017)), but rising temperature and drought will eventually reduce forage quality and digestibility (Barboza et al. 2009, Craine et al. 2010). Rising temperature will also outpace thermoregulation efficiency of bison, reducing growth rates (Martin and Barboza 2020*a*, *b*). Some indirect effects of climate change that will further challenge market viability that might encourage smaller body sizes and carcasses include decreasing availability and increasing production costs of feed stocks for finishing animals prior to slaughter—in short, incentivizing grass finishing of bison would be beneficial to the sustainability of bison conservation and to the resiliency of the bison coalition.

Consumer desire for sustainably produced meat is rising and 70% of bison managers indicated that they only supplement with hay and minerals, but not grain or other crops (Table 5.5). This practice helps reduce carbon emissions from transportation of grain and fodder, increases water and carbon sequestration if the hay is produced locally and without irrigation, and keeps input costs of production low. Two parallel markets for bison exist: grass-finished and grain-finished. The grass-finished market has established higher premiums, mostly because production is slower (2.5-3.5 years compared to 1.5-2.5 years, respectively) and consumer demand for grass-only produced meat is high and growing. Overall, bison production fairs a market value that ranges between 1.5 to 3.3-fold more than beef since 2000 (Carter 2019) and bison production is largely unsubsidized (i.e., few environmental externalities are being offset). Higher profit margins for bison markets help absorb costs for implementing climate change adaptations right now.

5.5.1. Recommendations and implications

Eighty percent of 372,000 bison in North American bison are maintained in the private sector, whereas the public bison population has remained at 20,000 animals since the 1940s. The private sector has been criticized for emphasizing predominantly provisional (e.g., meat production) ecosystem services (Geist 1988, Greenwald et al. 2013, Gooden and ‘t Sas-Rolfes 2019) at the cost of supporting, regulating and cultural services from the ecosystem. Consumptive uses do not detract from the number or the quality of bison on public lands (Tensen 2016). In contrast, evidence-based grazing, habitat, and land management practices that emphasize other ecosystem services (i.e., supporting, regulating, and cultural) build more robust and productive ecosystems (Kareiva and Marvier 2012, Kareiva and Fuller 2017, Gooden 2019, Wang et al. 2020), that is, provisional services enhance rather than detract from other ecosystem services (Foley et al. 2005). Moreover, Barboza and Martin (2020) illustrated that overlaying concept maps of the components of private and public sectors of bison management fully complement each other, further supporting formalization of the bison coalition; in short, production and conservation are inextricable. This establishes that the private sector has a major responsibility regarding bison conservation with improved land, habitat, and wildlife stewardship and requires a more comprehensive understanding of the perspectives and vulnerabilities of those that manage these lands. Conversely, because public lands are more climatically stressed than private lands, the public sector bears major responsibility to distribute "climate resistant seed stock" to other sectors as a source of hardy genetics for increasingly harsh environments. Values and attitudes of ecology and economy are shared among bison managers, suggesting that integration and collaboration between sectors is likely. Trust among other bison managers is high compared to other sources of bison-related information. Further integration of bison sectors into a more inclusive coalition would likely initiate creation of novel adaptive solutions to the effects of changing climate and culture.

By year 2050, environmental change will further degrade productivity of the Great Plains, hence increasing exposure and sensitivity of bison managers. Lack of adaptation or mitigation of exposure and sensitivity will increase vulnerability for bison and their managers. For bison managers, reducing sensitivity and vulnerability requires improving adaptive capacity through achieving high levels of communication and coordination between sectors and among individuals, increasing access to leasing grazing lands during drought, and improving monitoring of pasture and wildlife diversity and abundance. A system similar to the bison coalition can achieve conservation of native prairie biomes across the Great Plains, which are predominantly privately owned (Fuhlendorf et al. 2018, Huffman 2019). Integration of wildlife conservation across all sectors (or establishment of new sectors) will reduce vulnerability to changing climate and culture in the 21st Century.

The founder of wildlife conservation, Aldo Leopold, called for an improved and increased land ethic but feared that it would require a loss of nature's intrinsic beauty and biodiversity to force society to change approximately 70 years ago (Leopold 1939, 1949). A cultural shift in America has been occurring since Leopold's call to action in 1948 for improved conservation of working lands, wildlife and land stewards are tapping into markets that demand sustainable production and holistic conservation goals. We find ourselves at the precipice of losing biodiversity and natural beauty because of climate change land use decisions.

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6. CONCLUSIONS

Grasslands comprise nearly 40% of global land mass and are the predominant ecoregion biome for ungulates, hoofed animals (Foley et al. 2005, FAO 2015). Ungulates are relied upon as a food source for human consumption and widely used as grazing tools for grasslands (McMichael et al. 2007, Zeder 2012). The Great Plains and adjacent prairie ecosystems are the largest biome in North America and are approximately 2.9 million km^2, or 14% the landmass of US and Canada (Pieper 1994, 2005). The Great Plains hosts approximately 15.8 million people (4%) of the US and Canadian populations, and approximately 700 (28%) terrestrial vertebrate species are found in the Great Plains compared to the 2100 terrestrial vertebrate species in the US (Johnsgard 2003). Climate change, particularly warming and drought, is more of a driver of environmental change in the grasslands of the Great Plains than human land use, human population, pollution, and invasive species (Bowler et al. 2020)—though conversion of grasslands to croplands should not be trivialized. With this in mind, more than ever, understanding the biological and ecological consequences of climate change are essential. Body size is a functional trait, or common currency, for estimating ecological demands of nutrients, energy, and water for individuals, populations, communities, and entire ecosystems (Peters 1983, McGill et al. 2006, Polly et al. 2011).

6.1. Summary of findings

My data and findings from the fossil record (Martin et al. 2018), decadal datasets (Martin and Barboza 2020*a*), and seasonal observations (Martin and Barboza 2020*b*) indicate that *Bison* body size change is driven by rising temperatures and increasing droughts. For the Great Plains by 2100, local annual and seasonal temperatures are expected to increase an additional 2-5°C depending on location (Wuebbles et al. 2017) and droughts are expected to reach durations of multiple decades, termed 'megadroughts' (Cook et al. 2015). As result, by 2100, bison are expected to nearly halve in body mass under a global warming scenario of 4°C (IPCC's RCP8.5 model (IPCC-AR5 2013)); a decrease from 665 kg to an expected 357 kg (Martin et al. 2018, Martin and Barboza 2020*a*). Reduced productivity across various ecosystem services will likely hinder economic and social stability for those who make their living on the Great Plains (Parton et al. 1995, 2007, Ojima et al. 2015).

My data and findings from the survey of bison manager vulnerabilities to environmental change suggest that both sectors scored poorly on measures of monitoring environmental variation, gender diversity, grazing leases, bison population, and harvest. These low scores increase overall vulnerability to environmental change. Overall, exposure and sensitivity between sectors do not vary but adaptive capacity varied significantly. Adaptive capacity is the ability to reduce sensitivity to exposure of environmental change and measures of adaptive capacity, specifically: information exchange, external revenue, and grazing leases, offer pathways to build social resiliency to environmental changes as described in Martin et al. (2020) and Chapter 5.

6.2. Implications of findings

The synthesis of data and findings presented in the previous chapters of this dissertation lend themselves to be used by the bison coalition and bison coalition and beyond. I briefly provide a summary of 3 topics that I will delve into further: 1) Conservation—bison are figurative “canaries in the coalmine” but for the prairie states. Changes that they display are useful for monitoring ecological changes upon the prairie. 2) Production—bison can be privately owned and thus provide a mechanism for private land conservation, they have market viability and potential that other species lack, and there are associated concerns of private captivity of animals leading to domestication. 3) Paleobiology and ecology—debates about extinctions, macroevolution, and evolutionary adaptation rates to avoid extinction.

6.2.1. Conservation—sentinels of the prairie

Bison are expected to have mature body mass decline of 41 ± 10 kg per 1°C of global mean temperature rise, to an estimated body mass of 357 ± 54 kg with a 4°C rise over the 20th century average, essentially half the body mass they are today (as estimated in Martin et al. (2018) and Chapter 2). More specifically female bison will average 252 kg and male bison will average 446 kg (as estimated in Martin and Barboza (2020*a*) and Chapter 3). This is important, because, for terrestrial mammals with body mass less than ~300 kg, reproductive strategies shift from more *K*-selection type to more *r*-selection type (Famoso et al. 2018), that is, reproduction rates are expected to shift from one or less than one offspring annually to more than two offspring annually—given that body maintenance and metabolic demands are met to enable reproduction (Barboza et al. 2009). It is unlikely that body maintenance costs will be offset because of declining productivity of rangelands and grasslands due to effects of climate change—forage quality and quantity are expected to decline with rising temperature and drought (Derner et al. 2018, 2020, Augustine et al.

2018). Keying in on subtle changes of body mass over long-term datasets such as those from Wind Cave National Park presented in Martin and Barboza (2020*a*) in other large-bodied taxa are crucial for monitoring outcomes of ecosystem productivity leading through the 21st century. Martin and Barboza (2020*a*) indicate that their models of temperature, drought, and asymptotic body mass account for between 80–96% of variation in body mass. Correctly accounting for residual variation is critical for anticipatory conservation, where ecological restoration techniques that rely on accurate estimates of biological changes are implemented on the expectation of certain outcomes and consequences. For example, assisted species translocation should target the leading edge of a biome and not the lagging edge (Wingard et al. 2017).

6.2.2. Production—markets and opportunities for agricultural land conversion and conservation

The Northern Great Plains are approximately 70% privately owned and are in cattle operations; 50% of all cattle in North America are in the Great Plains (Parton et al. 2007, Ojima et al. 2015). Across the plains, 85% of the farms and ranches have fewer than 100 head of cattle, more than 46% have fewer than 50 head of cattle. Stocking rates of cattle operations vary little from bison operations which also average between 51-100 head of bison (Chapter 5 (Martin et al. 2020)), these bison herd sizes match those of cattle operations on the Great Plains. Since 2004, market carcass prices of bison ($211–509/ 100 lbs (cent weight or "cwt")[**]) have been 1.5–3.3 times higher than cattle ($148–270/ cwt)

[**] All prices have been corrected to 2018 US dollar equivalents (U.S. Bureau of Labor Statistics 2020).

with bison prices 2.4-fold higher since 2004 and 1.7-fold higher since 2008 (Carter 2019, USDA 2020). However, keep in mind, we predict that body mass will halve from 665 kg to 357 kg, resulting in skin surface area to also decline by 34% from approximately 4.2 m^2 to 2.8 m^2.

Granted, the production for bison lacks agricultural subsidies that are privy to cattle production. Subsidies in the cattle production industry largely incentivize inflated production at the cost of environmental degradation, or referred to as externalities. Bison, on the other hand, with the lack of subsidies, has become sensitive to environmental degradation and thus environmentally conscious. Therefore, the value of bison and their carcasses more likely reflects the cost of externalities which are subsidized in cattle production. Profits margins for bison (and likely cattle) are expected to decline as a result of climate change without adaptive measures but may be more sensitive to environmental degradation and thus more adaptive by altering stocking rates to match shifting carrying capacity.

Conversion costs for heavy-duty equipment, facilities upgrades, and perimeter fence may be limiting for many cattle ranchers to transform their properties for bison conservation, thus incentives for conservation conversion may be most effective—cattle operations that average between 50 and 150 head are ideal for converting to bison. All of this is to say that Great Plains cattle operations are likely to be the best targets for efficient transformation of working lands into conservation hotspots, especially given that grasslands productivity will decline (Craine et al. 2010, Seager et al. 2018*a*, *b*). Though, infrastructure grants to offset the high costs for improving perimeter fencing are available through local offices of Natural Resources Conservation Services of the United States Department of Agriculture. While start-up costs are high for bison, the lower daily operating expenses over the long-term favor bison production over cattle production.

6.2.2.1. Private land conservation

Private land conservation (PLC) has positive and negative implications that have been extensively reviewed by Gooden and colleagues (Gooden 2019, Gooden and ‘t Sas-Rolfes 2019, Gooden and Grenyer 2019) and Stolton and colleagues (Stolton et al. 2014, Mitchell et al. 2018). Briefly, Gooden and ‘t Sas-Rolfes (2019) describes three major criticisms of PLCs, including economic inefficiency, value conflict, and implementation effectiveness. Essentially, what is explored in those previous studies and here is the concept of the “land ethic” and the “farmer as the conservationist,” described by Aldo Leopold (1939, 1949). Leopold philosophically preferred public lands for conservation of fauna, flora, and physiography over private lands, but he acknowledged that effective conservation practices on private working lands had major potential for lowering unsustainable harvest and extraction rates (Licht 1997). Leveraging private lands for effective conservation hinge on the use of policy instruments that extol autonomy and self-determination, because in the end, private land conservationists participate in conservation because it is a leisure activity that is both enjoyable and productive (Gooden 2019).

Implementing successful private working lands conservation requires more than acquiring land and providing agro-tourism, eco-tourism, recreational, or hunting opportunities; gate fees are inadequate to cover accumulating deferred maintenance costs (U.S. National Park Service 2018). Access to liquid, regenerative, renewable assets that have market value would benefit private conservation entities economically. Decoupling agriculture from regenerative conservation requires new un-subsidized markets that value carbon sequestration, erosion control, and water preservation.

The bison coalition utilizes bison as the liquid asset to generate revenue through meat and breeding stock sales. Transfers between individuals and sectors are daily common place transactions, public herds such as Custer State Park in South Dakota and Antelope Island in Utah participate in fair-bid auctions for harvest and destocking. Tribal nations building their bison herds, some since the 1930s (Zontek 2007*a*, *b*), have access to bison stock through public herd repatriation as well as fair-bid auctions. Tribal herds are becoming desirable stock for the private sector to acquire because of the climate hardy characteristics of the bison from these austere environments. Inter-sector trade of bison stock is essential for gene swapping and adaptation to forthcoming climate change conditions in various physiographic regions of North America; again, increasingly xeric.

6.2.2.2. Captivity and domestication

Captive bison have been privately owned commercially in relatively large numbers since the 1960s (USDA 2016). Captive animals, in general, are subject to aspects of domestication either intentionally or unintentionally. Domestication of bison is not necessarily a good or bad thing in of itself, but it does present ethical and conservation considerations as we progress with continued captivity of wild animals, not just bison. For example, domestication may ultimately lead to the loss of the wild morphology or wild behaviors that are evolutionarily advantageous such as aggressive and dominate behaviors that produce more protective individuals against predators like wolves.

Captivity has been attributed to having 5 major tenets: constraint, segregation, protection, taming, and dependency (Boice 1981). Constraint being that the animal is limited in it typical pattern of movement, segregation being the animal is removed from its original habitat, protection being the animals are protected against predators including the use fencing and cages, taming being the reduction of the animal's flight distance and increased tolerance of use (i.e., use for shearing, milking, etc.), and dependency being the dependence on the supply from humans of water and food stuffs to captives for survival (Zeder 1982). Of these, ranched bison likely fall under some level of constraint, protection, and taming, but, in all fairness, so too do public bison herds where they are often fenced in (i.e., otherwise it is open season shooting outside of Yellowstone Park boundaries in Montana (Geremia et al. 2011)) and the bison have become largely habituated to visitor presence and to vehicular noise (Borkowski et al. 2006). The accumulation of tolerance traits drives a species towards domestication.

National Parks and wildlife reserves are considered *in situ* (Latin: in position or on site) conservation strategies, but conservation or captive breeding is viewed as *ex situ* conservation (Aune et al. 2017, Teletchea 2017). Privately owned bison then are considered *ex situ*—even though the majority of ranched bison are in their original habitat—counter to the definition of *ex situ*, semantics would suggest that privately owned bison are in fact *in situ* or in their original position/habitats. Semantics aside, captivity of wild animals are feared to be on the path towards domestication. Domestication, as mentioned above, is the culmination of multiple aspects of captivity that perpetuate through several generations of captive animals, especially if all or most of the life cycles of an animal are controlled in captivity and begin to display certain traits of desirability (Zeder 2012, Teletchea 2017).

The path to domestication is long and arduous for both the captives and capturers, involving several generations to complete the transformation of genetic and phenotypic change, of course reversal can still occur—feralization (Zeder 2012). Teletchea (2017) describes the process of domestication along a graduated captivity condition continuum (Figure 6.1). Starting with 0) wildlife species in their native habitats (capture/harvest activities being hunting or fishing), 1) habituation of the captured animal to the new captive habitat, 2) parts of the life cycle taking place in captivity, 3) entire life cycles in captivity with some wild genetic inputs, 4) entire life cycles in captivity with no inputs of wild genetics, and 5) selective breeding program used for specific goals of perpetuating desired traits. Teletchea indicates that animals at captive condition levels 4 and above are essentially domesticated (Figure 6.1).

