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Variation in American Bison (Bison Bison) Ecological Functionality across Management Sectors: Implications for Conducting Conservation Assessments

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VARIATION IN AMERICAN BISON (*BISON BISON*) ECOLOGICAL FUNCTIONALITY ACROSS MANAGEMENT SECTORS: IMPLICATIONS FOR CONDUCTING CONSERVATION ASSESSMENTS

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DEDICATION

This thesis is dedicated to my father, the late Randy Ray Rogers. Throughout his career he worked tirelessly to restore the largest land mammal in the Western Hemisphere, wood bison, to the state of Alaska. Though he was unable to witness the success of his work after a courageous battle with cancer, his passion and dedication towards wood bison lives on through me. Every day I spend working with these animals I feel closer to you, dad.

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ABSTRACT

The American bison (*Bison bison* subspp.), once on the verge of extinction, now number in the hundreds of thousands. Despite an understanding of their numerical recovery, a comprehensive survey of bison herds and how their management varies between sectors has never been completed, and neither has a critical evaluation of the level of ecological recovery of the species. I surveyed bison managers from all major sectors, collecting extensive information about each bison situation. I identified significant proportional differences between management sectors among my survey questions using Freeman-Halton-Fisher exact tests of independence. I visualized and grouped individual herds based on their adherence to the 2017 RLA criteria using a multiple correspondence analysis and hierarchical clustering analysis. I then used this information to conduct three nested iterations of the novel IUCN Green Status Assessment (GSA) with inclusion of herds in each iteration based on progressively relaxed definitions of “wild” from the most recent RLA criteria. In the end, I identified that inclusion of more bison herds in the assessment may increase GSA scores due to numerical recovery, but may lead to lower levels of perceived ecological recovery, posing important questions as we look into the future of bison conservation over the next 100 years.

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CHAPTER I

INTRODUCTION

American bison (*Bison bison ssp.*) hold a significant place in human political, economic, and social history. Bison have been and continue to be, an important cultural and utilitarian resource for indigenous peoples. Bison were also a source of conflict between indigenous peoples and European colonizers through the 18-19thth Centuries, which lead to bison being a target of purposeful eradication and near extinction in the wild by the end of the 19th Century (Shaw 1995; Boyd 2003; Sanderson et al. 2008). In modern times, bison are an icon of species recovery and wildlife conservation in North America as well as a distinct and sustainable private sector production commodity. Most recently, bison have been recognized as a cornerstone of indigenous peoples self-determination and the United States' first and only national mammal (Malainey & Sherriff 1996; Shaw & Lee 1997; Aune & Plumb 2019).

Accompanying this long history were large variations in geographical distribution and abundance. An estimated 60 million individuals inhabited a range from the Atlantic to Pacific coasts, north into Alberta, Canada, and south into Northern Mexico before European settlement (Shaw 1995; Sanderson et al. 2008). By the late 19th Century, less than 1,000 individuals remained in small isolated herds (Shaw & Lee 1997). Aune et al. (2017) recently estimated that over 300,000 bison exist in North America. However, there is no consensus as to the true number of bison in North America, but it is very likely in the hundreds of thousands (Gates et al. 2010).

Current Status and Data Gaps

Despite previous knowledge of bison populations in North America through independent research and assessments, there has never been a comprehensive bison population estimate. This issue is not shared for the closest relative of American bison, the European bison (*B. bonasus* subspp.). European bison in Europe and Russia are almost entirely accounted for by the regularly updated European Bison Pedigree Book (*European Bison Pedigree Book* 2020; Plumb et al. 2020). In North America, international conservation assessments regularly update the numerical status of bison in public and private conservation-oriented herds (Aune et al. 2017). Previous research in the early 2000s provided the most recent broad estimates for the entire population of American wood (*B. b. athabascae*) and plains bison (*B. b. bison*) (Boyd 2003; Sanderson et al. 2008). Multiple bison generations have occurred since these estimates, suggesting an updated assessment is necessary (Aune et al. 2017). Additionally, past research was focused on herds considered conservation-oriented, leaving out a clear picture of herds outside this designation, including meat-producing and tribal herds. Estimates for bison in the meat-producing sector are documented by both the Canadian and American governments through agricultural surveys (Canada Agriculture 2016; US Department of Agriculture 2017). Tribal sector bison herds are increasing rapidly in both the number of herds and the number of individual bison but are not recorded in a centralized database.

No estimate has ever been made for bison herds outside of their native continent, such as in zoos or other private operations throughout the world, although the Association of Zoos and Aquariums in North America and Species 360 have records for most bison held in zoos globally (Association of Zoos and Aquariums 2019; Species 360 2019). Bison are used as a livestock species outside of their native habitat in some countries. Australia supports a growing plains bison industry, and The American Bison Association of Australia has records for the number of bison held by its members (All About Bison 2020; National Bison Association 2021). Combining known data, updating previous information, and filling known data gaps is a valuable first step towards creating a complete picture of bison population estimates across the globe.

IUCN Assessments

Compiled information for a species' population numbers, demographics, and management can be used to conduct conservation assessments such as the Red List Assessment (RLA) of the International Union for Conservation of Nature (IUCN). As the only international observer organization in the United Nations, the IUCN provides scientific expertise on environmental issues (Rodríguez et al. 2011). The RLA evaluates the risk of extinction for a species based on past and expected future trends (IUCN 2019).

The most recent RLAs completed for American and European bison assessed each as near-threatened (Aune et al. 2017; Plumb et al. 2020). While these metrics are valuable for assessing risk of extinction, an individual RLA does not evaluate temporal population trends and does not incorporate the species' ecosystem function, both of which are needed for a holistic view of species recovery. Additionally, the RLA may lead to perverse incentives (Akçakaya et al. 2018). For example, downgrading a species from vulnerable to threatened between subsequent assessments may show that the species is recovering numerically. However, this may lead to reduced funding for ongoing and future research and management (Ogden 2019). This creates a financial incentive to assess species as more at risk-than-would-be-otherwise-justified (Ogden 2019). To address these issues, the IUCN has recently developed an additional tool, the Green Status Assessment of Species (GSA), to be used in conjunction with the RLA (Akçakaya et al. 2018). This new tool incorporates both temporal population trends and ecological function, or the role of species in the ecosystem. When both assessments are completed for a species, positive changes in the RLA can be qualified by the GSA in a more holistic picture of species conservation.

Green Status Assessment Approach

Though the IUCN RLA and GSA are valuable assessments, there exists issues with their application to American bison. In these frameworks, there is a discrepancy between which populations can be considered "wild" conservation herds and how their information can be used in the assessment. In 2014, there were approximately 3,000 independent operations managing a total of several hundred thousand bison in North America, yet the 2017 RLA only used 21 herds comprising 18,000 bison (Aune et al. 2017). Despite this large number of operations, 99% of the herds were excluded because: 1) they are not managed for species conservation or the public interest; 2) they are very small (<300 individuals) and managed on small landscapes; or 3) they are managed behind fences. This first point addresses why commercial bison operations, which constitute 90% of the total bison operations in livestock management settings, were excluded from the assessment. The second point precludes herds that may have been eligible for assessment due to meeting one or more approved IUCN exceptions, such as requiring management on a small landscape in order to keep the herd in a protected area. The third point identifies a fundamental difference in how species conservation is expected to occur in a one-size-fits-all assessment versus the reality that a large-bodied ungulate like bison experience. There are few bison herds in North America that qualify as self-sustaining, conservation-dependent, or lightly managed as required by the IUCN, due to the level of management involved with most herds. Bison are, and have historically been, managed to a higher degree than most other wildlife species, suggesting that some of the IUCN criteria is not applicable to this specific species (Wheat 1967; Morgan 1980). Most bison herds in North America classify as intensively managed or captive but also meet one or more of the exceptions. These exceptions are most notably the use of translocations between herds to maintain genetics and range restriction to keep the herds in protected areas. Therefore, further research is required in order to identify whether more herds may qualify for the GSA and RLA than previously used.

Application of the Green Status Assessment

Determining which bison herds should qualify for an IUCN RLA and GSA requires a deep understanding of each herd. This includes information on genetic integrity, management intensity, presence of diseases, and ecological function. Here, I used an online survey distributed via email and social media to bison managers throughout North America to obtain this information, providing a clear picture of bison from which to evaluate their conservation through internationally recognized assessments.

Management information collected from a survey of American bison herds provided additional insight into which herds should and should not qualify for the assessments. In the development phase of the IUCN GSA, American bison have routinely been used as an example of a functionally extinct species (Sanderson et al. 2008; Akçakaya et al. 2019). Functional extinction is when a species' abundance is too low, or its demographic structure is unsuitable to fulfill its ecological role (Sanderson et al. 2008). A trial assessment using a subset of data suggested that the designation of functionally extinct may not be warranted for American bison (Grace 2020). A full, comprehensive GSA of American bison is required in order to accurately assess the conservation, recovery, and ecological function of the species in a non-biased, empirical way.

OBJECTIVES

My first objective (Chapter Two) was to update and summarize the status of bison herds in North America by their various management sectors through a widely distributed survey of bison managers on the continent. I then evaluated the proportional adherence of herds in these management sectors to criteria presented in the most recent RLA and quantified if significant differences in herd structure and management truly exist. I illuminated for the first time where excluded sectors fall on the continuum of bison situations across North America, ranging from fully captive livestock in private production herds that are trending toward domestication to large, free-ranging wildlife populations on large landscapes subject to the full suite of natural selection pressures, and addressed the validity of perceptions regarding the similarities or differences in bison management among sectors.

My second objective (Chapter Three) was to complete three nested iterations of the IUCN GSA based on progressively relaxed definitions of criteria for “wild” presented in the most recent RLA (Aune et al. 2017). In doing so, I tested the variation in species recovery scores of this tool when herds were included or excluded. This highlighted its sensitivity to these changes and provided a foundation for future assessments of American bison and species with similarly diverse continuums of management situations.