While PLC promises a pathway to grow conservation areas (Kamal et al. 2015), private wildlife conservation has not been discussed for fears of unintended domestication (Teletchea 2017), among others. The sectors within the bison coalition—zoo herds, Tribal herds, public herds, private herds, and NGO herds—already spans the continuum of captivity (Figure 6.1). Public herds are likely the few herds that are still considered wild animals (scored as 0 on the continuum) and being habituated to their new enclosures with some level of containment and tameness (scored as 1–2), especially those that have perimeter fencing or some other means of hard selection at park boundaries. Tribal and NGO herds are likely in the spectrum of 1–3, while privately ranched bison herds are likely scored between 1–4 with some wild inputs from state herd transfers and some herds practicing no wild inputs. Zoo herds, because they are 100% dependent on human supply of food and water and are highly controlled for their breeding, are likely scored between 3–5. It is in the best interest for the bison coalition to limit the amount of intentional and unintentional domestication for bison.

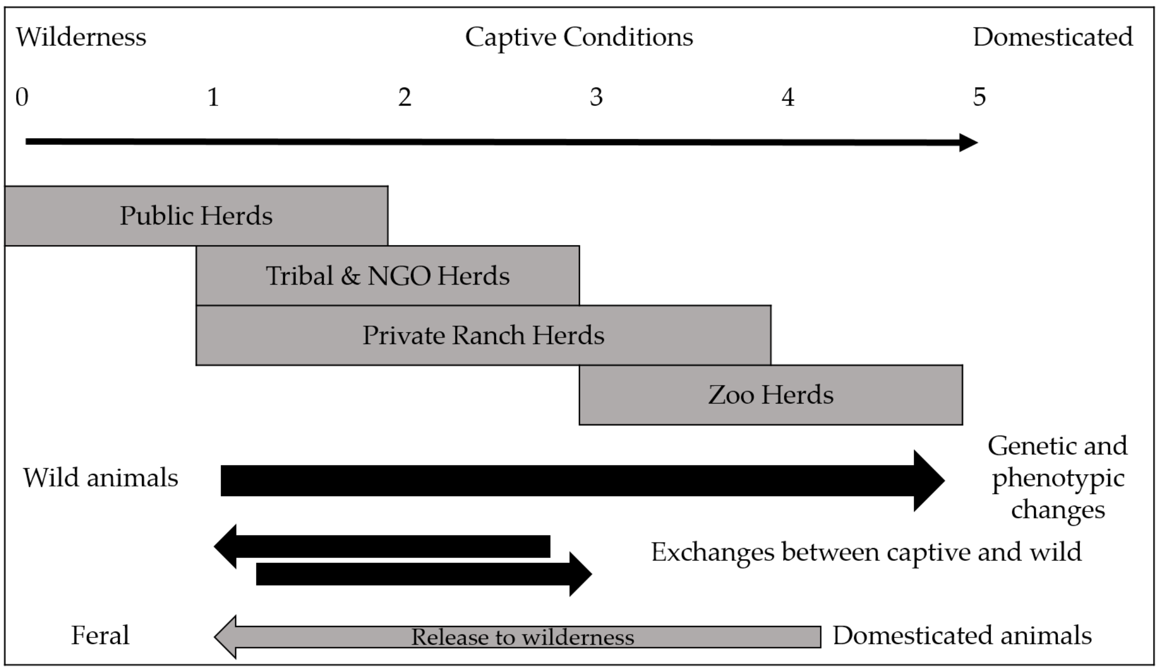

Figure 6.1. Conceptual figure of bison sectors and their adaptation of wildlife species to domestic species along a continuum of captivity. See text for definitions of captive condition scores. Adapted from Teletchea (2017).

6.2.3. Paleobiology and ecology—extinction and adaptation rates

Decades long debates about the causes of terminal Pleistocene extinctions remains unsettled (Martin and Klein 1984, Martin 1990, Koch and Barnosky 2006). Recent publications have described populations of mammoth that survived beyond the end of the

Ice Age mass extinctions were living as diminutives on islands in cold regions of the Russian Arctic Ocean until approximately 3,500 years ago and that transitional body sizes recording the diminution of mammoths has been documented on Santa Rosa island, California (Muhs et al. 2015, Semprebon et al. 2016, Rogers and Slatkin 2017). The ability to scale body size down is largely to do with generational time to adapt to new climatic pressures (Sander et al. 2011, Evans et al. 2012, Smith et al. 2018, Rozzi et al. 2020).

Islands are subject to the maritime effect with minimal temperature change throughout the year including cooler summers and moderate winters due to oceanic wind patterns and heat sink traits of oceanic water and currents in that, extreme temperature and temperature swings are less intense and less frequent. Muted and delayed effects of climate change appear on islands (i.e., long term sea level rise and relatively small changes in temperature) compared to adjacent continental biomes. The delayed and muted warming on islands likely contributed to the ability for mammoths to have adequate habitats of relief, or thermal refugia, from the effects of extreme warming that occurred on continents, globally.

Applying a dynamic framework for body size scaling of endotherms in relation to global climate change vastly changes interpretations of megafaunal extinctions of the last Ice Age, and, accordingly, would predict that isolated populations of megafauna to persist beyond the mass extinction because of muted and delayed local climatic change relative to continental trends. Reducing heat stressors reduces heat flux cost, especially for megafauna; allowing for mammoths to survive on islands with diminished body sizes because they were able to adapt through generations—even though their generation times are large—in large part due to reduced thermal costs and increased thermal refugia in their locations.

6.2.3.1. Case study of adaptation rates

In Table 6.1, I present a summary table of observed and expected body mass adaptation rates for both sexes of mature bison ranging over the fossil record reported in Chapters 2 (Martin et al. 2018) and over decadal trends reported in Chapter 3 (Martin and Barboza 2020*a*). Generation times for bison vary between 3 and 10 years (Martin et al. 2018) and thus give a minimum and maximum rate of body mass change per generation (kg/gen). Martin et al. (2018) indicated that bison may have changed between 0.2 and 0.8 kg/gen over a duration of 3,000 years of warming at the termination of the last Ice Age. Decadal datasets of bison from Wind Cave National Park from 1966 to 2015, duration of 50 years, reported in Chapter 3, however, suggest that female bison have lost between 2.9–9.6 kg per generation and males lost between 11.2–37.4 kg/gen (Table 6.1). Similarly, at Santa Catalina Island, female bison lost between 4.1–13.7 kg per generation and males lost between 2.2–7.3 kg/gen. Climate projections for mid- to late-21st century anticipate hotter drier conditions based on climate models using representative concentration pathways (RCP) of atmospheric radiation equivalent to 4.5 and 8.5 watts/m^2 (IPCC-AR5 2013). The expected timeframe for the same level of warming (~2°C globally) is by 2100 for RCP4.5 emissions for the less severe stabilization scenario, or by 2070 for RCP8.5 emissions for the more severe business-as-usual scenario. Hence, equating to a mean warming of 3-4°C for the northern Great Plains and mean warming of 2-3°C for the southern Great Plains (Wuebbles et al. 2017).

Northern female bison average 373 kg asymptotic body mass and are expected to decrease to 269 (Martin and Barboza 2020*a*), a loss of 104 kg (-28%) and northern male bison average 594 kg and are expected to decrease to 463 kg, a loss of 131 kg (-22%). Depending on generation time of 3 or 10 years, generational adaptation rates for northern Great Plains bison to decrease their asymptotic body mass range for females between 3.9–13.0 kg/gen for RCP4.5 or 6.2–20.8 kg/gen for RCP8.5, respectively, and for males between 4.9–16.4 kg/gen for RCP4.5 or 7.9–26.2 kg/gen for RCP8.5, respectively (Table 6.1).

Southern female bison average 369 kg asymptotic body mass and are expected to decrease to 252 (Martin and Barboza 2020*a*), a loss of 117 kg (-32%) and southern male bison average 543 kg and are expected to decrease to 446 kg, a loss of 97 kg (-18%). Depending on generation time of 3 or 10 years, generational adaptation rates for southern Great Plains bison to decrease their asymptotic body mass range for females between 4.4–14.6 kg/gen for RCP4.5 or 7.0–23.3 kg/gen for RCP8.5, respectively, and for males between 3.7–12.2 kg/gen for RCP4.5 or 5.8–19.5 kg/gen for RCP8.5, respectively (Table 6.1).

Table 6.1. Summary table of observed and modeled adaptation of body mass for both sexes of *Bison* over the fossil record and over decadal trends from Wind Cave National Park (WICA) and Santa Catalina Island (SCI). Two scenarios are presented for adaptation rates with generation times varying between 3 years (short generation times, "S") and 10 years (long generation times, "L"). Abbreviations: BM, body mass (kg); gen, generations; NGP, Northern Great Plains; SGP, Southern Great Plains; RCP4.5, stabilization scenario from IPCC AR5; RCP8.5, business-as-usual scenario from IPCC AR5; Δ, change; and %Δ, percent change.

Sex	Herd	Model	Time (y)	#gen (S)	#gen (L)	Initial (kg)	Final (kg)	ΔBM (kg)	%Δ	ΔBM/ gen (S; kg)	ΔBM/ gen (L; kg)
Both	North America	Fossil (observed)	3000	1000	300	906	670	236	-26%	-0.2	-0.8
F	WICA 1966-2015	Decadal (observed)	50	17	5	445	397	48	-11%	-2.9	-9.6
M	WICA 1966-2015	Decadal (observed)	50	17	5	798	611	187	-23%	-11.2	-37.4
F	SCI 1970s – 2000s	Decadal (observed)	30	10	3	362	321	41	-11%	-4.1	-13.7
M	SCI 1970s – 2000s	Decadal (observed)	30	10	3	534	512	22	-4%	-2.2	-7.3
F	NGP - by 2100	RCP4.5 (projected)	80	27	8	373	269	104	-28%	-3.9	-13.0
F	NGP - by 2070	RCP8.5 (projected)	50	17	5	373	269	104	-28%	-6.2	-20.8
M	NGP - by 2100	RCP4.5 (projected)	80	27	8	594	463	131	-22%	-4.9	-16.4
M	NGP - by 2070	RCP8.5 (projected)	50	17	5	594	463	131	-22%	-7.9	-26.2
F	SGP - by 2100	RCP4.5 (projected)	80	27	8	369	252	117	-32%	-4.4	-14.6
F	SGP - by 2070	RCP8.5 (projected)	50	17	5	369	252	117	-32%	-7.0	-23.3
M	SGP - by 2100	RCP4.5 (projected)	80	27	8	543	446	97	-18%	-3.7	-12.2
M	SGP - by 2070	RCP8.5 (projected)	50	17	5	543	446	97	-18%	-5.8	-19.5

In summary, the required body mass loss for projected warming of 2-3°C for northern and southern Great Plains bison by 2070 and 2100 ranges between -4 to -26 kg/generation which is within reasonable historical contexts of the observed change at WICA over the past 50 years, a range of mass loss between -3 to -37 kg/generation (Table 6.1).

6.2.4. Hope is still a bison—the future of the bison system and the bison coalition

The bison system already extols cooperation between and among sectors of the bison coalition. State bison herds sell bison to private entities and Federal bison herds seed NGO and other public herds and repatriate bison to Tribal herds. Tribal and private entities buy and sell bison from each other. Intentionally or unintentionally, the exchange of bison has also resulted in the exchange of ideas and management strategies. The exchange of ideas and practices have likely allowed the coalescence of values and attitudes (as discussed in Chapter 5) of bison managers across sectors. There is an annual meeting of bison managers that is inclusionary of all sectors, though not all participate in full. The annual conference focuses on continuing education seminars and lectures about bison handling, welfare, and husbandry (National Bison Association 2015). Recent efforts have focused on building educational resources for managers to learn to manage for and reinforce supporting and regulating ecosystem services like increasing landscape vegetation heterogeneity, wildlife diversity and abundance, prescribed burning, and improving erosion control by implementing rotational grazing management practices. To this end, strengthening of inter-sector connections is occurring organically, that is, there are already some 27% of public/NGO bison managers that also privately own bison. This may be an indication of sector integration, leading to further innovation in practice application, as illustrated in Figure 6.2.

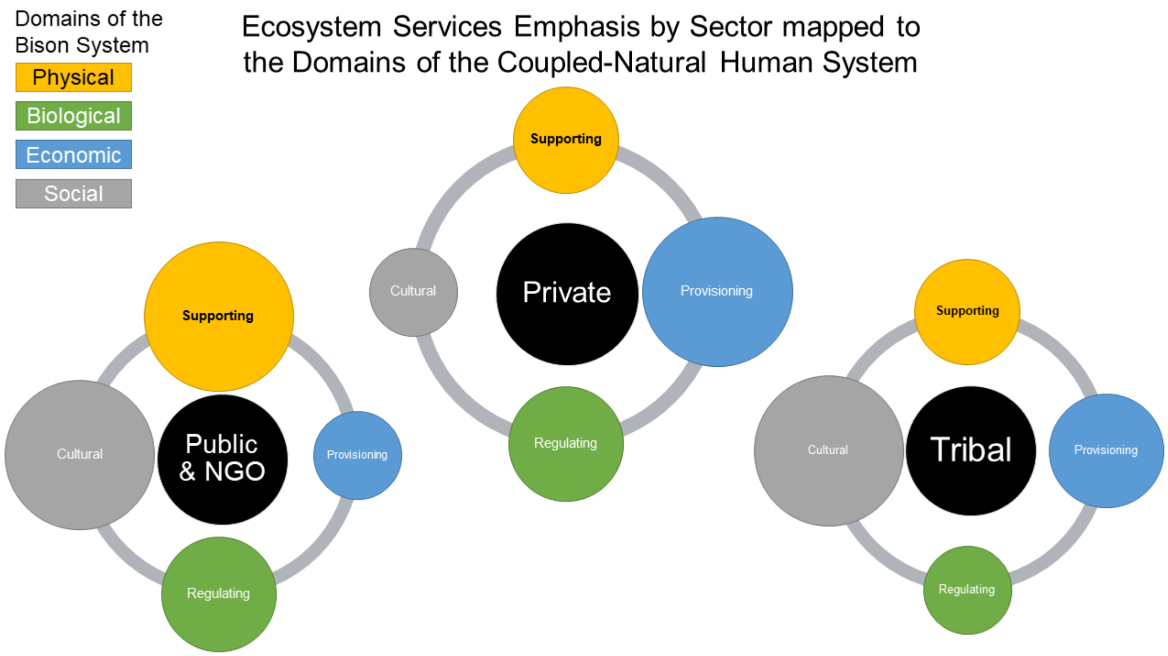

Figure 6.2. Conceptual framework of complementary sectors of wildlife management in North America including public/NGO, private, and tribal systems. Each sector emphasizes different ecosystem services (relative size of each circle) and each of the ecosystem services are attributed to the four domains presented in Barboza and Martin (2020). Supporting services map to the physical domain, regulating services map to the biological domain, provisioning services map to the economic domain, and cultural services map to the social domain. Note: regulating services are depicted small in all sectors because little is known about the full impacts on water and carbon cycles that bison management may affect.

The establishment of the Center of Excellence in Bison Studies at South Dakota State University should help further integrate a crucial element to the above Figure 6.2, academic institutions and land grant university systems. Although much of the established research literature about bison revolves around biophysical and historical aspects, which are necessary and a wealth of information, my hope is that future research of the bison coalition will include more cultural and social disciplines because there are some incredible people contributing to the conservation and preservation of *Bison* across North America. The American Bison Society, lead by Theodore Roosevelt and William T. Hornaday, of the early 20th century also stepped out once their mission was met, they executed an exit plan. This is what allowed for the successful and diverse conservation that we see with bison today. The stories of bison conservationists today are just as important and compelling as stories of Roosevelt and Hornaday witnessing the last of the buffalo commons—the difference, the people saving bison today for future generations are ordinary people.

I hope to see bison restoration and conservation on mass scales by the end of my lifetime that occupy and restore native prairie grasslands along the Great Plains that include Tribal, private, public, zoo, and NGO herds. The opportunity will present itself across the Great Plains as the humid-arid line of the 100th meridian continues to migrate east, leaving behind it an increasingly xeric grassland that suits bison well. Converting agricultural lands to bison range will be the likely scenario, that is if bison remains economically viable and desirable.

6.3. Closing remarks

Public lands are warming and drying at accelerated rates compared to the rest of the continent (Gonzalez et al. 2018) and are likely to continue through the remainder of the 21st century. Consequences of the accelerated warming and drying for bison on public lands is that they will shrink faster than other regions. Although we know that bison adapt to warming, it remains unknown the maximum adaptation rate that bison can achieve (Table 6.1). Private working lands and private bison, then would become a conservation bank, of sorts, for public herds.

Ostensibly, public lands cannot operate solely as sources for wildlife, nor do they exist in a vacuum free from cultural and natural stressors from recreational use, land use, or climate change. Integration of the public, NGO, zoo, tribal, and private sectors under one common theme for conservation was done for bison more than a century ago by President Theodore Roosevelt (Aune and Plumb 2019) and has persisted to this day. However, the bison system has fallen out of focus of researchers for improving the North American model (NAM) for wildlife management (Barboza and Martin 2018, 2020), despite NAM being originally developed for bison as a species. The bison coalition framework has worked with success for more than one hundred years in North America, its principles of shared conservation costs over more than 1,000 stakeholders makes it a viable option for other species, land, and ecosystem-wide conservation organizations.

Broadly speaking, this interdisciplinary dissertation applies to disciplines of ecology, evolution, vertebrate paleontology, wildlife biology, and conservation science. Interdisciplinary research is often riddled with challenges of reconciling disciplinary lexicons, clarifying underlying disciplinary assumptions, and abandoning foundational disciplinary traditions to reach scientific consensus for the sake of advancing scientific discovery.

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APPENDIX A

SUPPORTING DATA FOR CHAPTER 1 – INTRODUCTION

The following Table 7.1 and Table 7.2 are supporting data for Figure 1.1. Table 7.1 displays data of the average value for each bison, assuming a constant average body mass of 281 kg (620 lb). Table 7.2 displays data for events that pertain to bison conservation, including natural pressures, social pressures, economic pressures, legislation concerning bison, and implementation of recovery efforts. These data are also available here, DOI: 10.6084/m9.figshare.12314777. Jeff M. Martin ORCID: 0000-0002-4310-8973.

Table 7.1. Value of each bison from 1870 to 2019 (Hornaday 1889, USDA 2020) converted to 2018 dollar equivalents (U.S. Bureau of Labor Statistics 2020). 2018 base refers to the conversion multiplier for converting prices. Average body mass of 281 kg.

Year	$/ea	2018$/ea	2018 base	Bison pop.
1868	$ 2	$ 36	0.054876	30,000,000
1870	$ 5	$ 99	0.050376	5,500,000
1884	$ 192	$ 5,078	0.037872	350
1901	$ 120	$ 3,672	0.032814	800
1902	$ 714	$ 21,507	0.033213	723
1907	$ 250	$ 6,891	0.036279	100
1908	$ 441	$ 12,420	0.035522	1,592
1919	$ 300	$ 4,355	0.068894	6,013
1920	$ 430	$ 5,388	0.079806	8,448
1921	$ 287	$ 4,026	0.071284	8,448
1924	$ 115	$ 1,689	0.068098	12,264
1944	$ 75	$ 1,074	0.070089	20,013
2004	$ 784	$ 1,042	0.752260	231,950
2005	$ 848	$ 1,091	0.777747	398,049
2006	$ 923	$ 1,150	0.802835	448,827
2007	$ 951	$ 1,152	0.825694	448,827
2008	$ 1,142	$ 1,331	0.857393	415,111
2009	$ 1,182	$ 1,383	0.854367	415,111
2010	$ 1,481	$ 1,706	0.868384	415,111
2011	$ 2,052	$ 2,291	0.895783	344,525
2012	$ 2,119	$ 2,317	0.914301	344,525
2013	$ 2,047	$ 2,207	0.927721	317,960
2014	$ 2,153	$ 2,283	0.942774	317,960
2015	$ 2,333	$ 2,472	0.943889	317,960
2016	$ 2,592	$ 2,712	0.955796	312,132
2017	$ 2,760	$ 2,828	0.976146	312,132
2018	$ 2,747	$ 2,747	1.000000	372,502
2019	$ 2,562	$ 2,516	1.018120	372,502

Table 7.2. Summary table of Table 7.3 by decade, used for Figure 1.1D.

Decade	Natural	Social	Economic	Legislation	Recovery
Pre-European Contact	13	18	3	0	0
980-1799	3	14	3	0	0
1800-1829	0	4	5	2	0
1830-1839	0	3	2	1	1
1840-1849	0	2	3	2	0
1850-1859	0	1	1	0	0
1860-1869	0	5	3	2	2
1870-1879	1	8	6	9	7
1880-1889	0	6	3	7	5
1890-1899	0	1	1	5	4
1900-1909	0	0	1	7	8
1910-1919	0	0	0	2	4
1920-1929	0	0	0	0	1
1930-1939	1	1	0	1	4
1940-1949	0	2	0	2	1
1950-1959	0	0	0	1	1
1960-1969	0	0	0	0	1
1970-1979	0	0	0	3	2
1980-1989	0	0	0	0	3
1990-1999	0	0	3	0	5
2000-2009	1	1	1	0	4
2010-2019	0	0	1	2	3

Table 7.3. Conservation timeline events ranging across domains of natural, social, economics, legislation concerning bison (‘authorization’), and recovery efforts (‘implementation’).

Year (CE)	Natural Pressures	Social Pressures	Economic Pressures	Legislation (Authorization)	Recovery Efforts (Implementation)	References
985		Erik the Red founds settlement in Greenland for the Vikings				(Zorich 2017)
1000		Leif Erikson explores Atlantic coast of North America: First European to see North America.				(Enterline 2002)
1492		Christopher Columbus lands in Caribbean for Spain				(Columbus and Cummins 1992)
1497		John Cabot lands in Newfoundland Canada for Britain				(Fardy 1994)
1500-1800		Vore Buffalo Jump in Wyoming				(Reher 1985)
1519	Hernando Cortes brought horses to Mexico					(Isenberg 2000)
1521		Conquistador Hernan Cortes first European to see captive bison in southern Mexico				(Dolin 2010)
1528		First European to see wild bison in North America. Alvar Nunez Cabeza de Vaca in eastern or central Texas between 1528-1533.				(Reed 1952)
1540	Cattle introduced to North American, along with their various diseases - leading to the demise of bison in the late 1880s Horses at large in North America		Spanish exploration of Mexico and American Southwest by Francisco Vasquez de Coronado			(Barnosky et al. 2014, Stoneberg Holt 2018)
1570		Madison Buffalo jump in Montana				(Nathan 2018)
1612		The first Englishmen see bison for the first time				(Dolin 2010)
1670		Hudson's Bay Company chartered	Hudson's Bay Company trapping, hunting, and trading furs of many animals including bison robes.			(Pinkerton 1931)
1673		Jacques Marquette and Louis Jolliet explored the Mississippi and Illinois Rivers describing bison herds at large in central North America				(Petersen 1968)
1712		As Euro-Americans settled the country, moving westward from the east coast, they brought changes to native habitat through plowing and farming. Introduced cattle diseases and grazing competition with feral	Steam engine invented and catalyzes the development of the Transcontinental Railroad			(Isenberg 2000, Andrew 2015)

		horses also impacted bison prior to direct impact by Euro-Americans.				
1750	The great bison belt, a tract of rich grassland that ran from Alaska to the Gulf of Mexico, east to the Atlantic Seaboard (nearly to the Atlantic tidewater in some areas) as far north as New York and south to Georgia and per some sources down to Florida, with sightings in North Carolina near Buffalo Ford on the Catawba River as late as 1750					(Hornaday 1889)
1800			Bison leather is strong and durable and was a major commodity for the production of flat belts. Flat belts were widely used for in line shafting to transmit power in factories. They were also used in countless farming, mining, and logging applications, such as bucksaws, sawmills, threshers, silo blowers, conveyors for filling corn cribs or haylofts, balers, water pumps (for wells, mines, or swampy farm fields), and electrical generators.			(Soper 1941, Isenberg 1992, Gates et al. 2010)
1802		Bison gone from Ohio				(McHugh 1972)
1803		Lewis and Clark expedition Last buffalo was pushed out of modern day Buffalo, NY		Louisiana purchase - Great Plains added to United States which included the natural bison range		(U.S. National Archives & Records Administration 1803)
1804			Steam engine train locomotion invented			(Trevithick 1872)
1805			Invention of refrigeration			(Pearson 2005)
1815		Last two bison shot east of the Allegheny Mountains	Demand for bison robes and fur rise through 1840s			(Garretson 1934, Dolin 2010)
1818				United States and Great Britain sing the Convention of 1818 that extends the boundary between U.S and Canada on about the 49th parallel		(Bevans 1968)
1819		Native Americans tribes, forced off land in the east, bring horses and guns to the Great Plains and increased pressure on bison.				(Jahoda 1975)
1825			First public railway created in Britain			(Kirby 1993)
1830		Mass destruction of the once great herds of bison began.		U.S. Indian Removal Act "Trail of Tears"		(Hornaday 1889, Cave 2003)

				Proclamation to kill bison in army correspondence		
1831			First train in United States			(Snell 2010)
1832		Last bison shot east of the Mississippi River in southwest Wisconsin				(Lueck 2002)
1834					The *American Journal of Science* calls for a rapid decline of fur trade to preserve animals in North America	(Dolin 2010)
1836		The push west of Missouri begins with the exploration of the Oregon Trail by the Whitman-Spalding group				(Dary 2004)
1837			Economic depression in U.S. spurs immigration to Texas (Known as Panic of 1837)			(Rousseau 2002)
1840		West of the Rocky Mountains, bison (never in large numbers) disappeared. Native Americans market hunters concentrated on cow bison, because of their prime hides for trading.				(Hornaday 1889)
1843		Oregon Trail begins from Independence, Missouri	Oregon Trail begins			(Dary 2004)
1845			Texas becomes 28th state	June 1845 Asa Whitney led a team along the proposed central route for the Transcontinental Rail to assess its capabilities. Whitney then traveled widely to solicit support for the rail line, printed maps and pamphlets, and submitted several proposals to Congress.		(Office of the Historian Bureau of Public Affairs n.d., Brown 1933)
1846				Smithsonian Institution founded in Washington, D.C.		(Boren 2006)
1848			California gold rush begins			(Bingham 1981)
1850	Little Ice Age terminates		Texas cedes land and becomes its current shape			(Hamilton 2015, Solomina et al. 2016)
1860		Railroads built across the Great Plains during this period divided the bison into two main herds - the southern and the northern. Many bison were killed to feed the railway crews and Army posts. During this time, Buffalo Bill Cody gains fame.				(McHugh 1972, Dolin 2010)
1861		United States Civil War begins				(Engle 2019)
1862				The House of Representatives voted for the Transcontinental Rail line on May 6, 1862, and the Senate		(The Pacific Railway Act 1862)

			on June 20. Lincoln signed it into law on July 1.		
1864			Idaho State Legislature passed the first law to protect the bison - 24 years after bison were gone from the state.		(Brownell 1987)
1865	United States Civil War ends				(Plante 2015)
1866				In 1866, Charles Goodnight, at the request of his wife, captured a few free ranging bison calves and began a captive herd on his ranch in Texas. The bison were sold shortly after, unbeknownst of Mr. Goodnight.	(Lueck 2002)
1867	Buffalo Bill Cody kills 4,282 bison in 18 months for the Kansas Pacific Railroad on contract. In an 8-hour competition, Cody killed 69 bison compared to Bill Comstock's 46.	Cattle drives from Texas to railhead in Kansas Refrigeration rail cars first used to ship products and meat			(Carter 2000, Snell 2010)
1868	General William Sherman reinforces the call for hunting bison to extinction in his June 17th letter to his brother, United States senator John Sherman.	Bison bones were used in refining sugar, and in making fertilizer and fine bone china. Bison bones brought from $4.00 to $12.00 per ton. Based on an average price of $8 per ton they brought $2.5 million dollars into Kansas alone between 1868 and 1881. Assuming that about 100 skeletons were required to make one ton of bones, this represented the remains of more than 31 million bison.		Lincoln Park Zoo in Chicago, IL established.	(Isenberg 2000, Rosenthal et al. 2003)
1869		Golden Spike: First Transcontinental Railroad across the United States connecting the Central Pacific and Union Pacific railroads on May 10, 1869, at Promontory Summit, Utah Territory.			(Galloway 1989)
1870	An estimated two million bison were killed this year on the southern plains. England and Germany had developed a process to tan bison hides into fine leather. Homesteaders collected bones from carcasses left by hunters.	Bison in Prairie Canada were nearly extirpated. Hornaday estimated a waste of 15-20 million dollars which equates to 235-313.5 million in 2019 conversion. Bison Robes become fashionable Railroad companies offered "hunting		It became obvious in the 1870's that owning bison was profitable. More and more people were capturing free ranging bison to establish private herds.	(Hornaday 1889, McHugh 1972, Dobak 1996, Taylor 2011, Hill 2014, Kolipinski et al. 2014)

	Bison robe trade begins to decline in Canada. People, traders, trappers, and hunters, all depended on bison for their own sustenance.	specials" across the plains where passengers were welcome to shoot as many bison from the comfort of their train car. the was pushed by rail companies because bison were destroying the tracks during their migrations			
1871	This year marked the beginning of the end of the southern herd. The greatest slaughter took place along the railroads. One firm in St. Louis traded 250,000 hides this year. With newly discovered tanning process, bison were now hunted year round.	Demand for bison skins escalated as a Pennsylvania tannery began commercially tanning bison hides.	Territorial delegate R.C. McCormick of Arizona introduced a bill that made it illegal for any person to kill a buffalo on public lands in the United States, except for food or preserving the robe. The bill indicated that the fine be $100 for each buffalo killed. Mysteriously, this document disappeared and thus was not passed. Wyoming passed a law prohibiting the waste of bison meat and passed another that created a closed season on bison. since such laws were not enforced, they did little to protect the bison.		(Hornaday 1889, Hill et al. 2008, Moloney and Chambliss 2014, Aune and Plumb 2019)
1872	During this year and the next two, an average of 5,000 bison were killed each day, every day of the year, as ten thousand hunters poured onto the plains. One railroad shipped over a million pounds of bison bones. Bison hunting became a popular sport among the wealthy.	1.2 million bison harvested annually A 315,000 ft^3 Union Pacific shed filled to the top with bison hides that is estimated to be 44,333 hides (15,750 hides-72,917 hides)	The Kansas legislature passed a law prohibiting the wasting of bison meat, but the Governor vetoed it. Colorado passed a law prohibiting the wasting of bison meat; it was not enforced. Montana territorial legislature passed an act that established a closed season for "mountain buffalo, moose, elk, black-tailed deer, white-tailed deer, mountain sheep, white Rocky Mountain goats, antelope, or hare, between the 1st of February to the 15th of August." This was passed, however, not enforced. The federal legislation creating Yellowstone National Park provided against the wanton destruction of the fish and game found in said park. Staffing and funding were not provided to enforce this law.	Yellowstone National Park created by President Ulysses S. Grant	(Brownell 1987, Isenberg 1992, Moloney and Chambliss 2014, Aune and Plumb 2019)

1873	Lincoln Park Zoo in Chicago, IL exhibits 2 bison for first time. May have helped normalized social norms of conservation	On the southern plains, slaughter reached its peak. One railroad shipped nearly three million pounds of bones. Hides sold for $1.25 each, tongues brought $0.25 each - most of the bison was left to rot. A railway engineer said it was possible to walk a 100 miles along the Santa Fe railroad right-of-way by stepping from one bison carcass to another.	1.2 million bison harvested annually. Prices fell to $1.25 per robe (In today's economy $1.25= $26.16) Hind quarters of Buffalo were worth $0.01 while the fore quarters were worthless	Columbus Delano, Secretary of the Interior, under President Grant, wrote in his 1873 report, "The buffalo are disappearing rapidly, but not faster than I desire. I regard the destruction of such game as Indians subsist upon as facilitating the policy of the Government, of destroying their hunting habits, coercing them on reservations, and compelling them to begin to adopt the habits of civilization."	In 1872 or 1873 with the aid of his wife Sabine, Walking Coyote, a Pend d'Oreille Indian, acquired some bison calves, bringing them into the Flathead Valley with the intent of starting a bison herd. Fredrick Dupree capture 9 bison on Yellowstone River in Montana and brought them to South Dakota. This herd will be later owned by James "Scotty" Philip. In Canada, west of Winnipeg, James McKay acquired five bison and established a small herd.	(Hornaday 1889, Wood 2000, Moloney and Chambliss 2014)
1874		This year marked the seeming end of the great southern herd. Auctions in Fort Worth, Texas were moving 200,000 hides every day or two. One railroad shipped nearly 7 million pounds of buffalo bones.	1.2 million bison harvested annually. Barbed wire fences introduced to open range.	Congress advanced their efforts to save the bison. Both the House and Senate passed a bill "to prevent the useless slaughter of buffaloes within the Territories of the United States." The first section made it unlawful for any person not an Indian to kill a female buffalo and the second prohibited the killing of more males than could be used for food or marketed. However, President Grant refused to sign the bill.	Around this time, William and Charles Alloway of Manitoba, Canada, with the aid of a milk cow, captured three bison calves to start their own herd. Philadelphia Zoological Garden opens with bison on exhibit.	(Hayter 2012, Tolles 2013, Stoneberg Holt 2018, Aune and Plumb 2019)
1875				Few bison remained in Texas when the state legislature moved to protect the bison. However, General Phil Sheridan appeared before the assembly and suggested that every hunter be given a medal with a dead buffalo on one side and a discouraged Indian on the other. He added that once the animals were exterminated, the Indians would be controlled and civilization could advance.	Cincinnati Zoological Gardens opens with one (1) bison as exhibit, among many other species.	(Cincinnati Zoo & Botanical Garden n.d., Dolin 2010)
1876		The estimated three to four million bison of the southern plains were now dead. The Northern Pacific Railroad,	Hides went for $2.50 each (in 2018 dollars: $58.67)	Montana revised its previous wildlife protection bill to prohibit the killing of animals "for the purpose of procuring the hide only"		(Brownell 1987, Isenberg 1992)