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CHAPTER II

STATUS OF AMERICAN BISON (*BISON BISON*) HERDS BY MANAGEMENT SECTOR IN RELATION TO IUCN "WILD" CRITERIA

ABSTRACT

The American bison (*Bison bison* subspp.), at one point critically endangered, have recovered numerically and now number in the hundreds of thousands. However, the last attempt at a population estimate occurred almost two decades ago, and a new inventory is due. Additionally, a comprehensive survey of bison herds and how their management varies between sectors has never been completed. A comprehensive understanding of the species is necessary in order to address assumptions that have historically excluded bison herds from specific sectors in standardized international assessments such as the International Union for Conservation of Nature (IUCN) Red List Assessment (RLA). To address these issues and fill data gaps, I surveyed bison managers from all major sectors, collecting extensive information about each bison situation. I identified significant proportional differences between management sectors among my survey questions using Freeman-Halton-Fisher exact tests of independence. I visualized and grouped individual herds based on their adherence to the 2017 RLA criteria using a multiple correspondence analysis and hierarchical clustering analysis. I found that state or provincial and federal sector herds had the highest proportional adherence to the RLA criteria, while zoo and private sector herds had the lowest proportional adherence, with intermediate proportional adherence in the non-profit sector herds. I also found that 23.1% of non-profit and 7.8% of private

sector herds existed within the cluster of large herd and range sizes with light management practices, suggesting that the complete exclusion of these sectors from assessments may be unwarranted and that future evaluations should consider including these herds and capturing and including their conservation value in future species assessments.

INTRODUCTION

The history of American bison (*Bison bison* subspp.) in the 1900s is an example of concerted efforts to recover a species from near-extinction to widespread abundance across much of its historic range (Shaw 1995; Boyd 2003; Freese et al. 2007). In the 1800s, the once millions of bison in North America were subject to extreme hunting pressure and reduced to small isolated populations totaling fewer than 1,000 bison (Shaw 1995; Gates et al. 2010). Through a reversal of policy and perception, colonial Americans transitioned from exterminating to conserving bison. Because of this change bison today have numerically recovered and are no longer threatened with extinction (Gates et al. 2010; Aune et al. 2017).

Today, there are hundreds of thousands of bison in existence, yet there is a lack of comprehensive and repeated survey efforts to understand in detail the population size and situations within which these bison exist, leading to widely varying estimates of their status (Boyd 2003; Gates et al. 2010). In contrast, European bison (*B. bonasus* subspp.) are surveyed annually and have extensive documentation on population sizes, resulting in the most recent exact count of 8,927 total individuals among 421 herds distributed over three continents (*European Bison Pedigree Book*

2020; Plumb et al. 2020). Though there have been previous attempts to complete similar inventories for the American species, these attempts took place nearly two decades ago, and a new updated inventory is needed to encompass the current state of bison in North America (Boyd 2003; Sanderson et al. 2008; Gates et al. 2010).

Despite the numerical abundance of bison today, large discrepancies in herd population, range sizes, and management intensity between management sectors have been assumed in previous conservation research (Gates et al. 2010; Redford et al. 2011; Aune et al. 2017). In particular, the private sector, which holds more than 90% of the total abundance of bison, is assumed by conservation researchers to differ significantly from the state or provincial and federal sectors as heavily managed and manipulated animals trending towards domestication (O'Regan & Kitchener 2005). Because of this assumption, the private sector has been excluded from conservation assessments such as the International Union for Conservation of Nature (IUCN) Red List Assessment (RLA), resulting in a lower-than-would-otherwise-be-expected designation (near-threatened; Aune et al. 2017). The large majority of bison herds established since the 1950s exist in the excluded private sector, while the included federal and state or provincial sectors have had very little change, resulting in a perceived conservation plateau of the species over the past several decades (Boyd 2003; Boyd & Gates 2006; Gates et al. 2010). Excluded herds may hold conservation value but are assumed to not meet the rigid "wild" criteria set by IUCN and the most recent RLA, yet these assumptions have not been critically evaluated for their accuracy with empirical evidence (Table 1.1).

My objective was to summarize the status of bison herds in North America by their major management sectors through the first standardized and widely distributed survey of bison managers on the continent. I then evaluated the proportional adherence of herds in these management sectors to criteria presented in the most recent RLA and quantify if significant differences truly exist. This analysis provided new information on where excluded sectors fall along the continuum of bison situations across North America, ranging from fully captive livestock in private production herds that potentially are trending toward domestication to large, free-ranging wildlife populations on large landscapes subject to the full suite of natural selection pressures, and addressed the validity of perceptions regarding the similarities or differences in bison management among sectors.

METHODS

I collected extensive individual herd information from bison managers through an online survey hosted at bisonsurvey.com from January 22, 2020, until September 15, 2020 (University of Nebraska at Kearney Institutional Review Board Protocol #010920-2). This survey contained 53 questions regarding the location, population size, management sector, disease, genetics, management intensity, use, and cultural significance for each herd surveyed (Appendix A). Participation was both anonymous and confidential and participation was incentivized by the option to receive results when completed and be entered into a drawing for a chance to be randomly selected for one of five $50 VISA gift cards.

Managers for federal, state or provincial, private, zoo, and non-profit herds in North America (Canada, USA, and Mexico) were eligible to take the survey. I contacted these individuals and encouraged them to complete the survey via various membership associations, such as the National Bison Association, Canadian Bison Association, Intertribal Buffalo Council, regional bison associations, IUCN Bison Specialist Group, and the Association of Zoos and Aquariums, through social media platforms such as Facebook or through direct communication by email and phone. I estimate that I reached approximately 3,000 managers through these methods. Additionally, the Mexican Bison Working Group translated a subset of the questions from my survey into Spanish and directly contacted all known bison managers in Mexico to obtain their information (Esquer pers. Comm 2021).

After data were collected, I removed duplicates for the same bison herd and largely incomplete surveys (n=83) following Jamsen & Corley (2018). I identified duplicate responses using the IP addresses of the respondents or specific notes in the responses (ex. “this is the X herd”) or via the exact locations provided by the respondent. Duplicate responses were then compared for completion and accuracy with additional follow-up with managers if necessary when the managers were known. The most complete and accurate survey response was used for analysis.

I analyzed herd information by management sector. These included federal, state or provincial, private, non-profit, zoo, and tribal herds. For herds that selected multiple management sectors, I reviewed and assigned the best-fit sector to avoid double counting the survey responses. These were primarily state or provincial and federal herds, which also identified as non-profit, but whose best-fit management sector was the former. I did not use tribal herds for further analysis due to a less than 10% response rate of herds in the tribal sector (n=6). This is likely due to the onset of a global pandemic that limited the ability of tribal nations to participate in this research.

I obtained the total minimum bison population count by calculating the sum of the lower bounds of the population size options (e.g. 51 individuals used when "51-100 individuals" was selected) and any herds whose managers provided an exact population number. I determined significant proportional differences between management sectors among my survey questions using Freeman-Halton-Fisher exact tests of independence with an α of ≤ 0.05 and a Bonferroni correction factor in program *R* version 4.0.2 (Shaffer 1995; Lydersen et al. 2007). I omitted from my analyses null (no answer) responses as well as "unknown" and "I prefer not to answer" responses on a question-by-question basis (Jamsen & Corley 2018). For some questions, I pooled groups of answers based on similar thresholds presented in Aune et al.'s (2017) RLA. For example, the range size threshold presented in criteria 1.1 (range size) of the 2017 RLA is 4,000 ha. I used the closest value to this threshold possible from my survey, which was 5,000 ha. I did not specifically address criteria 2.4 and 2.5 regarding genetic testing in relation to heterozygosity, allelic diversity, and cattle gene introgression in my survey, but I asked whether the herd had genetic testing conducted as the closest proxy. I did not survey criteria 4.1 regarding legal documentation for the perpetuation of a herd >400 individuals into the long-term.

I visualized surveyed bison herds through a multiple correspondence analysis (MCA) using the nine surveyed criteria in Aune et al.'s (2017) RLA (Table 1.1; Greenacre & Blasius 2006; Abdi & Valentin 2007). For this analysis, I set "NA" if there was no response or "I prefer not to answer" for one of the nine criteria. I included the centroid of each management sector with a 95% confidence ellipse (Greenacre & Blasius 2006; Abdi & Valentin 2007). I then grouped individual herds regardless of management sector through hierarchical clustering using only the principal axes of the MCA (Audigier et al. 2017). The number of clusters was determined based on maximizing between-class variability and minimizing within-class variability using Ward's method and Huygens theorem (Audigier et al. 2017; Strauss & Maltitz 2017).

RESULTS

I received 442 attempts to complete my survey either online or via the Mexican National Bison Working Group's Spanish version directly answered by Mexican herd managers. After removing duplicates and largely incomplete responses, 359 surveys remained with a total minimum count of 102,124 individual bison (Figure 1.1). In five of the nine RLA criteria presented by Aune et al (2017) that were surveyed, the state or provincial management sector had the highest proportion of herds meeting the criteria of any management sector (Table 1.1). The federal management sector had the highest proportion of herds meeting RLA criteria in the other four out of nine criteria surveyed. Non-profit, zoo, and private herds did not have the highest proportion of herds meeting RLA criteria in any of the nine criteria surveyed. Conversely, zoo herds had the lowest proportion of herds meeting RLA criteria in seven out of the nine criteria surveyed. Private herds had the lowest proportion of herds meeting RLA criteria in two out of the nine criteria surveyed. Additionally, significant differences exist between management sectors for several non-RLA characteristics (Table 1.2).

My MCA accounted for 14.11% of the total variation in the survey data (Fig. 1.2). The first dimension of my MCA was primarily weighted by the range size, future range size, population size, and future population size (Appendix B). The second dimension of my MCA was primarily weighted by the frequency of supplemental feeding, amount of fencing, whether there was human-managed breeding, and sex ratio. This roughly translates to an x-axis defined by the herd and range size (small to large), and a y-axis defined by the management intensity (high to low).

I obtained three clusters from my MCA cluster analysis (cumulative inertia=0.65). The first cluster contained the majority of the zoo herds (67.9%), followed by small proportions of non-profit (23.1%), private (11.2%), state or provincial (7.7%), and federal (4.3%) herds (Appendix C). This cluster is mainly characterized by surveys containing large amounts of "NA" responses to the RLA criteria, but also the smallest herds (1-10 individuals) on the smallest landscapes (0-5 ha). This first cluster accounts for the majority of herds that are only supplementally fed.

The second cluster contains the majority of herds in the private (81.0%) and non-profit (53.8%) management sectors, followed by a minority of herds in the zoo (32.1%), federal (30.4%), and state or provincial (26.9%) management sectors. The majority of herds that contain >10 but < 400 individuals on >12 and <10,000 ha range sizes are within this cluster. Additionally, the majority of herds that have not had genetic testing conducted, are supplementally fed more than solely during handling or emergencies but <365 days per year, have sex ratios outside 1 adult male: 1-5 adult females, have movement restricted by full perimeter and internal fencing, and have documented sexual reproduction are within this cluster.

The third cluster contains the majority of herds in the state or provincial (65.4%) and federal (65.2%) management sectors, followed by herds in the non-profit (23.1%) and 7.8% of the private management sector. None of the herds in the zoo management sector are included in this cluster. The majority of herds with >400 individuals are contained within this cluster, as well as the majority of herds with range sizes >10,000 hectares and are only supplementally fed during handlings, emergencies, or never. The majority of herds with only a partial perimeter fence to restrict their movements are present in this cluster.

DISCUSSION

I estimate there are approximately 3,000 herds containing a total of 350,000-400,000 bison in private, non-profit, tribal, and public herds in North America (Canada Agriculture 2016; US Department of Agriculture 2017; Association of Zoos and Aquariums 2019; Gates et al. 2010; Aune et al. 2017). Outside of their native continent, 1,618 American bison are documented in 178 zoo and private herds on all continents except Antarctica (Association of Zoos and Aquariums 2019, All About Bison 2020). Based on this estimation and my minimum count, I surveyed approximately 10% of the total number of bison herds in North America, but at least 25% of the total number of bison. My survey distribution methods and network of contacts likely resulted in capturing most if not all of the large bison herds containing 1,000 or more individuals in North America. In addition to this, the directed effort by the Mexican National Bison Working group to contact and survey Mexican bison managers resulted in the first comprehensive inventory of the country's bison herds. This was an important first step for understanding the recovery of bison in the country that will lead to future conservation directions.

The Freeman-Halton-Fisher exact tests of independence support the argument that, in general, the state or provincial and federal management sectors have bison that are the most "wild" according to IUCN's definition in general (Sanderson et al. 2008; Redford et al. 2011; Aune et al. 2017). State or provincial and federal herds tend to have large population and range sizes and relatively light management practices. These herd qualities are the most in-line with conservation goals to perpetuate the species as wildlife with long-term genetic integrity (Boyd 2003; Freese et al. 2007; Sanderson et al. 2008; Aune et al. 2017). Conversely, the majority of bison in the private and zoo management sectors exist in herds below a minimum viable population of 400 individuals and on landscapes <5,000 ha with captive to intensive management practices, which are settings that promote domestication and a reduction in genetic integrity (Dorn 1995; O'Regan & Kitchener 2005; IUCN 2014). Interestingly, the non-profit management sector did not have the highest or lowest proportion of herds meeting each of the nine surveyed RLA criteria. This intermediate position between the most and least managed sectors demonstrates the larger average variation of situations within which non-profit herds exist compared to the other management sectors.

The three clusters obtained from my MCA can be considered the grouping of herds based on their general rather than specific adherence to Aune et al.'s (2017) RLA for "wild" bison populations. The first cluster primarily contains herds with large amounts of "NA" responses, but also the smallest herds, held on the smallest landscapes, which are captively managed. The second cluster holds the majority of herd situations in North America, which are small to medium population and range sizes as well as intensive management practices. The third cluster contains the largest herd and range sizes, and the lightest management. This makes the third cluster the most closely related to the "wild" and "wild with limitations" categories of the most recent RLA criteria, and cluster one the least closely related, which is supported within the literature (Aune et al. 2017).

Overall, the MCA corroborates most of the findings of the Freeman-Halton-Fisher exact tests of independence but identifies herds in both the non-profit and private management sectors that exist within the third cluster most closely aligning with all of the RLA criteria. While these herds may not specifically meet every RLA criteria required to be included in assessments, they are similar enough to herds that do meet all the criteria to be grouped together. However, no herds from either of these management sectors have ever been included, which is a contributing factor to why bison are perhaps underestimated in their conservation status (Boyd & Gates 2006; Sanderson et al. 2008; Gates et al. 2010; Aune et al. 2017). With the development of new assessments such as the IUCN Green Status Assessment, which includes ecological function, the lack of inclusion of these management sectors may have an even more profound impact (Akçakaya et al. 2019; Grace 2020). More inclusion of these herds, whether in the official assessments or in additional iterations of the assessment with reduced or relaxed requirements, should be considered to fully encompass the entire bison situation. Otherwise, we risk overlooking a large portion of the conservation of the species.

Collecting information regarding every bison herd was difficult to accomplish; some bison managers were not reachable through the methods provided, and some were simply not willing to participate. Additionally, most of the data collection occurred during the COVID-19 global pandemic, creating unique challenges for contacting bison managers. Specifically, the global pandemic resulted in a very low response rate from the tribal management sector, which prevented us from reliably analyzing their proportional adherence to Aune et al.'s (2017) RLA criteria and how it differs from other management sectors. I had a similar but different issue concerning zoo herds, the majority of which were surveyed by the Mexican Bison Working Group. Though I was able to obtain enough survey responses from this management sector to statistically analyze there were many "NA" values due to managers withholding information they felt uncomfortable sharing. This resulted in a smaller dataset used in the Freeman-Halton-Fisher exact tests of independence and a potential skew in my MCA cluster analysis to three clusters instead of two with most of the herds with a large number of “NA” values falling in cluster one. In the future, post-pandemic world, obtaining buy-in from leaders in each management sector to fully cooperate will be important to replicate and improve this research.

Despite some of the limitations experienced I obtained enough information from each management sector other than the tribal sector to offer inferences backed by scientifically valid methodologies and techniques. As previously mentioned, state or provincial herds have generally large populations and ranges with light management practices. Additionally, state or provincial herds contain the least amount of fencing and the highest prevalence of large carnivores on the herd range, which are additional factors supporting their position as the model management sector for “wild” bison according to the IUCN (Gates et al. 2010; Aune et al. 2017). A significantly higher proportion of these herds have hunting opportunities, an important use of “wild” bison that is not observed at as high of frequency in other management sectors. One area of improvement for herds in these sectors is to expand education and outreach opportunities to further connection of the public with local “wild” bison populations, increasing their perceived value by the general public (Fulton et al. 2008). Model herds in this sector include the Aishihik, Mackenzie Sanctuary, and Innoko wood bison herds in Alaska and adjacent Yukon and

Northwest territories of Canada (Freese et al. 2007; Gates et al. 2010), and the Henry Mountains bison herd in Utah (Bates and Hersey 2016).

Like the state or provincial management sector, the federal management sector has herds with generally large populations and ranges as well as light management practices (Aune et al. 2017). In addition to this, the federal sector has provided education, outreach, and tourism opportunities for the public to experience bison and learn about them as wildlife. Beyond an educational resource, the federal management sector is one of the major sectors aiding the establishment of new tribal herds (*Department of the Interior Bison Conservation Initiative* 2020). This addresses the one major weakness of this sector, which is its limited ability to expand due to the limited remaining public land available for herd establishment. Model herds such as Yellowstone National Park and Greater Wood Buffalo National Park exemplify this sector (Freese et al. 2007; Gates et al. 2010).

The non-profit management sector is in a unique position relative to others. As I have documented, herds in this sector have the largest variation in bison situations, from small to large scale, and from captive to light management practices. This can partly be attributed to an equally large variation in uses of the herds in this sector, from grazing tools to meat production herds to educational animals. A major strength of this sector is its high number of cross-jurisdictional agreements, resulting in collaborative conservation efforts. Model herds in this sector include the American Prairie Reserve and the Nature Conservancy herds (Gates et al. 2010).

The private sector, though not generally adhering to management practices that qualify its herds as “wild”, has built a multimillion-dollar industry from the meat production of its bison (National Bison Association, 2020). Nutritious bison meat produced by this growing sector is distributed across the American continent and is thus available to most individuals in the USA and Canada at their local supermarket (Joseph et al. 2010; McDaniel et al. 2013). Because this sector has the least restrictions on establishment of new herds and the simplest and economically viable operational set-up, most bison are managed privately. However, this sector has, in general, significantly different adult sex ratios from every other sector. This is due to sector’s conventional wisdom of having individuals with “more rump, less hump” which is one of the most pervasive ways to manipulate species’ genetics toward domestication (O'Regan & Kitchener 2005; Hedrick 2009; Redford et al. 2011). Despite this weakness among many herds in this management sector, some model herds in this sector include Ted Turner Enterprises and Wild Idea Buffalo Company (Gates et al. 2010).

The zoo sector, while understandably not managing herds towards RLA criteria, have a strong network and stretch of bison herds across the globe, allowing people to experience bison in person, even if they live far away from their natural habitat (Association of Zoos and Aquariums 2019, Lecturer & Booth 2006). I recognize that small population and range sizes as well as captive management practices are required in order to facilitate such broad extent of operations, resulting in the least “wild” management of any sector. However, by exposing otherwise naïve individuals to bison, zoos are increasing the perceived conservation value of the species and potentially introducing new advocates to their conservation (Lecturer & Booth 2006). This advantage greatly outweighs the drawbacks associated with the herds in this sector.