	anxious to advance, ignored tribal treaties and sent in a survey party. Native Americans killed some of the men, and General George Custer was sent to investigate, making history with the Battle at Little Big Horn. Fort Benton alone sent 80,000 hides to market (Bring in $200,000)		and "not making use of the carcass ... for food, for himself or for the purpose of selling the same to others for food." Illinois Rep. Greenbury Fort introduced a bill banning Commercial Buffalo hunting in the Indian territories. after passing the House it stalled in a Senate committee		
1877	A few remaining free roaming bison were discovered in Texas and were killed.		A law was passed in Canada that forbade the use of pounds (corrals), wanton destruction, killing of buffalo under 2 years of age, and the killing of cows during a closed season.	Lt. Col. Samuel Bedson of Stoney Mountain, Manitoba (Canada) purchased bison from the Alloway herd, the McKay herd and from some Native Americans.	(Hornaday 1889)
1878	Bison in Canada were disappearing rapidly.		Canada repealed the 1877 law.	Charles Goodnight preserves a herd of wild bison in Texas. Descendants of these animals are allegedly at Caprock Canyons State Park. Charles Goodnight was known to crossbreed bison with cattle. In 1902, bison from this herd were introduced to Yellowstone by CJ "Buffalo" Jones.	(Isenberg 1997, Stoneberg Holt 2018, Aune and Plumb 2019)
1879			Wisconsin establishes Game Warden Office		(Gjeston 2013, Stoneberg Holt 2018)
1880	Slaughter of the northern herd had begun.		New Mexico passed a law to protect the bison; unfortunately the bison were already gone from this state.		(Crenshaw 2002, Stoneberg Holt 2018)
1881	This year's winter marked the largest slaughter of the northern herd. One county in Montana shipped 180,000 buffalo skins. Robes brought $2.50 to $4.00 each. The Northern Pacific alone shipped 50,000 hides	Southern transcontinental railway completed. Largely following modern Interstate 10	South Dakota makes it illegal to kill and leave any part of a deer, elk, buffalo, antelope, and mountain sheep on the prairie.		(U.S. National Park Service n.d., Hanner 1981, Stoneberg Holt 2018)
1882	Over 10,000 bison were taken during one hunt of a few days length in Dakota Territory in September. The fate of the northern herd had been determined. Hunters thought that the bison had moved north to Canada, but they hadn't. They had simply been eliminated.			Cincinnati Zoo had first bison born in captivity. Buffalo Bill Cody begins his Buffalo Bill's Wild West Show. Dupree herd is established.	(Isenberg 2000, Wood 2000, Stoneberg Holt 2018)

	The Northern Pacific alone shipped 200,000 hides				
1883	By mid-year nearly all the bison in the United States were gone. The Northern Pacific alone shipped 40,000 hides				(Stoneberg Holt 2018)
1884	The Northern Pacific shipped two carloads (300 bison from Dickson, North Dakota and none from Fort Benton)		Congress gives the Army the task of enforcing laws in Yellowstone National Park in an effort to protect the final few wild bison from poachers.	Charles Goodnight re-established his herd. Michel Pablo and Charles Allard of Montana purchased 13 bison from Walking Coyote for $2000 in gold.	(Wood 2000, Lueck 2002)
1885			Montana establishes Fish and Game Commission. Illinois establishes Game Warden Office. United States establishes Section of Economic Ornithology within the US Department of Agriculture, to become the U.S. Fish and Wildlife Service.		(Illinois Department of Natural Resources n.d., Brownell 1987, Schmidly et al. 2016)
1886	The Smithsonian Institute sent an expedition out to obtain bison specimens for the National Museum. After a lengthy search, some were found near the LU Bar Ranch in Montana. Twenty-five were collected for mounting and scientific study. (The original mounted specimens were brought to the Fort Benton (MT) Museum of the Upper Missouri in the mid-1990's, close to where the original bison were taken.)			William Hornaday promotes recovery of wild bison in Montana. CJ "Buffalo" Jones wrangles 18 bison calves in Texas panhandle and brings back to Kansas. CJ Jones and Charles Goodnight both work towards breeding bison with cattle to make beefalo and cattalo.	(Hornaday 1889, Wood 2000)
1887		One of the last lots of bison robes sold in Texas for $10 per robe.	Minnesota establishes Game Warden Office	Theodore Roosevelt founds the Boone & Crockett Club. The Smithsonian's National Zoo opened with bison as exhibit.	(Hornaday 1889, Palmer 1912, Regan 2018, Smithsonian's National Zoo & Conservation Biology Institute n.d.)
1888				Austin Corbin established a herd of bison on New Hampshire's Blue Mountain Game Preserve. Lincoln Park Zoo in Chicago, IL has bison born in captivity.	(Hornaday 1889, 1913)

1889		Last commercial shipments of hides anywhere in United States. Land Rush of Oklahoma "Sooners"-land ownership	Montana passed a law making it illegal to shoot any bison for ten (10) years within the territory - hires first Game Warden.		(Hornaday 1889, Howard 1889, Brownell 1987)
1891			Colorado establishes Game and Fish Department.		(Williams 1907)
1892				John Muir founds the Sierra Club	(Regan 2018)
1894			The Lacey Act of 1894 was passed. The National Park Protective Act (Chapter 72 of Lacey Act) imposed jail sentencing and fines ($1000 then; $27,500 in 2015 dollars) for poaching within the national parks, and became the first law to provide specific protection for bison within the National Park System. President: Grover Cleveland		(Lacey Yellowstone Protection Act 1894, Boyd and Gates 2006)
1895			Missouri establishes Game Warden Office. North Dakota establishes Office of the State Game Wardens Wyoming establishes Office of State Game Warden.	Wildlife Conservation Socity founded as the New York Zoological Society at the Bronx Zoo The Pablo/Allard herd in the Flathead Valley totaled about 300. Allard died from injuries	(Wyoming State Archives n.d., Palmer 1912, Kriegel 1998, McLain 2018, Aune and Plumb 2019)
1896		Klondike Canada gold rush		After Allard's death, his widow sold her portion to Charles Conrad of Kalispell, MT. It is likely that many of the 300 bison from the Pablo/Allard herd stocked many of the zoos and parks around the country, including, circuitously to Yellowstone via City Zoos. Lincoln Park Zoo sells 1 bull and 7 cows to US Government to stock Yellowstone.	(Morse 2009, Aune and Plumb 2019)
1897	last 4 Public (wild) bison killed in the United		Bitteroot Forest reserve established to protect bison in Idaho.		(U.S Forest Service n.d.)
1899			Idaho establishes Game and Fish Game Warden Office.	Bronx Zoo opens	(Wildlife Conservation Society n.d., Palmer 1912)
1900			The Lacey Act of 1900 was passed		(Lacey Act 1900)
1901		Alaska gold rush begins	Montana appoints first Game and Fish Warden	James "Scotty" Philip buys around 100 bison in South Dakota.	(Williams 1907, Brownell 1987, Wood 2000, Adams and Dood 2011)

	Nebraska establishes Game and Parks Commission.		
1902		CJ "Buffalo" Jones named as first Game Warden at Yellowstone National Park by President Theodore Roosevelt. CJ introduced the bison to Yellowstone with seed stock from Texas (Goodnight herd) and 20 from Montana (Pablo-Allard herd).	(Isenberg 1997, Lueck 2002)
1903	New Mexico establishes Fish and Game Warden Office	W.C. Whitney donates 26 bison and William Hornaday donates 7 bison to the Bronx Zoo	(Crenshaw 2002, Aune and Plumb 2019)
1905	Kansas establishes Fish and Game warden office	The American Bison Society (ABS) founded by private citizens to protect and restore bison in concert with the New York Zoological Society and Bronx Zoo. Ernest Harold Baynes, founder; William T. Hornaday, president; Theodore Roosevelt, honorary president. CJ "Buffalo" Jones crossbred bison with Galloway cattle on a government ranch on the North Rim of the Grand Canyon in the Kaibab Plateau, Arizona. Now known as House Rock Valley.	(Williams 1907, Lueck 2002, Martin et al. 2017)
1906	Antiquities Act of 1906	Pablo sold his bison herd to Canada, after Congress turned down funding for purchase for the United States. After 5 years of rounding up, a total of 672 animals were shipped to Canada. Pablo received more than $160,000.	(Antiquities Act 1906, Isenberg 1997)
1907	Texas establishes Game Department.	ABS shipped 15 bison from the Bronx Zoo to Wichita Mountains Wildlife Refuge and Game preserve in Oklahoma.	(Texas State Library and Archives Commission 2016, Aune and Plumb 2019)
1908		National Bison Range in Montana established for a permanent range for the herd of bison to be presented by ABS.	(Hornaday 1889, Isenberg 2000)
1909	Oklahoma establishes Game Warden Office.	Thirty-four bison purchased from the Conrad herd	(Oklahoma Department of

				South Dakota establishes Office of the State Game Wardens.	(Kalispell, MT) by ABS, donated and release on National Bison Range.	Wildlife Conservation n.d., Reffalt et al. 2008, Casper and Pieczko 2014)
1911					American Game Protective Association founded (Wildlife Management Institute). Scotty Philip died and some of his 1000 bison were sold to the State of SD to establish Custer State Park bison herd.	(Nesheim 2012, Regan 2018)
1912				Arizona establishes Game Warden Office		(Arizona State Library 2018)
1913					Wind Cave National Park (SD) received 14 bison from the New York Zoological Society (now the Wildlife Conservation Society). Custer State Park in South Dakota was established with bison herd. The ABS donated 6 bison to the Fort Niobrara Game Preserve.	(McHugh 1972, Wood 2000, Wind Cave National Park 2006)
1915				Arkansas establishes Game and Fish Commission		(Arkansas Game and Fish Commission n.d.)
1919					Grand Canyon National Park established. CJ "Buffalo" Jones dies. American Society of Mammalogists is formed. Austin Corbin donates bison to Pisgah National Forest and Game Preserve in North Carolina.	(Kersey 1958, Animal Care and Use Committee 1998, Aune and Plumb 2019)
1927					Arizona Game and Fish Department purchases bison for the House Rock Valley adjacent to Grand Canyon National Park in Arizona.	(Hoffmeister 1986)
1934	Droughts and Dust Bowl across Great Plains	Sioux (Pine Ridge) in South Dakota and Crow establish herds in Montana				(Isenberg 2000, Nesheim 2012)
1935					Because of the secure populations of bison in public herds, the American Bison	(Lueck 2002)

				Society votes itself out of existence.	
1936				National Wildlife Federation founded	(Regan 2018)
1937			Pitman-Robertson act - Federal Aid in Wildlife Restoration Act	The Wildlife Society founded	(Federal Aid in Wildlife Restoration act 1937, Regan 2018)
1939				Badlands National Park established.	(Gabrielson 1941, Badlands Natural History Association 1968)
1940			U.S. Fish and Wildlife Service (FWS) created after Bureau of Fisheries and Bureau of Biological Survey merge and are moved out of USDA into the Department of Interior.		(Nesheim 2012)
1941	U.S. enters WWII				(Declaration of state of war with Japan 1941)
1943	Buffalo meat used to feed Americans during war since Bison meat was considered "game" and didn't need a rations coupons to buy.				(Nesheim 2012)
1947			Canada establishes Canadian Wildlife Service		(Burnett 2003)
1949				Aldo Leopold's Sand County Almanac published	(Leopold 1949)
1950			National Science Foundation started	The ecologist union reorganizes its self and becomes The Nature Conservancy	(National Science Foundation Act 1950, Dexter 1978)
1966				National Buffalo Association established	(Popper and Popper 2006)
1971			Wild Free-roaming horses and burros act		(Wild Horses and Burros Act 1971)
1973			Endangered Species Act		(The Endangered Species Act 1973)
1975				American Bison Association established	(Popper and Popper 2006)
1976				Fort Niobrara refuge designated as Wilderness	(Designation of Wilderness Areas Within the National Wildlife Refuge System 1976)
1978			Theodore Roosevelt National Park established in North Dakota.		(Norland 1984)
1985				The Nature Conservancy (TNC) Samuel Ordway Memorial Preserve in South Dakota establishes herd of bison	(Pyne 2017, Aune and Plumb 2019)

					TNC Niobrara Valley Preserve in Nebraska	
1986					TNC reintroduced bison to the Cross Ranch Preserve in North Dakota	(Enright 2009)
1987					The Nature Conservancy introduced bison to the Konza Prairie Biological Station in Kansas	(Konza Prairie Biological Station n.d.)
1990					The Intertribal Bison Cooperative (ITBC) was formed by 57 tribes	(Gates et al. 2010)
1991					Congress appropriated funding for Tribal bison programs	(Gates et al. 2010)
1993			North American Bison Cooperative formed with 330 bison producer members		The Nature Conservancy reintroduced 300 bison to the Tallgrass Prairie Preserve in Oklahoma	(The Nature Conservancy n.d., McKee and Boland 2009)
1994			North American Bison Cooperative opens a Slaughter and processing facility and process 5,000 bison annually			(McKee and Boland 2009)
1995					National Bison Assocation formed with the merge of American Bison Association and National Buffalo Association	(Popper and Popper 2006)
1999			Due to increased demand the North American Bison Cooperative process 8,000 bison annually		The Nature Conservancy acquired the Medano Zapata Ranch in Colorado along with one of the largest bison herds in North America	(National Park Service et al. 2005, McKee and Boland 2009)
2000					The Nature Conservancy in Kanasas reintroduces bison to the Smoky Valley Ranch	(The Nature Conservancy Kansas 2016)
2005			The North American Bison Cooperative joins a contractual alliance with North Dakota Natural Beef, LLC.		Wildlife Conservation Society re-establishes American Bison Society	(Redford 2007, McKee and Boland 2009)
2006	Severe drought in much of the Southwest and Great Plains				Bison Summit is held in Denver to plot out bison's ecological future	(Boyd and Gates 2006, NOAA National Centers for Environmental Information 2007, Redford 2007)
2008		Meeting on "Building Blocks for Bison Ecological Restoration" held in Rapid City, S. D. Wood bison from Elk Island National Park in Canada arrived at their temporary new home at the Alaska Wildlife Conservation Center on June 19, 2008.				(Alaska Department of Fish and Game 2008, American Bison Society 2008)

2009			TNC Tallgrass Prairie National Preserve in Kansas adds to the bison herd. TNC Broken Kettle Grasslands in Iowa adds to the Bison herd 23 Plains Bison were translocated from WICA to TNC Ranchi El Uno Ecological reserve in Chihuahua State	(The Nature Conservancy 2008, Gates et al. 2010, Geremia et al. 2017)
2011			TNC Dunn Ranch in Missouri adds to the herd	(Lee 2014)
2013		TX Gov. Rick Perry signed Senate Bill 174, May 10. The measure was authored by Sen. Craig Estes, R-Wichita Falls, and was sponsored in the House of Representatives by Reps. Charles Anderson, R-Waco; Charles Perry, R-Lubbock; and Dan Flynn, R-Van. Both the Senate and the House voted unanimously for the bill. (Bill Relating to the control of stray bison and other strays)		(Control of stray bison and other estrays. Act of May 10th 2013)
2014			The Nature Conservancy reintroduced Bison to the prairie in Nachusa Grasslands in Illinois. Smithsonian's National Zoo in D.C. exhibits two (2) bison for the 125th Anniversary.	(Smithsonian's National Zoo & Conservation Biology Institute n.d., Kleiman 2016)
2016		May 9th President Obama signs bill, declaring bison as the national mammal.	TNC Kankakee Sands in Indiana.	(National Bison Legacy Act 2016, Higgs 2019)
2017	Bison meat sales top $350 million			(National Bison Association 2017)

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APPENDIX B

LIST OF STUDY PERMITS, PERMISSION, AND APPROVALS

Throughout the research, we thank the following organizations for permitting the various research:

- National Park Service: Wind Cave National Park (permit #2017-SCI-0007);
- United States Fish and Wildlife Service: National Bison Range (permit #RR005-17);
- South Dakota Game, Fish, and Parks: Custer State Park (permit #2017-302);
- The Nature Conservancy and Kansas State University: Konza Prairie Biological Station (permit #2017-476)

All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted and for use of restricted imaging technology:

- Texas A&M AgriLife Research, Agriculture Animal Care and Use Committee: Study #2017-015A
- Texas A&M AgriLife Research, Technology Control Plan: TCP #17-02-007

The survey used in Chapter 5 was submitted for approval to IRB; it was determined to comply with Common Rule (45 CFR 46.101(b)) and qualify for an exemption from further review:

- Texas A&M University, Institutional Review Board of the Human Research Protection Program: 2018-1654

APPENDIX C

SUPPORTING DATA FOR CHAPTER 3 – DECADAL HEAT AND DROUGHT

Data from this chapter are available on Dryad Data Repository (Martin and Barboza, 2020), here: https://doi.org/10.5061/dryad.nvx0k6dnf.