Though I did not survey most of the bison herds existing within the tribal management sector, I recognize that the largest potential for growth of bison herds that meet IUCN RLA criteria exist within this sector (Symstad et al. 2019; *Department of the Interior Bison Conservation Initiative* 2020). With several large reservations in the process of establishing or expanding bison herds onto their range, the tribal sector may be poised to make the largest short-term gains of any sector (Young 2019; *Department of the Interior Bison Conservation Initiative* 2020). Future American bison survey efforts may be more successful in capturing this expansion and highlighting its place as one of the great “wild” bison management sectors.

Despite the differences among these sectors and their strengths and weaknesses, these sectors do not differ significantly in their belief that their herds contribute to bison conservation. Leaders in each of these sectors of bison management have set goals and put forth visions for the future of the species such as the Vermejo statement and Bison 1 Million objective (Sanderson et al. 2008; National Bison Association, 2020). In order to reach these goals management sectors will likely need to work together like they did to save the species from extinction initially. Shared stewardship encourages innovative solutions to address the scale, complexity, and ecological and cultural significance of “wild” bison conservation and restoration through collaboration across management sectors (Ranglack & Du Toit 2016; *Department of the Interior Bison Conservation Initiative* 2020).

Shared stewardship is not a new idea for bison conservation. In fact, the Department of Interior (DOI) Bison Conservation Initiative explicitly states it as one of its five main objectives (*Department of the Interior Bison Conservation Initiative* 2020). The DOI has demonstrated the application of this initiative through Indian Buffalo Management Act and Iinnii Initiative with bison, which assist tribal governments with the establishment of bison herds on their reservations (Young 2019). In 2014, northern tribal groups convened to sign the Buffalo Treaty, which established intertribal cooperation towards the restoration of bison on tribal lands as well as co-managed public lands. Today, these tribes manage bison herds on approximately 2.5 million hectares of rangeland: a testament to the Buffalo Treaty's ability to achieve bison conservation in an ecologically meaningful way on tribal lands. More recently, the Iinnii Initiative between the Blackfeet Nation in Montana and Glacier and Waterton Lakes National Parks in the US and Canada seeks to restore bison herds on local tribal lands. To the east, the US DOI as well as World Wildlife Fund (WWF) have partnered with the Sicangu Lakota Oyate nation living on the Rosebud Indian Reservation in South Dakota to restore at least 1,500 bison on the reservation, which would make it the largest herd in the tribal sector.

The federal, non-profit, and private sectors have several high-level shared stewardship projects as well. Wind Cave National Park, which is restricted to a herd size <400 and unable to maintain genetic diversity on its own in the long term, has partnered with The Nature Conservancy (TNC) to establish multiple satellite herds totaling >1,000 individuals. To date, this TNC program has resulted in 13 preserves across the Great Plains. Other than TNC, the American Prairie Reserve in northeast Montana has a goal of managing 1.2 million contiguous hectares of private, public, and tribal lands with several thousand migratory bison. In the private sector, a partnership between the National Bison Association and World Wildlife Fund has resulted in Conservation Management Plans, a critical step towards improving “wild” management of bison in private herds. The goal of this new certification process is to promote the conservation of “wild” bison genetics, ecosystem function, and biodiversity without adversely affecting the economic viability of meat producing operations (World Wildlife Fund 2013).

Current shared stewardship practices continuously show the ability of cooperation and collaboration among management sectors to advance the multiple visions of bison conservation into the future. In the end, managers may consider the expansion of these current local shared stewardship projects and establishment of new ones where appropriate. In order to do this, we may need to adapt our mindset to include the range of bison situations along the continuum of bison conservation. We may also need to embrace new strategies and ideas such as local stewardship of public resources (Ranglack & Du Toit 2016). In doing so, we may be able to create herds that both adhere to RLA criteria and have the greatest strengths of each management sector, ending the plateau in conservation that have bison conservation has experienced in the past five decades and propelling it to new heights that were once thought to be impossible (Redford et al. 2016).

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FIGURES AND TABLES

Table 1.1: Survey results by management sector in relation to Aune et al.'s (2017) RLA criteria. Percentages represent the percent of herds that met the criteria based on the number of herds of that management sector that provided a response in my survey. The number of responses meeting the criteria out of the total number of responses received for the management sector are in parenthesis. Significant proportional differences among management sectors are indicated by superscripts; management sectors that share the same superscript letter are not significantly different from one another via a Freeman-Halton-Fisher exact test. If no superscripts are provided, there are no significant differences among any of the management sectors for that criterion.

Category		Criteria	Management Sector					
			Non-Profit	State/Provincial	Federal	Zoo	Private	Total
		Total Minimum Count	3,961	7,148	9,441	303	81,271	102,124
		Total Number of Herds Surveyed	27	26	25	28	253	359
Physical Environment (Range Resources)	1.1	Range area and resources can sustain a minimum viable population (MVP) or larger population without supplementation. Range size is 5,000 hectares or larger.	22.2%(6/27)[a]	64%(16/25)[b]	60.9%(14/23)[b]	0%(0/27)[a]	12.7%(29/229)[a]	19.6%(65/331)
		Range area and resources can sustain a minimum viable population (MVP) or larger population without supplementation. Range size will be 5,000 hectares or larger in the next 10 years.	33.3%(8/24)[abc]	73.9%(17/23)[c]	65%(13/20)[c]	0%(0/15)[a]	9.5%(20/210)[b]	19.9%(58/292)

	1.2	Bison have unrestricted access to resources within the entire range area. Fencing or other artificial structures or herding are not used to constrain daily or seasonal resource selection within the range area. This criteria does not apply to population distribution limits imposed for management purposes outside the range area.	4.5%(1/22)[ab]	68.2%(15/22)[c]	13%(3/23)[b]	0%(0/25)[a]	0%(0/228)[a]	5.9%(19/320)
Species Patterns	2.1	Sustainable herd population normally exceeds 1,000 individuals older than one year.	3.8%(1/26)	7.7%(2/26)	12%(3/25)	0%(0/28)	9.1%(23/253)	8.1%(29/358)
		Sustainable herd population will exceed 1000 individuals older than one year in the next 10 years.	3.8%(1/26)	8.3%(2/24)	9.1%(2/22)	0%(0/28)	10.5%(25/238)	8.9%(30/338)
	2.2	Sustainable herd population exceeds 400 individuals but is less than 1,000 individuals older than one year.	3.8%(1/26)[ab]	30.8%(8/26)[b]	28%(7/25)[b]	0%(0/28)[a]	5.5%(14/253)[a]	8.4%(30/358)
		Sustainable herd population will exceed 400 individuals but less than 1,000 individuals older than one year in the next 10 years.	15.4%(4/26)[abc]	41.7%(10/24)[c]	27.3%(6/22)[bc]	0%(0/28)[a]	8.4%(20/238)[ab]	11.8%(40/338)
	2.3	Herd has a mature male:mature female sex ratio between 1:1 and 1:5.	62.5%(15/24)[b]	72.2%(13/18)[b]	90%(18/20)[b]	75%(15/20)[b]	9.5%(24/252)[a]	30.8%(103/334)
	2.4	Sufficient infraspecific genetic variation exists for natural selection to operate on. Requires using multiple tests for heterozygosity and allelic richness employing current molecular technologies.*	81.8%(18/22)[bc]	86.4%(19/22)[c]	87%(20/23)[c]	36.4%(8/22)[ab]	29.2%(63/216)[a]	41.2%(128/305)
	2.5	Very low or low level of historic cattle gene introgression. Requires tests based on current molecular technology. Very low means < 1% cattle gene markers. Low means < 2%.	Not Surveyed					

Reproductive and Natural Selection Processes	3.1	Reproductive selection: No artificial selection of mates, either male or female. Mate selection within herd is achieved through competition among males and female choice, not by importation, bull rotation, or other artificial means.	95%(19/20)^{ab}	88%(22/25)^{ab}	100%(22/22)^{b}	56.3%(9/16)^{a}	80.1%(181/224)^{ab}	82.4%(253/307)
	3.2	Natural selection: spatial and temporal variation in resource abundance and quality are important factors influencing reproduction and survival. No supplemental forage is provided to sustain the population. Minerals or water are not intentionally provided to sustain the bison population. Baiting with forage for capture is not considered supplementation.	78.3%(18/23)^{b}	83.3%(20/24)^{b}	78.3%(18/23)^{b}	0%(0/27)^{a}	10.5%(24/228)^{a}	24.6%(80/325)
	3.3	Large carnivores are present in the range.	8%(2/25)^{ab}	64%(16/25)^{c}	43.5%(10/23)^{bc}	0%(0/23)^{a}	20%(45/225)^{ab}	22.7%(73/321)
Potential for maintaining environment, patterns and processes over meaningful evolutionary time	4.1	Legislation, regulations, policies, or legal agreements do not threaten the perpetuation of an MVP or larger wild population. This criterion relates to the potential for a wild population less than 400 and not allowed to increase above that threshold because of legislation, policy or regulation.	Not Surveyed					

*This criterion was not directly assessed but I used whether genetic testing had been conducted on the herd as a proxy.

Table 1.2: Survey results by management sector in relation to survey questions not related to Aune et al.'s (2017) RLA criteria. Percentages represent the percent of herds that met the criteria based on the number of herds of that management sector that provided a response in my survey. The number of responses meeting the criteria out of the total number of responses received for the management sector are in parenthesis. Significant proportional differences among management sector are indicated by superscripts; management sectors that share the same superscript letter are not significantly different from one another via a Freeman-Halton-Fisher exact test. If no superscripts are provided, there are no significant differences among any of the management sector for that criterion.

Category	Description	Management Sector					
		Non-Profit	State/Provincial	Federal	Zoo	Private	Total
Ecological Function	Intermittent heterogeneous grazing has been observed on the range of the bison herd by its manager.	80.0%(16/20)[ab]	91.7%(22/24)[b]	91.3%(21/23)[b]	38.1%(8/21)[a]	67.6%(152/225)[ab]	70.0%(219/313)
	Wallow pits have been observed on the range of the bison herd by its manager.	95.0%(19/20)	91.7%(22/24)	100%(23/23)	81.0%(17/21)	91.1%(205/225)	91.4%(286/313)
	Whole bison carcasses are allowed to decompose at the location where the animal deceased.	70.0%(14/20)[c]	79.2%(19/24)[c]	87.0%(20/23)[c]	0.0%(0/21)[a]	31.6%(71/225)[b]	39.6%(124/313)
	Non-human predation has been observed on the range of the bison herd by its manager.	4.3%(1/23)[a]	50.0%(12/24)[b]	18.2%(4/22)[ab]	5.9%(1/17)[ab]	4.6%(10/217)[a]	9.2%(28/303)
Use	Ecosystem and landscape restoration.	65.4%(17/26)[b]	50.0%(13/26)[b]	70.8%(17/24)[b]	7.1%(2/28)[a]	59.7%(151/253)[b]	56.0%(200/357)

	Culture.	26.9%(7/26)^{a}	34.6%(9/26)^{ab}	75.0%(18/24)^{b}	28.6%(8/28)^{a}	13.0%(33/253)^{a}	21.0%(75/357)
	Tourism.	38.5%(10/26)^{a}	57.7%(15/26)^{ab}	87.5%(21/24)^{b}	71.4%(20/28)^{b}	34.0%(86/253)^{a}	42.6%(152/357)
	Bison conservation.	57.7%(15/26)	84.6%(22/26)	83.3%(20/24)	67.9%(19/28)	58.5%(148/253)	62.7%(224/357)
	Meat production.	50.0%(13/26)^{b}	19.2%(5/26)^{b}	4.2%(1/24)^{ab}	0.0%(0/28)^{a}	92.1%(233/253)^{c}	70.6%(252/357)
	Education and outreach.	57.7%(15/26)^{a}	46.2%(12/26)^{a}	95.8%(23/24)^{b}	92.9%(26/28)^{b}	38.7%(98/253)^{a}	48.7%(174/357)
	Hunting.	7.7%(2/26)^{a}	61.5%(16/26)^{b}	16.7%(4/24)^{a}	0.0%(0/28)^{a}	16.2%(41/253)^{a}	17.6%(63/357)
Public Access to Herd	Public access to landscape and viewing of bison herd possible.	45.8%(11/24)^{ab}	91.3%(21/23)^{c}	87.0%(20/23)^{bc}	72.0%(18/25)^{bc}	25.8%(58/225)^{a}	40.0%(128/320)
Fire Occurrence on Range	Natural and/or prescribed fires occur on the range.	72.7%(16/22)^{bc}	84.0%(21/25)^{c}	95.5%(21/22)^{c}	11.1%(2/18)^{a}	46.4%(91/196)^{b}	53.4%(151/283)
Round Ups	Bison herd is never round up.	12.5%(3/24)^{ab}	54.2%(13/24)^{b}	26.1%(6/23)^{ab}	26.9%(7/26)^{ab}	12.2%(28/229)^{a}	17.5%(57/326)

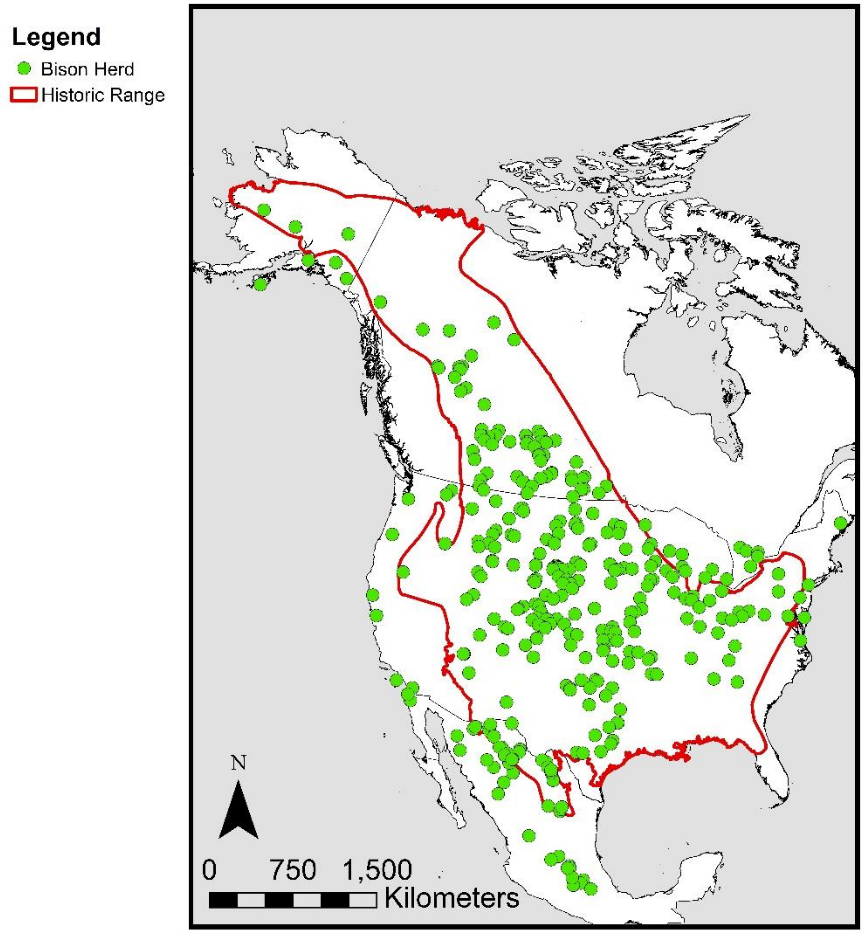

Figure 1.1: Map of surveyed bison herds in relation to the species' historic range. I updated the original range delineated by Aune et al. (2017) using new information from Plumb and McMullen (2018), the Mexican National Bison Working Group (List pers. Comm 2020), and the Canadian Wood Bison Restoration Team (Seaton pers. Comm 2020).

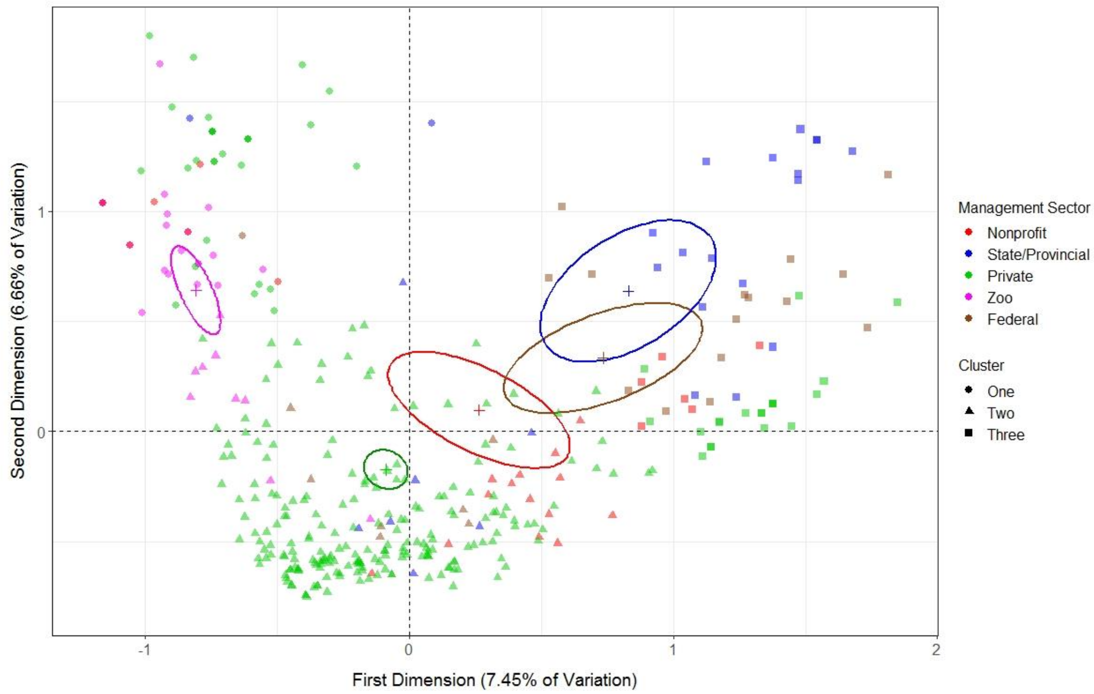

Figure 1.2: Two-dimensional MCA ordination and cluster analysis of the nine RLA criteria surveyed. Centroids for each management demographic are marked by a "+" symbol. Ellipses contain the 95% confidence of centroid locations.

CHAPTER III

VARYING DEFINITIONS OF "WILD" IMPACT AMERICAN BISON (*BISON BISON*) ECOLOGICAL RECOVERY SCORES USING THE NOVEL IUCN GREEN STATUS ASSESSMENT

ABSTRACT

The American bison (*Bison bison* subspp.), once on the verge of extinction, now number in the hundreds of thousands within and outside their historic range. These bison herds exist along a continuum of herd and range sizes as well as management intensity and natural selection pressures. Despite an understanding of their numerical recovery, a critical evaluation of the level of ecological recovery of the species has not been conducted. Furthermore, assessments that have been conducted for the species, such as the International Union for Conservation of Nature (IUCN) Red List Assessment (RLA), have excluded more than 95% of the herds based on strict criteria of a "wild" herd, underestimating the conservation of the species. The novel IUCN Green Status Assessment (GSA) provides a standardized tool to assess the level of ecological recovery of bison and how it varies based on the inclusion of previously excluded bison herds. I conducted three nested iterations of this new assessment with inclusion of herds in each iteration based on progressively relaxed definitions of "wild" from the most recent RLA criteria. I found that conservation metrics generally increased as more herds were included to my subsequent iterations with some notable discrepancies, identifying potential limitations to the new GSA criteria with regards to the unique situation of American bison. In the end, I identified that inclusion of

more bison herds in the assessment may increase GSA scores due to numerical recovery, but may lead to lower levels of perceived ecological recovery, posing important questions as we look into the future of bison conservation over the next 100 years.