Figures

Gompertz equations of body mass, height, and age

We determined the relationship of measured height to measured body mass in *Bison* from Wind Cave National Park (WICA) in the Black Hills, South Dakota. We modeled these relationships using Gompertz equations, Equations 3.3 and 3.4, in the article.

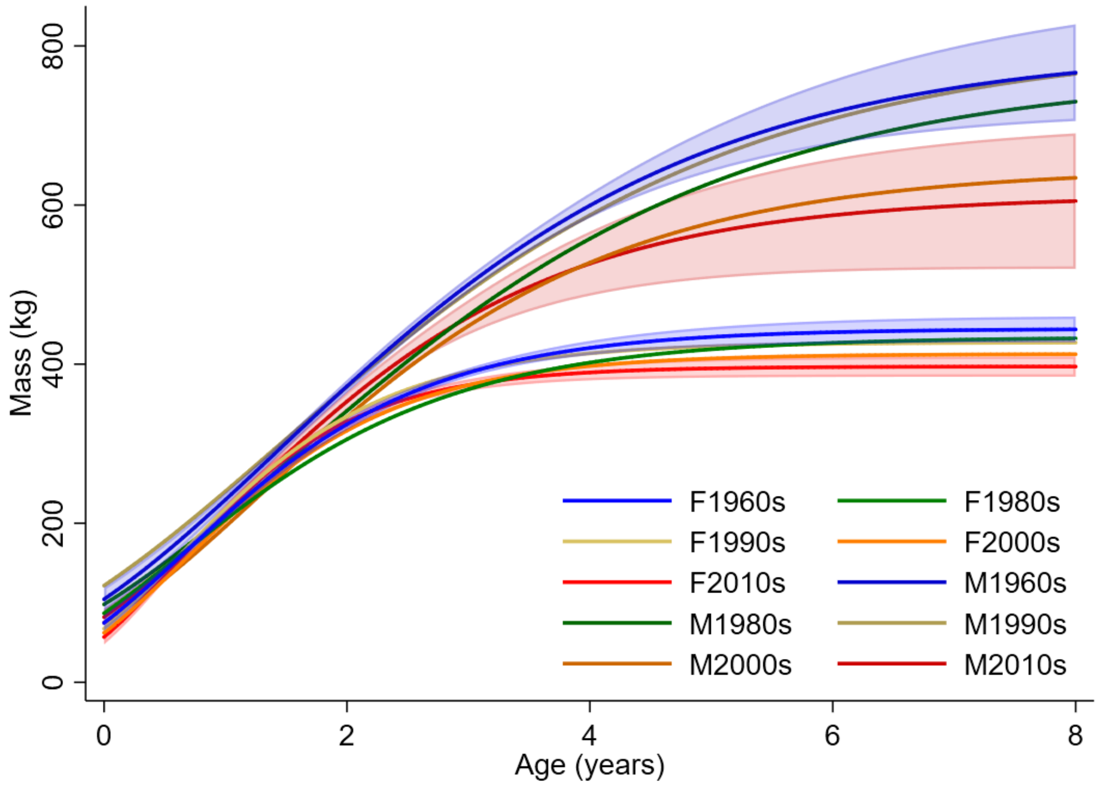

Figure 9.1. Growth of male and female *Bison* at WICA in decadal intervals.

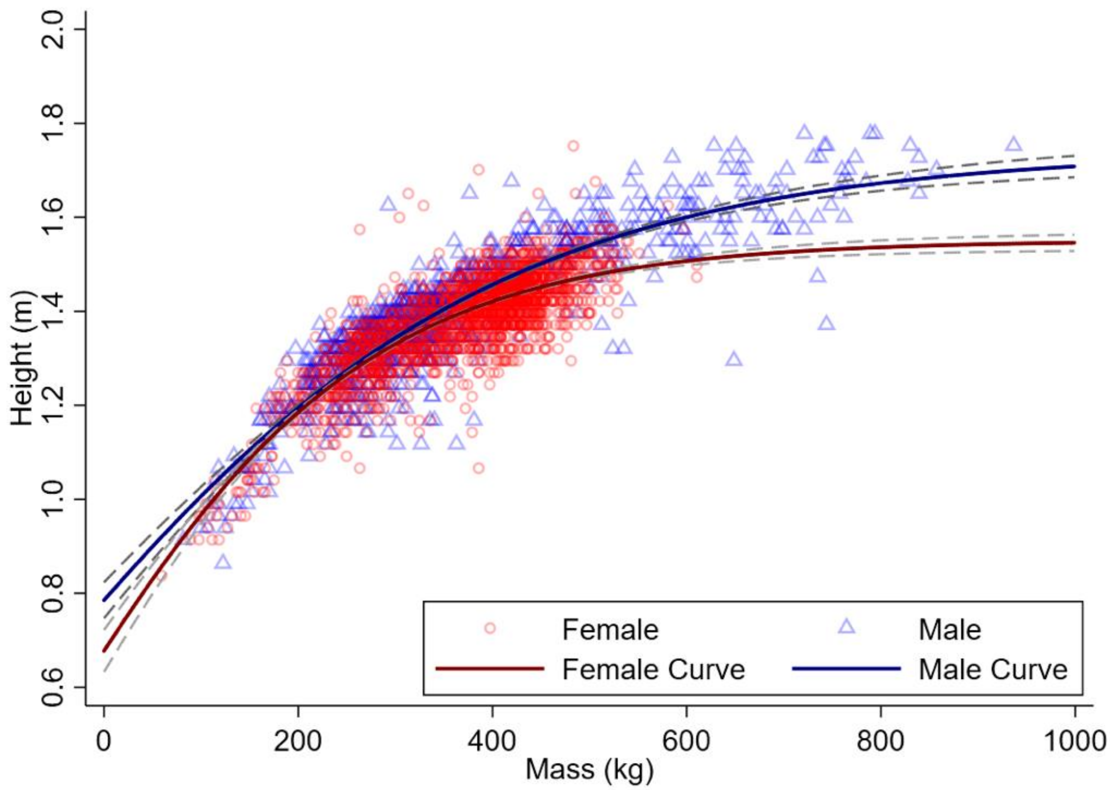

Figure 9.2. Gompertz curves of male (blue, *n* = 1042) and female (red, *n* = 2136) *Bison* body mass (kg) and height (m) from Wind Cave National Park (WICA), Black Hills, South Dakota. Confidence intervals (95%) are dashed lines, points are "jittered" to illustrate density of data.

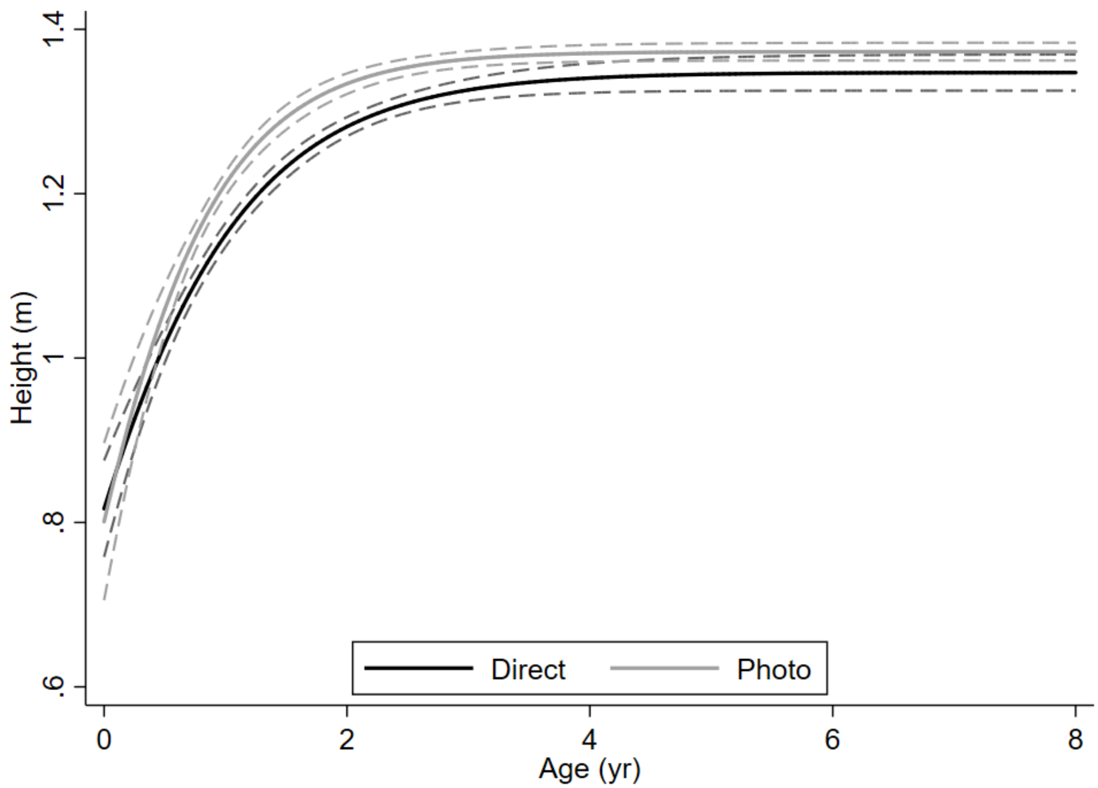

Figure 9.3. Growth of female *Bison* from the 2010s decade at WICA estimated by two methods: direct (Direct; solid black line) measurement in a handling chute and photogrammetric estimate (Photo; solid gray line). Broken lines indicate 95% confidence intervals for each relationship. Estimates of asymptotic body size do not differ between the two methods.

Photogrammetry validation

Two validations were performed. 1) We determined the optimal distance between the viewer and object, 2) we determine best estimate for body size of living bison in various postures, and 3) we determine intra-individual body size measure variation (2 animals, > 5 observations each in different postures).

1) We performed distance optimization for photogrammetry using a yard stick (0.9144 m, n = 77). Optimal distance was 40 ± 5 m. Efforts were made to maintain this distance in the field with *Bison* (Figure 9.4).

2) Individual variation of body size measures was performed to identify most consistent measures of body size using 2 individuals in several postures and positions. Body measures include: total height (H), ear to anus length, eye to nares, hock length, nares to anus, chest height, and surface area (Figure 3.3).
3) While working with live *Bison*, there are no known measures of body size. Of the evaluated measures, least variance (0.01) and skew (0.022) is height (H, n = 7, Figure 9.5).

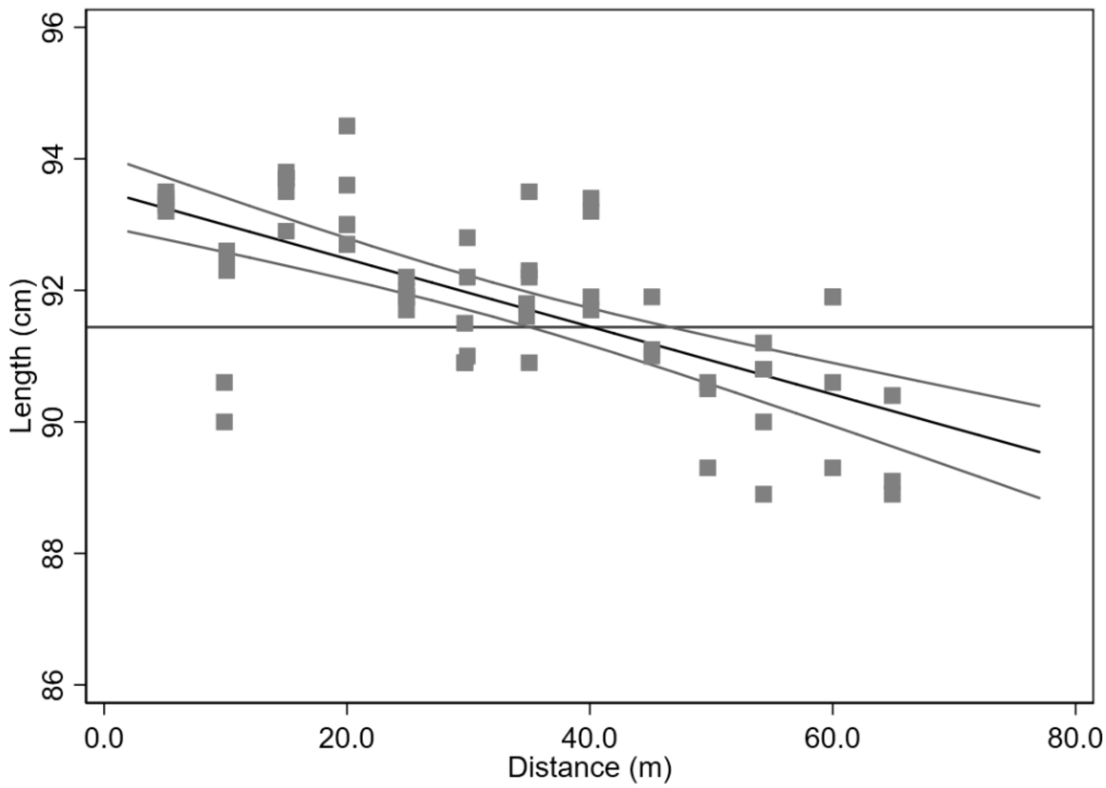

Figure 9.4. Photogrammetric estimate of the length of a yard stick (0.9144 m, solid horizontal line) in relation to the distance from the camera (± 0.05 m). The estimated length is the same as the reference length at 40 ± 5 m.

Figure 9.5. Variation in posture of an individual *Bison* photographed in the lateral view. Variation in the orientation of the head affected estimates of body length more than body height. For example, in this series of images, estimated body length varies by 0.05 SE (1.98 – 2.29 m), whereas estimated body height varies by 0.03 SE (0.48 – 0.60 m).

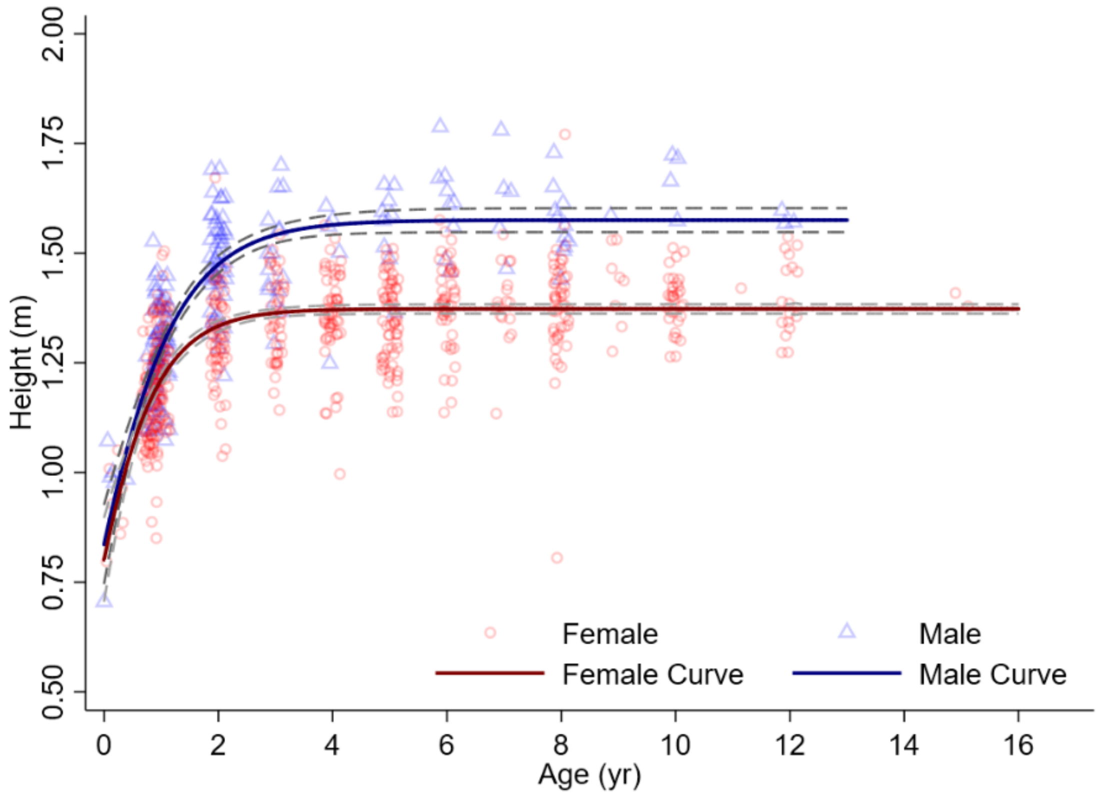

Figure 9.6. Growth of male (*n* = 194; blue symbols and lines) and female (*n* = 579; red symbols and lines) *Bison* along the Great Plains.

Tables

Table 9.1. Summary table of Gompertz equation parameters (Equation 2) in temporal (WICA 1960s to 2010s) and spatial (study sites 1-19 in 2017-2018) data series with covariables for site, sex (females, F; males, M), and decade of birth (DoB). Parameters include asymptotic body mass (*b*1; kg); instantaneous growth-rate at inflection point (*b*2); age at inflection point (*b*3; years).

Site	Sex	DoB	*b*1	SE	p	*b*2	SE	p	*b*3	SE	p	N	Adj. R^2
WICA	F	1960	444.45	8.55	0.00	0.87	0.05	0.00	0.67	0.03	0.00	338	0.99
WICA	F	1980	433.92	1.64	0.00	0.76	0.02	0.00	0.62	0.03	0.00	1356	0.99
WICA	F	1990	427.33	2.57	0.00	1.01	0.08	0.00	0.61	0.07	0.00	851	0.99
WICA	F	2000	412.81	3.30	0.00	0.98	0.04	0.00	0.65	0.02	0.00	674	0.98
WICA	F	2010	397.02	6.54	0.00	1.16	0.07	0.00	0.57	0.02	0.00	274	0.98
WICA	M	1960	797.93	41.89	0.00	0.49	0.04	0.00	1.45	0.12	0.00	252	0.99
WICA	M	1980	766.95	16.86	0.00	0.47	0.02	0.00	1.55	0.05	0.00	550	0.98
WICA	M	1990	806.97	31.32	0.00	0.45	0.03	0.00	1.43	0.09	0.00	535	0.98
WICA	M	2000	646.51	28.63	0.00	0.59	0.04	0.00	1.30	0.09	0.00	548	0.97
WICA	M	2010	611.82	47.52	0.00	0.65	0.07	0.00	1.08	0.13	0.00	190	0.97
3	F	2010	331.32	17.45	0.00	0.85	0.72	0.24	-0.14	1.17	0.91	44	0.95
4	F	2010	395.82	12.20	0.00	7.91	2.69	0.01	0.74	0.04	0.00	44	0.97
5	F	2010	346.97	13.29	0.00	4.75	1.82	0.01	0.72	0.06	0.00	30	0.97
8	F	2010	395.43	32.12	0.01	0.87	1.52	0.63	1.74	3.65	0.68	5	1.00
10	F	2010	361.93	13.21	0.00	1.89	1.69	0.27	0.23	0.56	0.68	33	0.97
11	F	2010	413.15	10.48	0.00	8.15	2.49	0.00	0.79	0.02	0.00	34	0.98
12	F	2010	372.20	18.20	0.00	0.64	0.27	0.02	-0.36	0.54	0.52	57	0.97
13	F	2010	363.08	18.84	0.00	1.09	0.58	0.07	0.19	0.44	0.67	31	0.96
14	F	2010	377.85	15.72	0.00	0.53	0.20	0.01	-0.38	0.47	0.42	41	0.98
15	F	2010	330.09	11.94	0.00	4.06	1.70	0.02	0.68	0.09	0.00	65	0.94
16	F	2010	390.49	18.70	0.00	0.96	0.34	0.01	0.20	0.31	0.51	32	0.97
17	F	2010	359.89	15.38	0.00	2.53	1.05	0.02	0.45	0.19	0.02	35	0.95
18	F	2010	371.23	10.91	0.00	1.56	0.31	0.00	0.50	0.08	0.00	44	0.98
19	F	2010	382.74	14.95	0.00	1.30	0.87	0.15	0.25	0.46	0.59	23	0.98
4	M	2010	719.69	126.13	0.00	0.30	0.16	0.09	0.83	0.60	0.19	13	0.98
5	M	2010	542.97	194.41	0.07	1.68	3.69	0.68	0.71	0.79	0.43	6	0.88
8	M	2010	598.38	130.28	0.02	0.27	0.16	0.19	2.21	1.19	0.16	6	0.97
9	M	2010	494.75	37.45	0.05	0.69	0.44	0.36	0.67	0.43	0.36	4	0.99
10	M	2010	582.38	96.21	0.00	0.46	0.32	0.17	-0.21	0.55	0.71	20	0.96
11	M	2010	512.78	92.31	0.00	0.77	1.29	0.57	-0.48	1.96	0.81	9	0.97
13	M	2010	746.90	209.27	0.02	0.40	0.23	0.15	1.23	0.73	0.15	8	0.99
14	M	2010	600.15	33.80	0.00	0.96	0.13	0.00	0.85	0.08	0.00	18	0.99
15	M	2010	510.25	20.41	0.00	4.45	--	--	0.83	0.03	0.00	11	0.99
16	M	2010	600.43	--	--	0.90	69.29	0.99	0.47	40.88	0.99	3	0.96
17	M	2010	499.91	134.38	0.00	1.42	1.55	0.38	0.68	0.26	0.03	14	0.93
18	M	2010	543.43	36.00	0.00	1.18	0.32	0.01	0.44	0.14	0.02	11	0.98
19	M	2010	505.84	35.78	0.00	0.63	0.25	0.04	0.39	0.44	0.40	11	0.98

Table 9.2. *Bison* image counts by locality and mean decadal temperature, precipitation, and Palmer Drought Severity Index (Vose *et al.*, 2014; NOAA, 2018).

Site number	State/ Province	Images captured (*n*)	Mean decadal temperature (°C)	Mean decadal precipitation (mm)	Decadal Palmer Drought Severity Index
1	Montana	5	5.46	807.52	-0.43
2	Montana	9	5.46	807.52	-0.43
3	Montana	44	4.46	547.20	-0.37
4	Saskatchewan	44	4.75	449.86	1.27
5	Wisconsin	32	7.28	942.93	2.18
6	Minnesota	17	7.45	958.20	2.43
7	South Dakota	25	8.89	482.04	2.53
8	South Dakota	4	7.11	553.97	1.37
9	South Dakota	4	7.11	553.97	1.37
10	Wyoming	33	7.72	391.87	0.89
11	Colorado	34	8.02	463.01	0.42
12	Kansas	57	11.74	521.32	-0.50
13	Kansas	31	12.42	855.27	-0.15
14	Kansas	41	14.03	720.32	0.11
15	New Mexico	65	8.98	405.33	-1.91
16	New Mexico	32	14.40	250.61	-1.96
17	Texas	35	15.67	465.55	-0.94
18	Texas	44	17.79	600.20	-0.66
19	Texas	23	19.34	1230.09	-0.69

Table 9.3. Summary statistics of female (F) and male (M) *Bison bison* data from Wind Cave National Park.

F	N	Mean	Std. Dev.	Min	Max
Age (y)	3698	5.0	4.6	0.5	23.5
Mass (kg)	3698	344.2	104.8	27.7	646.4
Height (m)	2136	1.38	0.10	0.84	1.75
M					
Age (y)	2083	2.0	1.4	0.5	17.5
Mass (kg)	2083	331.6	146.8	21.8	936.7
Height (m)	1044	1.39	0.14	0.86	1.78

APPENDIX D

SUPPORTING DATA FOR CHAPTER 4 – THERMAL BIOLOGY AND GROWTH

Data from this chapter are available on Figshare Data Repository (Martin and Barboza, 2020). DOI: 10.6084/m9.figshare.12084645.

Materials

Data sources

Climatic data are available from the United States National Oceanic and Atmospheric Administration (NOAA) Gridded Climate Divisional Dataset (CLIMDIV; version 1.0.0) database. doi:10.7289/V5M32STR & https://data.nodc.noaa.gov/cgi-bin/iso?id=gov.noaa.ncdc:C00005# (Vose et al. 2014). Ecoregions of North America shapefiles, including the Great Plains used in this study, are available from the United States Environmental Protection Agency: https://www.epa.gov/eco-research/ecoregions-north-america.

Methods

Photogrammetry

Distance measures of *Bison* for photogrammetric techniques were determined using a digital laser rangefinder [RX-1200i TBR/W (±0.46 m), Leupold & Stevens, Inc., Beaverton, Oregon, USA]. Photogrammetric calibration on each image was performed in FLIR ResearchIR Max software [version 4.40.1 64-bit; FLIR Systems, Inc., Wilsonville, Oregon, USA] using the built-in focal length (83.2 mm) and spatial calibration tool (17 µm pixel pitch). We used the upper rear leg of *Bison* as a standard target for distance measurement using the range finder, that is, we aimed for the center of the femur as our target for the distance measure. The hindquarters were chosen because of the reduced variability in distance measures in comparison with the forequarters, likely due to the increasing refraction of the laser in the dense, long hair of the forequarters (Martin, unpublished data).

Emissivity calibrations

We performed emissivity validation for seasonal changes in *Bison* hair coat-skin emissivity. Indeed, seasonal hair coats affect physical measures (Russell and Tumlison 1996). Emissivity (ε) is a measure of a material's radiating efficiency (Mason and Coleman 1967, Tattersall et al. 2009). An emissivity of 1.00 implies that the material is 100% efficient at radiating energy. An emissivity of 0.20 indicates that that the material absorbs 80% and radiates 20% of incoming radiant energy. Knowledge of emissivity is critical for directly comparing surface temperatures of materials. Emissivity values alter the measured temperature; the temperature is reliant upon accurate reports of the emissivity to give the true temperature of the object.

Following methods in FLIR Systems (2017), we applied 3M Scotch brand–88 black vinyl electrical tape to seasonal variants of both a hand-reared living *Bison* and hair-on *Bison* robes and allowed for all materials to thermally equilibrate. We targeted the pelvic-iliac anatomical position of both the living animal and the robe. Using FLIR ResearchIR Max (version 4.40.1; 64-bit) software, we adjusted the object of interest emissivity value until the mean temperature aligned with the mean temperature of the calibration material, here the 3M Scotch brand 88 black vinyl electrical tape, set at a known emissivity value—0.96 for the vinyl tape. Using the method described above, we confirmed the emissivity values of the textiles compared in Appendix Table 7.6 below and report *Bison* hair, skin, and Bison-merino sheep blend wool textile emissivity values (Braaten and Williams 1996, McGregor 2012). Generally accepted emissivity values of salient materials were compared (Mason and Coleman 1967, Zhang et al. 2009, Optotherm Thermal Imaging 2018). We report emissivity for *Bison* hair coat (winter) and skin (summer) to be $\varepsilon = 0.90$ and $\varepsilon = 0.94$, respectively. This aligns with known values of leather (0.95–1.00), human skin (0.98–0.99). We found that the emissivity compared directly to 3M Black electric tape (0.96).

Thermal conductivity

Thermal conductivity was a critical element to calculate thermal conductance and non-evaporative insulation-conductive heat transfer (hereafter, 'sensible heat' (McCafferty et al. 2011)). Total depth of insulation layer of *Bison* torso varies seasonally because of molt of woolly fur undercoat (Reinhardt 1985, Braaten and Williams 1996). Total torso insulation depth (d; m; see discussion in Supplemental Methods for torso mass composition and insulation depth estimation) averaged 0.0784 m in winter and 0.0371 m in summer. Total insulation averaged 0.6625 m^2•°C/W (Christopherson and Young 1981). Thermal conductivity averaged 0.118 (k; W/m•°C) and was calculated using Equation 10.1:

Equation 10.1. $$k = d/I$$

Sensible heat

Calculating total heat flux of insulated portions of endotherms required sensible heat (q_{sens}; W•m^{-2}). Sensible heat was calculated using thermal conductivity, insulation depth, average core body temperature, and surface temperature. Core body temperature (T_b), measured as rectal temperature, for *Bison bison* below ambient air temperature of 0 °C averaged 38.4 °C (Christopherson et al. 1979). While the upper limit threshold for *Bison* (dark brown color) was not well established in the literature, the value likely lies between that for black colored *Bos taurus* at 30 °C and that for black colored *Bos indicus* at 35 °C (Nielsen-Kellerman 2009, National Academies of Sciences • Engineering • Medicine 2016); lighter colors such as white fur raises the upper limit threshold for both cattle species—effectively increasing heat tolerance. Sensible heat was calculated using Equation 10.1:

Equation 10.2. $$\boldsymbol{q_{sens} = \frac{k}{d}(T_b - T_s)}$$

Total heat flux

Calculating total heat flux (q_{tot}; W•m^{-2}) follows Tattersall (Tattersall 2019) for q_{conv} and q_{rad}, where q_{rad} already included the difference between absorbed heat gain and radiative heat loss. We included q_{sens} as a term in Equation 4.3 (McCafferty et al. 2011, Clarke 2017). Total heat flux (q_{tot}) was calculated using Equation 10.3:

Equation 10.3. $$\boldsymbol{q_{tot} = (q_{rad} + q_{conv} + q_{sens})}$$

Total body surface heat loss

Total surface heat loss (Q; W) is the product of surface area and total heat flux. Calculating total body surface heat loss follows Clarke (2017). Total surface heat loss is calculated using Equation 10.4.

Equation 10.4. $$\boldsymbol{Q = SA \times q_{tot}}$$

Composition of torso mass and insulation depth

Because we focus on the effective thermal window of *Bison* (i.e., the torso), we estimated the mass of the torso. At one location, site 4, slaughtered *Bison* between the ages of 1.5 – 2.5 y had a live body mass that averaged 384 – 438 kg, respectively. We calculated torso mass to best estimate the mass of the effective thermal window of *Bison* as a horizontal cylinder for thermogrammetry and comprised the following body part components: 1) hot hanging mass— the untrimmed carcass missing viscera, distal podials, crania, and integument—averaged 235 – 272 kg (~61.5% of live body mass); 2) fresh skins (without crania) average approximately 45 – 56 kg (~12.3% of live body mass; M. Jacobson of North American Bison, LLC., pers. comm., 2020); and 3) viscera—including digesta—averaged 7 – 13% of live body mass (Huntington et al. 2019); generating an average torso mass to live body mass percentage of approximately 83.7%.

Total depth of insulation on the torso was the sum of subcutaneous fat, skin and fur. Total torso insulation depth (d; m) averaged 0.0784 m in winter and 0.0371 m in summer. Subcutaneous fat cover of the ribcage averaged 0.0221 m (Koch et al. 1995) and skin thickness averaged 0.015 m (McEwan Jenkinson and Nay 1975). Woolly hair covering the rib cage averaged 0.0413 m (Peters and Slen 1964) in the winter and $\leq$ 0.001 m in summer.

Instruments and databases

We used a mobile weather station mounted on a leveled tripod-vane standing 0.25-m above ground at each site to record dry bulb temperature (°C), dew point temperature (°C), wind speed ($m \cdot s^{-1}$), and temperature-humidity index (hereafter, heat index; °C) at 10 minute intervals during observations of *Bison* [Kestrel 5400AG Cattle Heat Stress Tracker; Nielsen-Kellerman Company, Boothwyn, PA, USA]. We used the nearest weather station to each site in the Daily Global Historical Climatology Network (GHCN; version 3.22; http://doi.org/10.7289/V5D21VHZ) from 1895 to 2018 (Menne et al. 2012) to obtain local daily measures of maximum temperature, minimum temperature, precipitation, snowfall, and snow depth. We used the NOAA Gridded Climate Divisional Dataset (nClimDiv; version 1.0.0; http://doi:10.7289/V5M32STR) database (Vose et al. 2014) to obtain annual, monthly, and regional measures of temperature (MAT), and precipitation (MAP).

Weather and climate: measures, databases, and indices

We directly measured daily weather on site for thermal camera calibrations and we obtained annual and seasonal measures of climate and weather from NOAA databases of seasonal and monthly weather, including dry bulb temperature, wind speed, and temperature-humidity index (hereafter, heat index). We used three spatial scales of weather observations because each one provides a slightly different measure of weather. We used latitude, mean annual temperature (MAT), and mean annual precipitation (MAP) to indicate annual climate at each site.

Figures

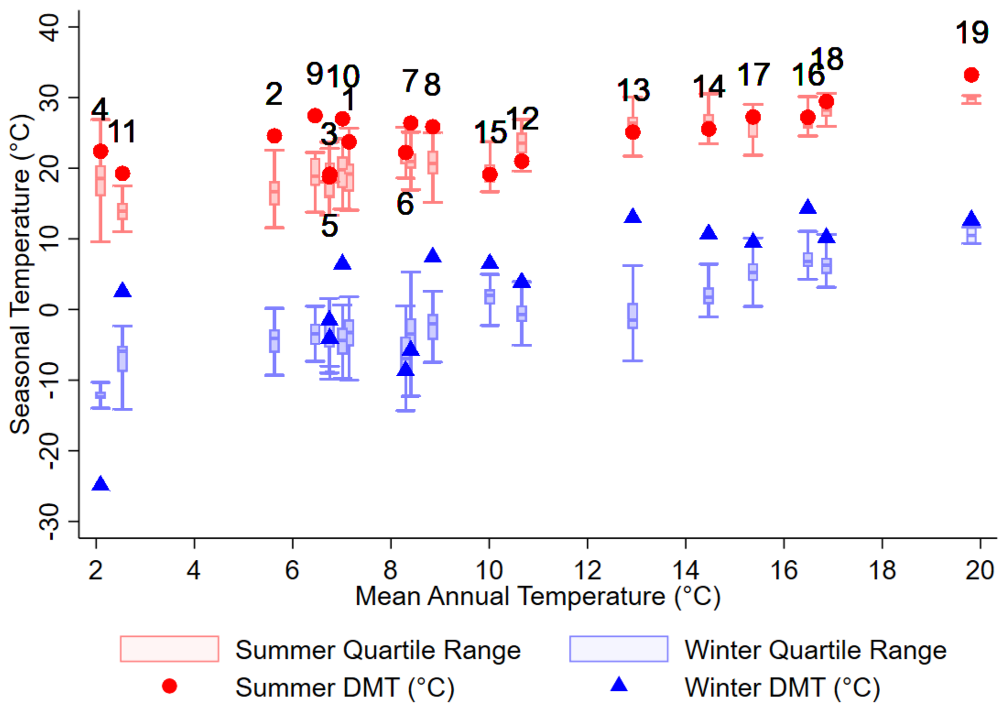

Figure 10.1. Boxplot of winter and summer range of temperature for each locality. Solid red circle indicates daily mean temperature on the day of the summer visit, whereas solid blue triangle indicates daily mean temperature on the day of the winter visit. Numbers refer to site number.