INTRODUCTION

The American Bison (*Bison bison* subspp.), once numbering less than 1,000 individuals and on the verge of extinction in the late 1800s, now have numerically recovered and are no longer threatened with extinction (Gates et al. 2010; Aune et al. 2017). Today, approximately 350,000 American bison (*B. bison* subspp.) exist in a total of approximately 3,000 herds on the continent in private, non-profit, tribal, and public herds (Chapter Two). Large variation in herd population and range size and management intensity exist among management sectors, creating a continuum of bison situations (Chapter Two; Boyd & Gates 2006; Redford et al. 2011). This continuum has created the possibility of divergent evolutionary pathways, with some potentially deviating from being “wild” and trending towards domestication (Boyd 2003; Boyd & Gates 2006; Gates et al. 2010; Gates 2014).

In particular, the private sector, which holds more than 95% of the total abundance of bison, largely consists of herds with small populations <400 individuals, on small landscapes <5,000 ha, with intensive or captive management practices (Chapter Two). These management practices include controlling herd movements via fencing or herding, manipulating sex ratios and controlling breeding opportunities among individuals and removing natural selection pressures such as predation and resource limitation (Sanderson et al. 2008; Gates et al. 2010). Conversely, state and provincially managed bison herds in North America have generally large populations, exist on large landscapes, and are relatively lightly managed (Chapter Two). Most non-profit, federal, and tribal herds exist in the middle of this continuum, and some herds in every management sector exist at both ends of the spectrum (Chapter Two). However, because of the pervasiveness of non-“wild” management practices used in the private sector and a lack of herd-level data proving otherwise, it has been excluded from conservation assessments such as the International Union for Conservation of Nature (IUCN) Red List Assessment (RLA; Aune et al. 2017). This assessment does not consider all bison, only those that meet the criteria as “wild” herds. This results in a lower-than-would-otherwise-be-expected designation based on total numerical abundance of the species (near-threatened in 2017; Redford et al. 2011; Aune et al. 2017).

In the most recent RLA, eighteen of the twenty-one bison herds included in the assessment were managed by the state or provincial sector, five herds were managed by the federal sector, and two were managed by the tribal sector, with several herds being co-managed by multiple sectors (Aune et al. 2017). All other non-profit, zoo, and private herds were excluded. Many of these excluded herds in the non-profit sector were evaluated against the criteria for “wild”, but none of the private sector herds were (Aune et al. 2017). Chapter Two evaluated approximately 10% of the private herds and 25% of the total private herd population and confirmed that none of the evaluated private herds met all of the strict criteria presented by Aune et al. (2017), but several met most. Some of these private herds, which constitute more than 90% of the total species abundance, may have important conservation value that may be overlooked (Chapter Two). Progressively reducing or relaxing the IUCN RLA criteria for "wild" via multiple iterations will include some of these private bison herds may provide insight into what the extent of the definition of "wild" impacts assessment scores (Chapter Two).

In addition to the RLA, the IUCN has recently developed the Green Status Assessment (GSA; Akçakaya et al. 2018, 2019; Grace 2020). This new assessment evaluates species' recovery through time, whereas the RLA examines extinction risk at one time state (Rodríguez et al. 2011; IUCN 2019). Additionally, the GSA is the first assessment by the IUCN to incorporate ecological function, or the role of the species in the ecosystem, in its assessment (Akçakaya et al. 2018, 2019). In the development of this assessment, bison have been used as an example of an ecologically extinct species due to restrictions of large-scale movements and their relatively small herd sizes instead of large herds historically observed (in the tens of thousands of individuals) on large, continuous landscapes (Sanderson 2006; Freese et al. 2007; Plumb et al. 2009). Out of the 3,000 bison herds in North America, only one population of plains bison (*B. b. bison*; Yellowstone National Park) and three populations of wood bison (*B. b. athabascae*; Greater Wood Buffalo National Park, Mackenzie, and Nisling River) in North America are considered ecologically restored (large numbers of individuals on large landscapes with all natural selection pressures and minimal management by humans; Gates et al. 2010). I aim to test if, in fact, these are the only herds in North America to be considered ecologically functional through the novel GSA tool.

My objective was to complete three nested versions of the IUCN GSA using three iterations of bison herds based on progressively relaxed definitions of and criteria for "wild" presented in the most recent RLA (Aune et al. 2017). In doing so, I aim to test the variation in species recovery scores of this tool when herds are included or excluded. This will highlight its sensitivity to these changes and provide a foundation for future assessments of American bison and species with similarly diverse continuums of management situations.

METHODS

To complete my GSAs, I used individual herd information collected in Chapter Two with supplementation from the most recent IUCN RLA (Aune et al. 2017) as needed. I updated the historic range map delineated by Aune et al. (2017) using new information from Plumb and McMullen (2018), the Mexican National Bison Working Group (R. List pers. Comm 2020), and the Canadian Wood Bison Restoration Team (C. T. Seaton pers. Comm 2020) as my original bison range circa 1750 CE (Figure 2.1). I conservatively set the benchmark year as suggested by the IUCN standard as a time period prior to major human impacts on species' abundance and distribution (IUCN 2020, 2021b). This original range of modern American bison stretched across most of North America, including modern-day Mexico, the United States of America, and Canada (Stephenson et al. 2001; Gates et al. 2010; Plumb and McMullen 2018; R. List pers. comm 2020; C. T. Seaton pers. comm 2020). The Great Plains contained the highest abundance of bison, but they were present as far east as Florida and New England, as far south as the Gulf of Mexico and northern interior Mexico, west onto the Colorado plateau, northern Nevada, and eastern Oregon, and north into Alberta, British Colombia, Saskatchewan, Manitoba, Northwest Territories, Yukon Territories, and Alaska (Figure 2.1; Stephenson et al. 2001; Gates et al. 2010; Plumb and McMullen 2018; R. List pers. comm 2020; C. T. Seaton pers. comm 2020). In addition to the original range of American bison at 1750 CE I added areas that are currently occupied by the species due to natural expansion or translocations (IUCN 2020, 2021b). These areas are also considered part of the indigenous range (Stephenson et al. 2019; IUCN 2020, 2021a). For the purpose of this study, I only included two of these herds outside of the original range, as they qualified as free-ranging "wild" populations by Aune et al.'s (2017) RLA criteria. These are the Chitina River and Copper River bison herds in Alaska. There are numerous bison populations that exist outside the original range of American bison which may contain significant conservation value, but they are not being considered for this study.

Per IUCN GSA criteria, the entire original and additional range of American bison was divided into spatial units using the Environmental Protection Agency Level One ecoregions or Level Two subecoregions, as they are meaningful ecological boundaries that span the entire original range of bison (Mcmahon et al. 2001; Omernik 2004; Omernik & Griffith 2014; Stephenson et al. 2019). There were 31 EPA level two subecoregions that intersected the original and additional range of bison. I clipped these subecoregions so that only the portion within the original and additional range remained. Next, I set a minimum spatial unit size of 20,000 km^2, the minimum size required to meet IUCN Regional RLA criteria of least concern and

IUCN GSA criteria of Functional (IUCN 2012b, 2020, 2021a). Any Level two subecoregions that were smaller than 20,000 km^2 were combined with their nearest neighbor that shared the same Level one ecoregion. This resulted in either combining Level two subecoregions into their Level One ecoregion or combining two subecoregions into a new unique subecoregion. I combined the Northern Arctic, Alaska Tundra, Brooks Range Tundra, and Southern Arctic Level Two subecoregions by their Level One ecoregion Tundra. I combined the Taiga Shield with its adjacent Level Two subecoregion which it shares the same Level One ecoregion, Taiga Plain. I combined the South Central Semiarid Prairies, Texas-Louisiana Coastal Plain, and Tamaulipas-Texas Semiarid Plain Level Two subecoregions, which share the same Level One ecoregion into a distinct Level Two subecoregion called the Southern Great Plains. I combined the Upper Gila Mountains, Western Sierra Madre, and Eastern Sierra Madre Level Two subecoregions, which share the same Level One ecoregion. Lastly, to encompass the two free-ranging "wild" herds in my additional range, I expanded the Boreal Cordillera subecoregion spatial unit. The majority of this ecoregion is contained within the original bison range. All of these modifications to my ecoregions and subecoregions resulted in 23 final spatial units.

After I delineated my spatial units, I created three iterations of bison herds based on their level of adherence to Aune et al.'s (2017) RLA criteria for a "wild" bison herd. These three iterations were nested within one another, such that First Iteration herds also qualified as Second Iteration and Third Iteration herds, and Second Iteration herds also qualified as Third Iteration herds. Only bison herds that exist within the original and additional range were considered for assessment (IUCN 2020, 2021b). For the First Iteration, I strictly followed Aune et al.'s (2017) RLA criteria as well as the IUCN standards, which only allows for inclusion of herds that would loosely fall under lightly managed or not managed (IUCN 2012a, 2019).

For the Second Iteration bison herds, I removed criteria 1.1 (range size), 1.2 (range restriction), 2.1 (>1,000 mature individuals), 2.2 (>400 mature individuals), and 3.3 (large carnivores present) from being requirements, allowing the inclusion of herds that loosely follow the definition of intensively managed (Redford et al. 2011; Aune et al. 2017). By allowing intensive management, I allowed herds that were rotated between pastures in order to be sustained on the natural resources within their range. I also allowed herds that are occasionally fed supplementally, provided it was only during roundups or handling events, or only in rare extreme weather events. Frequent yearly supplemental feeding (e.g. >30 days per year) is considered captive management (Redford et al. 2011) and herds that exhibited this were excluded in the Second Iteration. Nearly all bison in North America have their range restricted in some form, whether it is a physical or social boundary (Boyd & Gates 2006; Gates et al. 2010; Aune et al. 2017), therefore, I did not disqualify herds from the Second Iteration based on the presence of range restrictions and allowed the use of fences to restrict bison movements. Though bison are a large-bodied nomadic species that historically roamed long distances in large groups, replicating this is nearly impossible in the contiguous 48 United States, southern Canadian provinces, and Mexico in the modern era due to large human populations and development (Boyd

2003; Boyd & Gates 2006; Gates et al. 2010). However, recent advances in genetics provide the ability for populations below the minimum viability threshold of 400 individuals to have an effective population size via human conservation actions of translocating individuals and/or embryos (Dorn 1995; Barfield 2019; Hartway et al. 2020; Benham et al. 2021). Therefore, through intensive management these bison herds can still be valuable in establishing a metapopulation structure (Gates et al. 2010; Barfield 2019). Additionally, these herds can still carry out their ecological role on small landscapes, provided they are not supplementally fed excessively (Sanderson et al. 2008; Redford et al. 2011). I used the frequency of supplemental feeding as a proxy for this threshold between intensive and captive management.