Tables

Table 10.1. Summary table of body surface temperature (°C) in a multilevel mixed effects general linear model of black globe temperature (T_{Globe}; °C) interacting with season, wet bulb globe temperature (T_{WBGT}; °C) interacting with season, and wet bulb globe temperature. Abbreviations: *β*, beta coefficient; SD, standard deviation; SE standard error. Cross-validation support metrics using $k_{(10)}$-fold: pseudo-R^2 = 0.61, RMSE = 10.3, *N* = 779 individuals, *n* = 19 groups by site. Random effects (site) explained 0.26% of variance.

Parameter	*β*	SE	z	*p*	Lower CI	Upper CI
x_1, Season#T_{Globe}						
Summer	0.04	0.16	0.23	≤ 0.81	-0.28	0.36
Winter	0.51	0.12	4.26	< 0.001	0.28	0.75
x_2, Season#T_{WBGT}						
Winter	-0.80	0.29	-2.75	≤ 0.006	-1.38	-0.23
x_3, T_{WBGT}	1.07	0.25	4.31	< 0.001	0.59	1.56
β_0, intercept constant	10.47	1.45	7.20	< 0.001	7.62	13.32
ϵ, ‖ Site:	3.24	0.65	---	---	2.19	4.80
SD of whole model	9.71	0.25	---	---	9.23	10.21

Table 10.2. Summary table of ordinary least squares regressions of total body surface heat loss (*Q*; W) over estimated body mass (BM_E; kg) and log of absolute value of body surface heat loss ($log_{10}Q$; log_{10}-|*Q*|) over log of estimated body mass ($log_{10}BM_E$; log_{10}-kg). Abbreviations: *β*, beta coefficient; SE standard error. W: Adj. $R^2 = 0.31$, RMSE = 7914, *N* = 695 individuals; log-|*Q*|: Adj. $R^2 = 0.36$, RMSE = 0.13, *N* = 695 individuals.

Parameter	β	SE	z	*p*	Lower CI	Upper CI
Q						
x_1, BM_E	-52.0	2.9	-17.9	< 0.001	-57.7	-46.3
β_0, intercept constant	-9586.6	1018.6	-9.4	< 0.001	-11586.6	-7586.7
Log_{10}-|*Q*|						
x_1, $log_{10}BM_E$	0.63	0.03	19.85	< 0.001	0.57	0.70
β_0, intercept constant	2.82	0.08	35.28	< 0.001	2.66	2.98

Table 10.3. Summary table of total body surface heat loss (*Q*; W) in an ordinary least squares model of growth rate ($kg \cdot y^{-1}$). Abbreviations: *β*, beta coefficient; SD, standard deviation; SE standard error. *Q*: Adj-$R^2 = 0.25$, RMSE = 5964.9, *n* = 16 groups by site.

Parameter (*Q*)	β	SE	z	*p*	Lower CI	Upper CI
x_1, Growth rate ($kg \cdot y^{-1}$)	150.3	61.1	2.5	≤ 0.027	19.4	281.2
β_0, intercept constant	-39960.3	4901.7	-8.2	< 0.001	-50473.3	-29447.2

Table 10.4. Summary table of heat flux ($W \bullet m^{-2}$) in a multilevel mixed effects general linear model of latitude interacting with season and site as a random effect. Abbreviations: β, beta coefficient; SD, standard deviation; SE standard error. Cross-validation support metrics using $k_{(10)}$-fold: pseudo-R^2 = 0.12, RMSE = 64.6, N = 343 individuals, n = 19 groups by site. Random effects (site) explained 0.61% of variance.

Parameter $W \bullet m^{-2}$	β	**SE**	**z**	p	**Lower CI**	**Upper CI**
x_1, Latitude#Season						
$\text{Latitude}_{\text{Summer}}$	3.08	1.66	-1.86	≤ 0.063	-0.17	-6.32
$\text{Latitude}_{\text{Winter}}$	3.85	1.64	2.34	≤ 0.019	.63	7.07
β_0, intercept constant	-423.55	67.47	-6.28	< 0.001	-555.78	-291.32
ϵ, ‖ Site:	35.25	7.25	---	---	23.56	52.74
SD of whole model	61.17	2.39	---	---	56.66	66.03

Table 10.5. Parameters of bison body size, body and eye temperature, and reflectance of hair and bare skin.

Parameter	Abbreviation	Unit	Calculation or parameters used	Notes and references
Surface temperature	T_S	°C	---	Remotely measured with FLIR T1030sc.
Estimated height	H_E	m	$H_E = \frac{d(o \times s)}{f \times i}$	Where, *d* is measured distance from camera to object (m) obtained by a laser rangefinder; *o* is relative digital length of the object of interest in the photograph (pixels); *s* is sensor height of the camera (mm); *f* is focal length of the lens (mm); *i* is total picture height (pixels); and *H* is height of the animal (Martin and Barboza 2020). Remotely measured.
Body surface area	B	m2	---	Using the above equation above. Remotely measured.
Wind speed	V	m • s-1	---	---
Dew point temperature	DP	°C	---	---
Relative humidity	RH	0-1, fractional	---	Recorded as percent and converted to fractional.
Bison haircoat reflectance	ρ_0	0–1, estimated to be 0.37	If season == winter	Average of: 0.04–0.05 for black cattle (Holstein (*Bos taurus*) and Brangus (*B. taurus* × *B. indicus*), respectively), 0.44–0.58 for red coat cattle (Holstein and Simmental (*Bos taurus*), respectively), and 0.37 for marsh deer (*Blastocerus dichotomus*). Between the wavelength range of 300–850 nm (da Silva et al. 2003); table 1.
Bison bare skin reflectance	ρ1	0–1, estimated to be 0.23	If season == summer	Average of: 0.06–0.07 for black cattle (Holstein (*Bos taurus*) and Brangus (*B. taurus* × *B. indicus*), respectively), 0.23 for black water buffalo (*Bubalus bubalis*; who are relatively hairless), 0.28–0.44 for red coat cattle (Simmental and Holstein (*Bos taurus*), respectively), and 0.31 for marsh deer (*Blastocerus dichotomus*). Between the wavelength range of 300–850 nm (da Silva et al. 2003); table 2.
Standard reflected temperature	---	°C	Summer = 20 Winter = -20	---
Emissivity	ε	0–1	Summer bare skin is estimated to be 0.94 whereas, winter haircoat is estimated to be 0.90 using the emissivity calibration feature in FLIR ResearchIR Max software	Following emissivity calibration protocols (FLIR Systems 2017), see SI Table S6 below.
Shape of object	S	Sphere, hcylinder, vcylinder, hplate, vplate	"hcylinder" was chosen.	Horizontal cylinder was chosen because height (HE) is the characteristic measure of *Bison* representing the radius of the cylinder and height into the air column (Tattersall 2019).
Dry bulb temperature	Ta	°C	---	---
Wet bulb globe temperature	WBGT	°C	---	Used in place of effective temperature (T_E) (Bernard et al. 1994, Liljegren et al. 2008).
Daily maximum temperature	T_{max}	°C	max (T_{daily})	---
Daily minimum temperature	T_{min}	°C	min $(T_{daily\,(day+1)})$	T_{min} is often reported as the low temperature preceding to T_{max}, we have shifted the T_{min} to be the succeeding daily low temperature because it is more physiological relevant for dumping accumulated heat from the preceding heat stress (Nairn and Fawcett 2014)
Daily mean temperature	DMT	°C	$mean$ $(T_{max} + T_{min})$	---

Table 10.6. Emissivity (ε) of selected materials used in this study. Asterisk indicates: a material recommended by FLIR to determine emissivity because this material is consistent in both the short wavelength (3-5 µm) and long wavelength (8-12 µm) regions.

Material	Emissivity (ε)	References
Bison bare skin (summer molt)	0.94	This study
Bison hair (winter woolly fur undercoat)	0.90	This study
3M Scotch brand–88 black vinyl electrical tape*	0.96	(FLIR Systems 2017)
Human skin	0.98–0.99	(Optotherm Thermal Imaging 2018, ThermoWorks 2019)
Leather	0.95–1.00	(Optotherm Thermal Imaging 2018, ThermoWorks 2019)

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APPENDIX E

SUPPORTING DATA FOR CHAPTER 5 – BISON MANAGER SUVEY

Bison Manager Survey Questionnaire

Table 11.1. Bison Manager Survey
Informed Consent

Welcome to the Bison Manager Survey!

We are conducting a research study about bison manager decisions and practices as they relate to bison resiliency and vulnerabilities. You will be presented with questions relevant to bison management. Please be assured that your responses will be kept confidential. We do not ask any personal identifying information. Your recorded answers will not be associated with any digital identifying information (e.g. IP addresses). Results will be reported in a generalized format (averages and standard deviations) that will conceal individual information.

The study should take you around 10 minutes to complete. Your participation in this research is *completely voluntary*. You have the right to withdraw at any point during the study, for any reason, and without any prejudice. This study is approved by the Texas A&M University Institutional Review Board: IRB 2018-1654. If you would like to contact the Principal Investigator in the study to discuss this research, please e-mail Dr. Perry Barboza at psbarboza@tamu.edu.

By clicking the button below, you acknowledge that your participation in the study is voluntary, you are 18 years of age, that you are aware that you may choose to terminate your participation in the study at any time and for any reason.

Please note that this survey will be best displayed on a personal computer. Some features may be less compatible for use on a mobile device.

○ I consent, begin the study

○ I do not consent, I do not wish to participate

Skip To: End of Survey If 1 = I do not consent, I do not wish to participate

Survey Administration

Note: each possible answer to each question may either be numbered or be labeled as "•", indicating scoring measures. Additionally, a "•" indicates a "null", whereas incremental numbers indicate a higher "resiliency score" for that question. Some questions may not be scored at all.

1. Do you or have you ever managed bison?
    - Yes
    - No

Skip To: End of Survey If 1 = No

2. To which gender do you most identify?
    1. Male
    2. Female
    - Other
    - Prefer not to answer

Survey Questions

3. What is the predominant location of your bison herd(s)?
    - Northern (Canada, MT, ND, MN, WI, SD, WY, ID, WA, OR, MI)
    - Central (UT, NE, IA, IL, IN, OH, KY, TN, MO, KS, CO, NV)
    - Southern (CA, AZ, NM, TX, OK, AR, LA)
    - Eastern (ME, NH, VT, NY, RI, CT, MA, NJ, VA, NC, SC, GA, FL, MS, AL)
4. What is the predominant ecoregion for your bison herd(s)?
    - Tallgrass Prairie
    - Mixed grass Prairie
    - Shortgrass Prairie
    - Other ____
    - Prefer not to answer
5. What is the highest degree or level of school you have completed? If currently enrolled, highest degree received/earned?
    1. Less than high school
    2. High school graduate
    3. Some college
    4. 2 year degree
    5. 4 year degree
    6. Masters degree
    7. Professional degree
    8. Doctorate
    - Prefer not to answer

Display This Question: If 5 = 4 year degree Or 5 = Masters degree Or 5 = Professional degree Or 5 = Doctorate

6. What discipline was your degree in?
   - Social sciences (Economics, archaeology, sociology, etc.)
   - Natural sciences (Physics, chemistry, biology, etc.)
   - Formal or applied sciences (Computer sciences, mathematics, statistics, etc.)
   - Humanities (Arts, literature, philosophy, etc.)
   - Professions (Education, business, agriculture, medicine, law, engineering, etc.)

7. How long have you managed bison?
   1. 3 years or less
   2. 4-10 years
   3. 11- 20 years
   4. More than 20 years

8. In which sector of ownership is your bison operation?
   - Private (Typically for profit)
   - Non-governmental Organization (Private non-profit)
   - Governmental
   - Prefer not to answer

Display This Question: If 8 = Non-governmental Organization (Private non-profit) Or 8 = Governmental

9. Have you ever privately owned bison?
   1. No
   2. Yes
   - Prefer not to answer

10. What proportion of your net annual income is derived from owning or managing bison?
    1. Less than 10%
    2. 11 - 33%
    3. 34 - 67%
    4. 68 - 90%
    5. More than 90%
    - Prefer not to answer

11. Is non-agricultural income important to sustaining your bison herds?

	1. Not at all important	2. Neutral	3. Extremely Important
a. Tourism			
b. Recreation			
c. Off the farm employment			
d. Investment income			

12. In terms of productivity with your bison herd, when was your best year?
    - 2018
    - 2017
    - 2016
    - 2015
    - 2014
    - 2013

- Other ____

13. In terms of productivity with your bison herd, when was your worst year?
    - 2018
    - 2017
    - 2016
    - 2015
    - 2014
    - 2013
    - Other ____

14. In terms of productivity with your bison herd, how would you rank last year?
    - Extremely good
    - Somewhat good
    - Neither good nor bad
    - Somewhat bad
    - Extremely bad

15. Do you insure your bison?
    1. No
    2. Yes
    - Prefer not to answer

16. How much land do you manage?
    1. Fewer than 10 acres
    2. 11-50 acres
    3. 51-100 acres
    4. 101-250 acres
    5. 251-400 acres
    6. 401-750 acres
    7. 751-1000 acres
    8. 1001-2000 acres
    9. 2001-5000 acres
    10. More than 5000 acres
    - Prefer not to answer

17. How many people work with your bison herd(s)?
    1. More than 31
    2. 21-30
    3. 11-20
    4. 6-10
    5. 2-5
    6. 0-1
    - Prefer not to answer

18. How many bison herd(s) do you manage?
    1. 1
    2. 2
    3. 3
    4. 4
    5. 5
    6. More than 6
    - Prefer not to answer

19. What is the total population of bison you manage?
    1. More than 3000
    2. 2001-3000
    3. 1251-2000
    4. 1000-1250
    5. 501-1000
    6. 251-500
    7. 101-250
    8. 51-100
    9. 16-50
    10. 1-15
    - Prefer not to answer
20. What is your typical annual harvest rate?
    1. 31-50%
    2. 21-30%
    3. 11-20%
    4. 6-10%
    5. 0-5%
    - Greater than 50%
21. How important are economic balances to sustaining your bison herd?
    1. Strongly disagree
    2. Somewhat disagree
    3. Neither agree nor disagree
    4. Somewhat agree
    5. Strongly agree
22. How important are ecological balances to sustaining your bison herd?
    1. Strongly disagree
    2. Somewhat disagree
    3. Neither agree nor disagree
    4. Somewhat agree
    5. Strongly agree
23. Would you consider your work with bison as physically active?
    1. Strongly disagree
    2. Somewhat disagree
    3. Neither agree nor disagree
    4. Somewhat agree
    5. Strongly agree
24. Would you consider your work with bison as positive?
    1. Extremely negative
    2. Somewhat negative
    3. Neither positive nor negative
    4. Somewhat positive
    5. Extremely positive
25. Would you consider your work with bison as intellectually active?
    1. Strongly disagree
    2. Somewhat disagree
    3. Neither agree nor disagree
    4. Somewhat agree
    5. Strongly agree

26. Would you consider you work with bison as novel & innovative?
    1. Strongly disagree
    2. Somewhat disagree
    3. Neither agree nor disagree
    4. Somewhat agree
    5. Strongly agree

27. What are your attitudes towards the following ecological practices:?

	1. Negative	2. Positive
a. Hunting on your property (bison, deer, hogs, etc.)		
b. Prescribed burns for rangeland management		
c. Disease surveillance by necropsy of bison		
d. Disease surveillance by fecal analyses of bison		
e. Treating bison for intestinal parasites		
f. Vaccination of bison against disease		
g. Implement breeding stock selection procedures with registry tools		

28. What are your attitudes towards the following economic practices:?

	1. Negative	2. Positive
a. Cost sharing programs (i.e., absentee ownership, cooperatives)		
b. Agricultural subsidies (tax credits)		
c. Diversified livestock (cattle, goats, horses, poultry, etc.)		
d. Diversified land use (hay production, forest production, wetland conservation)		
e. Hunting on your property (bison, deer, hogs, etc.)		