For my Third Iteration I removed all criteria and included any herds that provided a location and sufficient information for assessment. These herds are considered captively managed, or are managed outside of normal sexual ratios and reproduction manner (Gates et al. 2010; Redford et al. 2011; Aune et al. 2017; Hartway et al. 2020). The Third Iteration is severely underrepresented due to a lack of information regarding herds in North America, resulting in larger uncertainties among the true states in each spatial unit than the other two iterations (Chapter Two).

Per IUCN criteria, herds used in each iteration of the GSA were aggregated by spatial unit (IUCN 2020, 2021a). Each spatial unit was assigned one of four green score categories using the GSA decision tree:

Absent (weight 0): There are no individuals of the assessed species within the spatial unit.

Present (weight 3): There are individuals of the assessed species within the spatial unit.

Viable (weight 6): In addition to being present within the spatial unit, the combined herds form a large, stable, healthy, genetically robust, replicated (more than one subpopulation within the spatial unit), demographically sustainable, resilient metapopulational structure that has adaptive capacity and is at very low risk of extinction. The spatial unit must meet criteria to be considered “least concern” by an IUCN regional RLA and not be undergoing a continuing decline (IUCN 2012a).

Functional (weight 9): In addition to being both present and viable within the spatial unit, the combined herds exhibit all of their main ecological interactions, functions, and roles in the ecosystem (IUCN 2020, 2021b). While there are many ecological functions of bison, the four main functions that hold across their range are: 1) creation of heterogeneous landscapes via intermittent grazing; 2) creation of edge habitat via wallowing; 3) creation of nutrient-rich microclimates via the decomposition of carcasses where an animal deceases; and 4) availability as a prey animal for large predators (Coppock et al. 1983; McNaughton 1984; Dinerstein 1989; Cid et al. 1991; Knapp et al. 1999a, 1999b; Gerlanc & Kaufman 2003; Melis et al. 2007; Jonas & Joern 2007; Bump 2008; Sanderson et al. 2008; Bump et al. 2009; Gates et al. 2010; Fox et al. 2012; Tastad 2014; Merkle et al. 2016; Wilkins et al. 2019; Geremia et al. 2019). I considered a spatial unit to be functional if the majority of individuals within the spatial unit existed in minimum viable populations of 400 mature individuals or more as well as a herd that exhibits all four main ecological functions.

The GSA process was completed on each spatial unit as a three-step procedure in which a lower (minimum), upper (maximum), and best estimate value was assessed to the spatial unit with 95% confidence that the true value lies between the upper and lower bounds (IUCN 2020, 2021a). In addition to this, the assessment on each spatial unit was carried out independently at six time states: 1) former; 2) current; 3) counterfactual current; 4) short-term future with conservation; 5) short-term future without conservation; and 6) long-term future. The former state was assessed at the year 1950 per IUCN GSA guidelines (IUCN 2020). The current state was assessed based off the best possible data of the species at present from Chapter Two. The current counterfactual state was estimated based on the hypothetical status of the species if no human-involved conservation occurred between the former and current state (IUCN 2020, 2021b). The short-term future state was defined as 10 years in the future. The short-term future state was estimated with information provided by herd action and management plans disseminated by their managers and combined by spatial unit. The short-term counterfactual state was estimated based on the counterfactual scenario that *all* human-involved conservation of the species ceased between the current state and the short-term future state (IUCN 2020, 2021b). The long-term future state was defined as 100 years from the present and is estimated using long term species action plans, possible scientific trajectories and publicly articulated goals such as the Vermejo Statement (Sanderson et al. 2008):

Scores for each ecoregion were separated by time state and aggregated by minimum, best estimate, and maximum values and then used in the GSA equation to produce percentages of full recovery (Akçakaya et al. 2018):

$$G = \frac{\sum_S W_S}{W_F \times N} \times 100$$

Where G is the percentage of full recovery at the time state, S is the spatial unit, WS is the weight of the state in the spatial unit (0 to 9) 0 being absent and 9 being functional), WF is the weight of the functional category (9), and N is the total number of spatial units (Akçakaya et al. 2018, 2019). The denominator is the maximum score possible with all spatial units being functional (Akçakaya et al. 2018).

As a result, each spatial unit had a total of eighteen Green Scores derived from 3 estimates (upper, lower, best) for each of the six time states (IUCN 2021a). The best estimate GSA score was used to show change in species recovery from the former state to the long-term future with associated counterfactual scenarios included. These quantified four important conservation metrics (Akçakaya et al. 2018):

Conservation Legacy: The difference in Green Score percentages between the current and current counterfactual.

Conservation Dependence: The difference in Green Score percentages between the current and short-term future counterfactual scenario.

Conservation Gain: The difference in Green Score percentages between the current and short-term future scenario.

Recovery Potential: The difference in Green Score percentages between the current and long-term future scenario.

These four metrics yielded visual and quantitative results of how human-involved conservation has improved species recovery from the past to present, and provided theoretical trajectories for the future based on more or less conservation actions directed towards the species for each of the three “wild” iterations (Akçakaya et al. 2018).

RESULTS

IUCN Green Status: First Iteration

For the First Iteration of the GSA I used 22 free-ranging American bison herds totaling 18,942 individuals that qualify for an official IUCN assessment based on IUCN criteria (IUCN 2012b, 2019) and Aune et al.’s (2017) criteria. These included the 21 free-ranging bison herds used in the 2017 RLA as well as the Innoko wood bison herd in western Alaska, which has since qualified due to being established more than 5 years prior to the assessment (IUCN 2019). The First Iteration very likely captures all bison herds in North America that qualify for an official IUCN assessment.

The species recovery category for this iteration was assessed as critically depleted, with the current species recovery score of 14% recovered (lower bound=13%, upper bound=16%; Fig. 2). Of the 23 spatial units, only six are currently occupied by at least one bison herd. The conservation legacy was assessed as high (lower bound=12%, most likely=14%, upper bound=16%; Fig. 3), indicating that without former conservation efforts, bison recovery would be currently at or near zero (extinction). The conservation dependence was also assessed as high (lower bound=7%, most likely=14%, upper bound=16%), indicating that without continued conservation actions, bison recovery would reach zero or near zero in the next ten years (extinction). The conservation gain was assessed as low (lower bound=1%, most likely=4%, upper bound=10%), indicating little potential for an increase in bison recovery over the next ten years. The recovery potential was assessed as medium (lower bound=22%, most likely=29%, upper bound=46%), indicating potential for a moderate increase in bison recovery over the next 100 years. It should be noted that the difference between the lower and upper bounds for this conservation metric is 24%, suggesting large uncertainty in the potential recovery of bison in this iteration. Based on my assessment, within their original range the greatest possible recovery for American bison meeting First Iteration criteria in the next 100 years is 59.4% recovered, which is the upper bound of the long-term aspiration value.

IUCN Green Status: Second Iteration

For the Second Iteration of the GSA, I included 31 herds in addition to the 22 herds used in the First Iteration, for a total of 53 herds and 29,835 individuals. I obtained a species recovery category of largely depleted for this iteration, with a current species recovery score of 25% recovered (lower bound=22%, upper bound=25%). At least one bison herd occupies 11 of the 23 spatial units. The conservation legacy was assessed as high (lower bound=20%, most likely=25%, upper bound=25%). Similar to the First Iteration, without former conservation efforts bison recovery would be at or near zero (extinction) currently. A high conservation dependence was assessed (lower bound=16%, most likely=25%, upper bound=25%), indicating that without continued conservation actions over the next ten years, extinction or near extinction would occur. Little increase in bison recovery over the next ten years is likely as indicated by low conservation gain (lower bound=0%, most likely=4%, upper bound=12%). The recovery potential was assessed as high (lower bound=36%, most likely=46%, upper bound=57%), which means that a large increase in bison recovery is possible over the next 100 years. Similar to the First Iteration, there is uncertainty (19%) between the lower and upper bounds of this estimation. From my assessment, I estimate that the greatest possible recovery for American bison within their original range meeting the Second Iteration criteria in the next 100 years is 78.3% recovered.

IUCN Green Status: Third Iteration

For the Third Iteration of the GSA I included an additional 190 bison herds to the 53 herds used in the Second Iteration, for a total of 243 herds and 60,906 individuals. The species recovery category for the Third Iteration was assessed as largely depleted, with the current species recovery score of 33% recovered (lower bound=32%, upper bound=33%). Out of the 23 spatial units, 17 contain at least one bison herd. Conservation legacy was assessed as high (lower bound=30%, most likely=33%, upper bound=33%), indicating that bison would likely be extinct or near extinct without past conservation efforts. Conservation dependence was high (lower bound=26%, most likely=33%, upper bound=33%), suggesting that bison recovery would reach zero or near zero in the next ten years (extinction) without continued conservation actions. Conservation gain was low (lower bound=3%, most likely=7%, upper bound=12%), indicating little potential for increase in bison recovery over the next ten years. Recovery potential was medium (lower bound=36%, most likely=39%, upper bound=45%), indicating potential for a moderate increase in bison recovery over the next 100 years. My assessment finds that within their original range the greatest possible recovery for American bison meeting the Third Iteration criteria in the next 100 years is 76.8% recovered.