29. How many cow/calf pairs can your ranch support on 10 acres in summer without hay (AUM)?
    1. Less than 0.5
    2. 0.6 - 1.0
    3. 1.1 - 3.0
    4. 3.1 - 5.0
    5. 5.1 - 10.0
    6. 10.1 - 15.0
    7. 15.1 - 20.0
    8. More than 20.0
    - Prefer not to answer

30. What supplement(s) do you use with your herd(s) (select all that apply)?

- No supplementation
- Grain
- Roughage cubes
- Minerals
- Hay
- Haylage/ Silage
- Other ____
- Prefer not to answer

31. In total, how many extreme weather events (e.g. Atlas Blizzard, Hurricane Katrina, greater than F3 tornado, Legion Lake Wildfire, hail storm, drought, heat wave, etc.) have you experienced in the last 10 years?
    1. 20+
    2. 11 - 19
    3. 6 - 10
    4. 2 - 5
    5. 1
    6. 0

Display This Question: If 31 != "0"

32. What extreme weather event did you experience (select all that apply)?
    - Blizzard
    - Hurricane
    - Tornado
    - Heat wave
    - Hail storm
    - Drought
    - Wildfire
    - Other ____

Display This Question: If 31 != 0

33. What losses have you suffered (select all that apply)?
    - Buildings
    - Animals
    - Grass/pasture/fence
    - Infrastructure (water, power, etc.)
    - Equipment
    - Other ____
    - None

34. In the last 10 years, have you observed directional changes to the following:

	1. Decreased/ later	2. No change	3. Increased/ sooner	•. Skip
a. Calf survival rates				
b. Pregnancy rates				
c. Parasite loads				

d. Disease rates				
e. Summer temperatures				
f. Winter temperatures				
g. Winter precipitation amount				
h. Spring precipitation amount				
i. Timing of spring green up				
j. Timing of bison winter coat shedding				
k. Timing of bison winter coat developing				

35. Does your operation regularly monitor:

a. Pasture conditions	1. No	2. Yes	•. Skip
b. Diversity of pasture plants	1. No	2. Yes	•. Skip
c. Diversity of wildlife	1. No	2. Yes	•. Skip
d. Population of wildlife	1. No	2. Yes	•. Skip

36. Where do you seek bison-related information that informs your practices (select all that apply)?
- Extension agent
- Bison associations
- Neighbors
- Bison producers (not neighbors)
- Public agents (wildlife officers, state park bison herd managers, etc.)
- Family members
- University professors and research scientists
- Other ____
- None
- Prefer not to answer

Display This Question: If 36 = Extension agent Or 36 = Bison associations Or 36 = Neighbors Or 36 = Bison producers (not neighbors) Or 36 = Public agents (wildlife officers, state park bison herd managers, etc.) Or 36 = Family members Or 36 = University professors and research scientists

37. How often do you seek their knowledge?
    1. Rarely (1 time per year or less often)
    2. Sometimes (2-3 times per year)
    3. Often (>4 times per year)

38. Have you leased grazing land in the last 3 years for bison?
    1. No
    2. Yes

- Prefer not to answer

39. What is your grazing management style?
    1. Continuous grazing (1-3 pastures)
    2. Ultra-high-density rotational grazing (>2 AU/acre, for less than 15 days in each pasture)
    3. Rotational grazing (>3 pastures with low to moderate stocking rates)
    - Other ____
    - Prefer not to answer

40. Do you have access to natural water features for your bison herd?
    1. No
    2. Yes
    - Prefer not to answer

41. Do you provide water to your animals?
    1. No
    2. Yes
    - Prefer not to answer

42. Do you have a drought plan (i.e., alter stocking rates, or purchase hay with below normal rain)?
    1. No
    2. In development
    3. Yes
    - Prefer not to answer

43. Is there anything you would like us to know? You may provide comments below.

____

Tables

Table 11.2. Corresponding region and ecosystem of respondent bison managers' predominant location. Displayed as "total # (public/NGO #/ private #)."

Region	Shortgrass	Mixed Grass	Tallgrass	Other	Total
Northern	10 (1/9)	40 (1/39)	3 (--/3)	5 (--/5)	58 (2/56)
Central	10 (2/8)	25 (2/23)	8 (3/5)	6 (--/6)	49 (7/42)
Southern	4 (--/4)	12 (1/11)	2 (1/1)	1 (--/1)	19 (2/17)
Eastern	--	2 (--/2)	1 (--/1)	3 (--/3)	6 (--/6)
Total	24 (3/21)	79 (4/75)	14 (4/10)	15 (--/15)	132 (11/121)

Table 11.3. Summary descriptive statistics of select questions and measures of interest from the vulnerability scoping diagram survey with comments indicating the meaning for specific median scores.

Question	N	Median	SD	Min	Max	Response code	Comments
Rely on tourism for sustaining bison management	125	1	0.67	1	3	1. Not at all important 2. Neutral 3. Extremely important	Most do not rely on tourism to sustain bison
Rely on recreation for sustaining bison management	123	1	0.64	1	3	1. Not at all important 2. Neutral 3. Extremely important	Most do not rely on recreation to sustain bison
Rely on off farm income for sustaining bison management	128	2	0.86	1	3	1. Not at all important 2. Neutral 3. Extremely important	Off-farm income reliance is even distributed, but most (*n*=52) are dependent on the income to sustain bison
Rely on investment for sustaining bison management	126	2	0.76	1	3	1. Not at all important 2. Neutral 3. Extremely important	Most are neutral or do not rely on investment income to sustain bison
Insure bison	123	0	0.46	0	1	0. No 1. Yes	Most do not insure their bison
How much land is managed	126	6	2.69	2	10	1. Fewer than 10 acres 2. 11-50 acres 3. 51-100 acres 4. 101-250 acres 5. 251-400 acres 6. 401-750 acres 7. 751-1000 acres 8. 1001-2000 acres 9. 2001-5000 acres 10. More than 5000 acres	Size of property is bi-modal, with most between 101-750 acres or between 1000->5000 acres.
How many people work for the bison operation	126	5	0.50	2	6	1. More than 31 2. 21-30 3. 11-20 4. 6-10 5. 2-5 6. 0-1	Most have less than 5 employees that derive their income from managing bison
How many herds	126	1	1.46	1	6	1. 1 2. 2 3. 3 4. 4 5. 5 6. More than 6	Most have only 1 herd of bison
How many bison	123	3	2.44	1	10	1. 1-15 2. 16-50 3. 51-100 4. 101-250 5. 251-500 6. 501-1000 7. 1000-1250 8. 1251-2000 9. 2001-3000 10. More than 3000	Most have less than 250 bison, with a median herd size of 51-100 bison
Rate of harvest	122	3	1.83	1	6	1. Greater than 50% 2. 31-50% 3. 21-30% 4. 11-20% 5. 6-10% 6. 0-5%	Harvest rates are diverse and equally distributed, ranging from less than 5% and greater than 50%
Prioritize economic balance	125	4	0.84	1	5	1. Strongly disagree 2. Somewhat disagree 3. Neutral 4. Somewhat agree 5. Strongly agree	Most prioritize economic balance (*n*=100; 76%)
Prioritize ecological balance	125	5	0.78	1	5	1. Strongly disagree 2. Somewhat disagree 3. Neutral 4. Somewhat agree 5. Strongly agree	Most prioritize ecological balance (*n*=108; 82%)
View job as physically active	126	4	0.94	1	5	1. Strongly disagree 2. Somewhat disagree 3. Neutral	Most view their job as physically active

						4. Somewhat agree 5. Strongly agree	
View job as positive	125	5	0.33	3	5	1. Strongly disagree 2. Somewhat disagree 3. Neutral 4. Somewhat agree 5. Strongly agree	Most view their job as positive
View job as intellectually stimulating	126	5	0.58	3	5	1. Strongly disagree 2. Somewhat disagree 3. Neutral 4. Somewhat agree 5. Strongly agree	Most view their job as intellectually stimulating
View job as novel	126	5	0.82	1	5	1. Strongly disagree 2. Somewhat disagree 3. Neutral 4. Somewhat agree 5. Strongly agree	Most view their job as novel or innovative
Attitude towards hunting on premise	122	2	0.46	1	2	1. Negative 2. Positive	Most view hunting positively
Attitude towards prescribed burning on premise	120	2	0.45	1	2	1. Negative 2. Positive	Most view prescribed burning positively
Attitude towards disease monitoring using necropsy	120	2	0.37	1	2	1. Negative 2. Positive	Most view necropsy positively
Attitude toward disease monitoring using fecal tests	122	2	0.36	1	2	1. Negative 2. Positive	Most view fecal testing positively
Attitude toward treating internal parasites	123	2	0.33	1	2	1. Negative 2. Positive	Most view treating parasites positively
Attitude toward vaccinating against disease	122	2	0.39	1	2	1. Negative 2. Positive	Most view vaccinating positively
Attitude toward using breeding/genetic tools	122	2	0.50	1	2	1. Negative 2. Positive	Views for breeding/genetic tools are split, with a slight skew towards positive
Attitude toward cost-sharing	122	2	0.50	1	2	1. Negative 2. Positive	Views for cooperatives are split, with a slight skew towards positive
Attitude toward Ag. subsidies	123	2	0.49	1	2	1. Negative 2. Positive	Views for ag. subsidies are split, with a moderate skew towards positive
Attitude toward diverse livestock	122	2	0.49	1	2	1. Negative 2. Positive	Views for diverse livestock are split, with a moderate skew towards positive
Attitude toward diverse land use	122	2	0.29	1	2	1. Negative 2. Positive	Most view diverse land use positively
How many cow/calf pairs can your ranch support on 10 acres in summer without hay (AUM)?	121	6	1.52	1	8	1. Less than 0.5 2. 0.6 - 1.0 3. 1.1 - 3.0 4. 3.1 - 5.0 5. 5.1 - 10.0 6. 10.1 - 15.0 7. 15.1 - 20.0 8. More than 20.0	Most have moderately low stocking rates, averaging between 1.1-3.0 cow/calf pairs per 10 acres
In total, how many extreme weather events (e.g. Atlas Blizzard, Hurricane Katrina, greater than F3 tornado, Legion Lake Wildfire, hail storm, drought, heat wave, etc.) have you experienced in the last 10 years?	124	4	1.02	1	6	1. 20+ 2. 11 - 19 3. 6 - 10 4. 2 - 5 5. 1 6. 0	Most have experienced between 2-5 extreme weather events over the last 10 years
Regularly monitor pasture conditions	119	1	0.13	0	1	0. No 1. Yes	Most regularly monitor pasture conditions
Regularly monitor pasture plant diversity	119	1	0.37	0	1	0. No 1. Yes	Most regularly monitor pasture plant diversity
Regularly monitor wildlife diversity	117	1	0.42	0	1	0. No 1. Yes	Mold regularly monitor wildlife diversity
Regularly monitor wildlife population	118	1	0.47	0	1	0. No 1. Yes	Mold regularly monitor wildlife population
How often do managers seek knowledge from others	118	2	0.73	1	3	1. Rarely (1 time per year or less often) 2. Sometimes (2-3 times per year) 3. Often (>4 times per year)	Many seek information and communicate more than 2-3 times per year with mentors, and most seek information more than 4 times per year
Leased land for expanding bison grazing in the last 3 years	119	0	0.44	0	1	0. No 1. Yes	Most have not leased grazing land for sustaining bison in the last 3 years

Grazing management style	120	2	0.95	1	3	1. Continuous grazing (1-3 pastures) 2. Ultra-high-density rotational grazing (>2 AU/acre, for less than 15 days in each pasture) 3. Rotational grazing (>3 pastures with low to moderate stocking rates)	Grazing management style is bi-modal, split equally between continuous grazing (*n*=50) and rotational grazing (*n*=53)
Natural water features present on property	120	1	0.41	0	1	0. No 1. Yes	Most have natural water features on their property for bison use
Provide water for bison consumption	120	1	0.33	0	1	0. No 1. Yes	Most provide drinking water to bison
Have a drought plan prepared	131	3	0.78	1	3	1. No 2. In development 3. Yes	Most have a drought plan created (*n*=95) and some are in-development of one (*n*=13)

Table 11.4. Summary statistics of vulnerability exposure, sensitivity, adaptive capacity and overall resiliency scores of bison managers from different regions, ecosystems, and sectors (displayed as median score (standard error)). Indicators: * = statistically different groups ($p \leq 0.05$), in multiple pairwise comparison of margins with Bonferroni's adjustment method.

Trait	Group	Exposure	Sensitivity	Adaptive Capacity	Overall Resiliency
Region	Northern	5.9 (0.2)	6.1 (0.2)	5.7 (0.3)	5.8 (0.2)
	Central	5.9 (0.2)	6.2 (0.2)	5.9 (0.3)	6.2 (0.2)
	Southern	5.4 (0.3)	6.1 (0.4)	6.0 (0.5)	6.0 (0.3)
	Eastern	5.8 (0.6)	6.9 (0.6)	6.0 (0.9)	6.5 (0.6)
Ecosystem	Shortgrass	5.5 (0.3)	6.6 (0.3)	5.8 (0.4)	6.1 (0.3)
	Mixed grass	5.8 (0.1)	6.1 (0.2)	5.9 (0.2)	5.9 (0.2)
	Tallgrass	6.3 (0.3)	5.8 (0.4)	6.1 (0.6)	6.5 (0.4)
	Other	6.0 (0.3)	6.6 (0.4)	5.1 (0.6)	5.8 (0.4)
Sector	Private	5.8 (0.1)	6.1 (0.1)	6.0 (0.2)*	6.0 (0.1)
	Public/NGO	6.2 (0.4)	6.6 (0.5)	4.0 (0.6)*	5.8 (0.4)

Table 11.5. Cross-tabulation summary table of education level and education discipline. Only 74/132 of bison managers reported having earned college degrees. Examples of education disciplines were as follows: social sciences (economics, archaeology, sociology, etc.), natural sciences (physics, chemistry, biology, etc.), formal or applied sciences (computer sciences, mathematics, statistics, etc.), humanities (arts, literature, philosophy, etc.), and professions (education, business, agriculture, medicine, law, engineering, etc.).

Education	Discipline					
Level	Social	Natural	Applied	Humanities	Professions	Total
4-year degree	4	11	2	2	19	38
Masters	3	6	1	1	13	24
Professional	--	1	--	--	4	5
Doctorate	1	2	--	--	4	7
Total	8	20	3	3	40	74

APPENDIX F

CARBON EMMISSIONS STATEMENT

I travelled in excess of 27,700 miles to collect more than 800 organ tissue samples from 190 individual bison from the northern-most and southern-most extents of the Great Plains, and captured more than 2100 thermal images of bison in summer and in winter from 19 bison herds in the Great Plains, ranging from central Saskatchewan to southeast Texas. That's a carbon footprint of 14.3 metric tons (CO_2) driving and 4 metric tons (CO_2) flying, summing to 18.3 metric tons of CO_2, worth approximately $520 (USD-2019).

To offset this carbon, I owned on average 15 bison for the past 18 years on approximately 180 acres of converted cropland to pastures, which sequester approximately 176 metric tons of carbon annually (14.7 metric tons monthly; http://grazingguide.net/research/soil-carbon-sequestration-in-pastures.html). One to two months of bison grazing offsets the carbon output for this travel. The conversion of croplands to pasture usually adds 0.2 to 0.5 tons of soil C per acre each year and the farm has been in operation for about 18 years at the time of writing this. Between 700 and 1800 metric tons of carbon have been sequestered at my parent's ranch by converting the property to pastureland from cropland.

Calculations derived from: https://www.myclimate.org/; 36,532.1 km driven, in a car with 9.35 km/l for driving and flying roundtrip to Fargo, via Denver, from College Station, twice. Equivalencies calculated from: https://www.epa.gov/energy/greenhouse-gas-equivalencies-calculator.

Table 12.1. Table of carbon equivalencies produced from this research project.

Output and Remediation Equivalencies			
Greenhouse gas emissions from:	**CO_2 emissions from:**	**Greenhouse gas emissions avoided by:**	**Carbon sequestered by:**
4 passenger vehicles driven for one year	2,059 gallons of gasoline consumed	6.2 tons of waste recycled instead of landfilled	303 tree seedlings grown for 10 years
45,409 miles driven by an average passenger vehicle	1,798 gallons of diesel consumed	0.889 garbage trucks of waste recycled instead of landfilled	23.9 acres of U.S. forests in one year
---	20,0164 pounds of coal burned	779 trash bags of waste recycled instead of landfilled	0.124 acres of U.S. forests preserved from conversion to cropland in one year
---	0.242 tanker trucks' worth of gasoline	0.004 wind turbines running for a year	---
---	2.1 homes' energy use for one year	695 incandescent lamps switched to LEDs	---
---	3.1 homes' electricity use for one year	---	---
---	0.101 railcars' worth of coal burned	---	---
---	42.4 barrels of oil consumed	---	---
---	748 propane cylinders used for home barbeques	---	---
---	2,333,840 smartphones fully charged	---	---