DISCUSSION

My three GSA iterations reflect the varying levels of recovery based on which bison herds are considered for assessment. Unsurprisingly, the GSA scores increased significantly from the First Iteration to the Third Iteration for both the current and future with conservation time states due to the inclusion of more bison herds and larger number of individuals. However, in the long-term aspiration time state, Second Iteration and the Third Iteration were significantly greater than the First Iteration, but not significantly different from one another. For the Third Iteration I assessed that within 100 years every spatial unit could at least reach present and almost every spatial unit could reach viable, which is due to an overall greater numerical recovery across the original range of bison than the First or Second Iteration. However, due to the lower management restrictions and lower reported frequency of ecological functions in the private sector (Chapter Two), I estimated that fewer spatial units would reach the functional state in the Third Iteration than the Second Iteration because the majority of bison would be held in private herds not observing all four ecological functions. The change in ecological recovery scores between the Second and Third Iterations present a fundamental challenge for bison recovery. Numerical recovery and distribution may be obtained if any management intensity, range size, or herd size is considered "wild" for assessment purposes, but it may come at the cost of ecological recovery of the species (Gates et al. 2010).

Within my three GSA iterations the former, current counterfactual, and ten-year future counterfactual Green Scores were the same. Because of a lack of information regarding the date of establishment and status of the Second Iteration and the Third Iteration bison herds at the former time state, I held the GSA scores assessed for the First Iteration herds at this state constant among all three iterations. Bison are entirely dependent upon conservation actions, and without previous or current conservation, bison would be almost certainly be extinct or critically endangered (Sanderson et al. 2008; Aune et al. 2017). Only a few individuals in the most remote herds may have survived to the current state or future counterfactual state in the absence of conservation actions. Across all three iterations in both time states I assessed the lower bound and most likely state as absent and the upper bound as present within only a few select remote spatial units in Alaska and northern Canada.

One issue with the GSA criteria specific to bison that I encountered was the assessment of viable to a spatial unit. There was no evidence of a continuing population decline of 30% of more in any of my spatial units at any time state other than the former. Due to the isolated nature of bison herds, there is no sign of a natural, non-human intervention caused rescue effect from an adjacent spatial unit (IUCN

2020, 2021b). This essentially made the decision of whether a spatial unit was assessed as present or viable dependent on if it contained <1,000 or >1,000 total mature individuals (IUCN 2020, 2021a). This number represents a large total population size that can persist long-term without significant loss of genetic diversity (Halbert & Derr 2008; Cherry et al. 2019). However, all bison herds are range restricted in some form (Boyd & Gates 2006; Gates et al. 2010). This is fundamentally different from many other wildlife species, and the current GSA one-size-fits-all criteria and protocols do not account for this. As a result, even though 1,000 total mature individuals may exist in several herds within a spatial unit, they may also be isolated from one another and have no genetic exchange. In the future, my findings suggest that the GSA criteria for viability should consider whether there is a natural or management-induced genetic connection between herds containing the majority of individuals within a spatial unit in addition to containing >1,000 mature individuals. This criterion may also provide a meaningful ecological justification for which herds should exchange individuals for the purpose of genetic maintenance, since exchange should take place within similar ecosystems to ensure environmental adaptations are maintained (Hedrick 2009; Hartway et al. 2020).

One additional change for the current GSA protocols I suggest in the future is the time of the former state: 1950 or when conservation actions began taking place, whichever is later (IUCN 2020, 2021a). The birth of the modern environmental movement took place in the 1950s, yet, by this time, much of the recovery of bison had already occurred (Gates et al. 2010). The American Bison was one of the first species in the United States to have a concerted effort to save from extinction in the late 1800s and early 1900s, occurring decades before the modern environmental movement (Gates et al. 2010). By rigidly requiring 1950 to be the earliest possible time of the former state, the true conservation legacy metric of bison may be underestimated. I suggest that the IUCN allow the former state to occur prior to 1950 in order to allow assessors to capture the true conservation legacy of species with early conservation efforts.

In the development of the IUCN Green Status protocols, the American bison has have been used as an example of a species that has recovered numerically but is considered ecologically extinct (Sanderson 2006; Freese et al. 2007; Plumb et al. 2009). Based on the criteria I have defined for functionality, American bison are currently functional in two spatial units for the First Iteration, three spatial units for the Second Iteration, and three spatial units for the Third Iteration. The presence of ecologically functional spatial units across all three assessments provides some refutation to bison as an example of an ecologically extinct species, because although bison do not fill their ecological role across their entire original range or even throughout their functional spatial units, they do fulfill their ecological role within several of the protected areas they currently reside. Future conservation and management efforts could further expand the recovery of American bison and establish the species an example of an ecologically functional species, rather than ecologically extinct.

The historic range of bison sits largely on developed land, and it is unlikely that bison will ever recover to pre-European settlement conditions (Gates et al 2010). Even so, conservation efforts have led to restoration over the last 100 years. With a vast continuum of bison situations present in North America resulting in potentially divergent paths for the species, the recovery objectives and goals over the next 100 years need to be critically evaluated (Sanderson et al. 2007). Current shared stewardship practices have shown the ability of cooperation and collaboration among management sectors to overcome many of the issues limiting bison conservation in the 21st Century (Sanderson et al. 2007; Gates et al. 2010 Ranglack and du Toit 2015). The embrace of new management strategies, expansion of local shared stewardship projects, and establishment of new ones where appropriate may be one of the prime ways to advance the multiple visions of bison conservation into the future. By working together American bison managers can lead conservation into a new era of cooperation and collaboration, creating the best possible situation for the wildlife species to proliferate into the long-term future.

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FIGURES AND TABLES

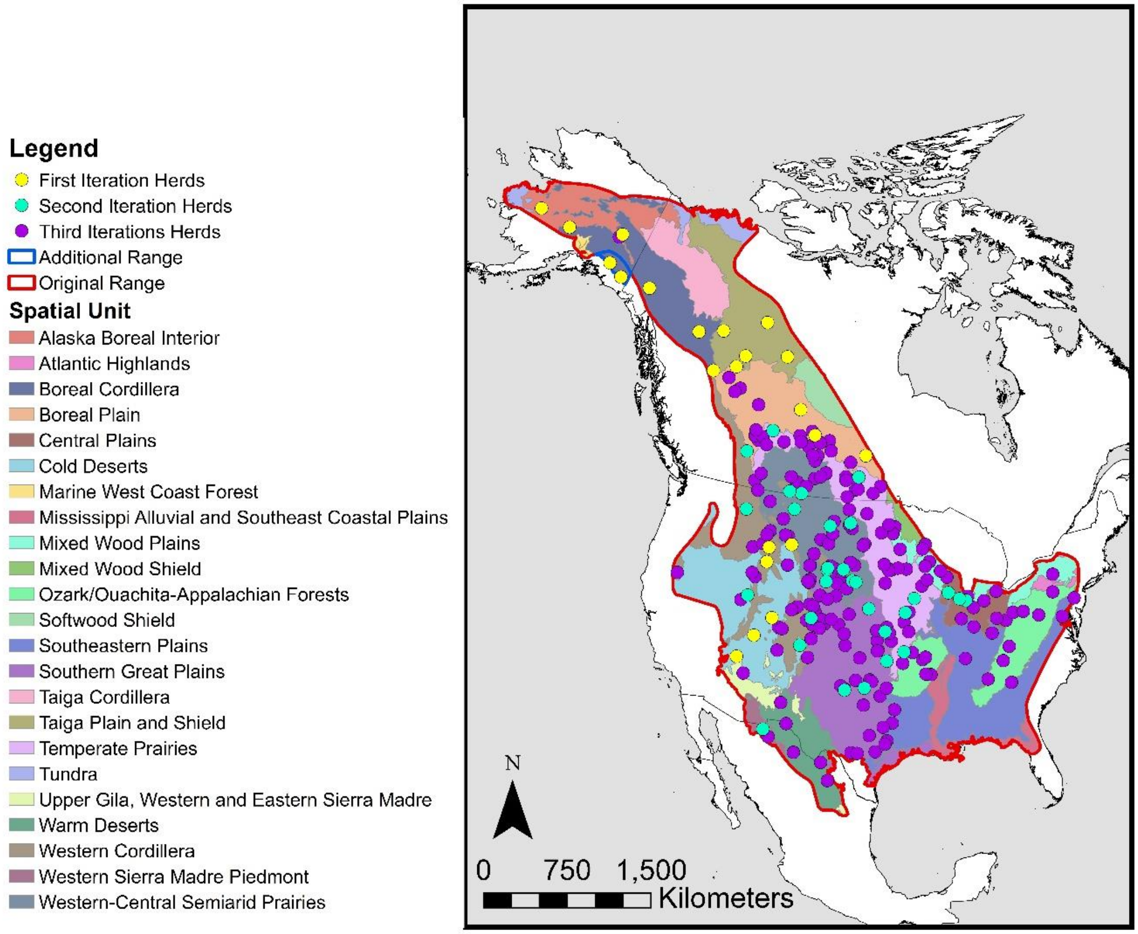

Figure 2.1: Surveyed American bison herds by iteration in relation to their spatial unit contained within the historic and additional range. Bison herd iterations are nested within one another, such that the First Iteration herds are also the Second Iteration and the Third Iteration herds, and the Second Iteration herds are also the Third Iteration herds. Herds outside the historic and additional range are not included in any iteration. Spatial units are derived from the U.S. Environmental Protection Agency level one ecoregions and level two subecoregions. Historical range is adapted from

Aune et al. (2017) with updated information from the Mexican Bison Working group (R. List pers. comm 2020), Canadian Bison Working Group (C. T. Seaton pers. comm. 2020) as well as Plumb and McMullen (2018). Additional range encompasses two bison herds qualifying for the First Iteration within the Boreal Cordillera subecoregion bound by the Alaska-Canada border in accordance with IUCN protocol (IUCN 2021b).

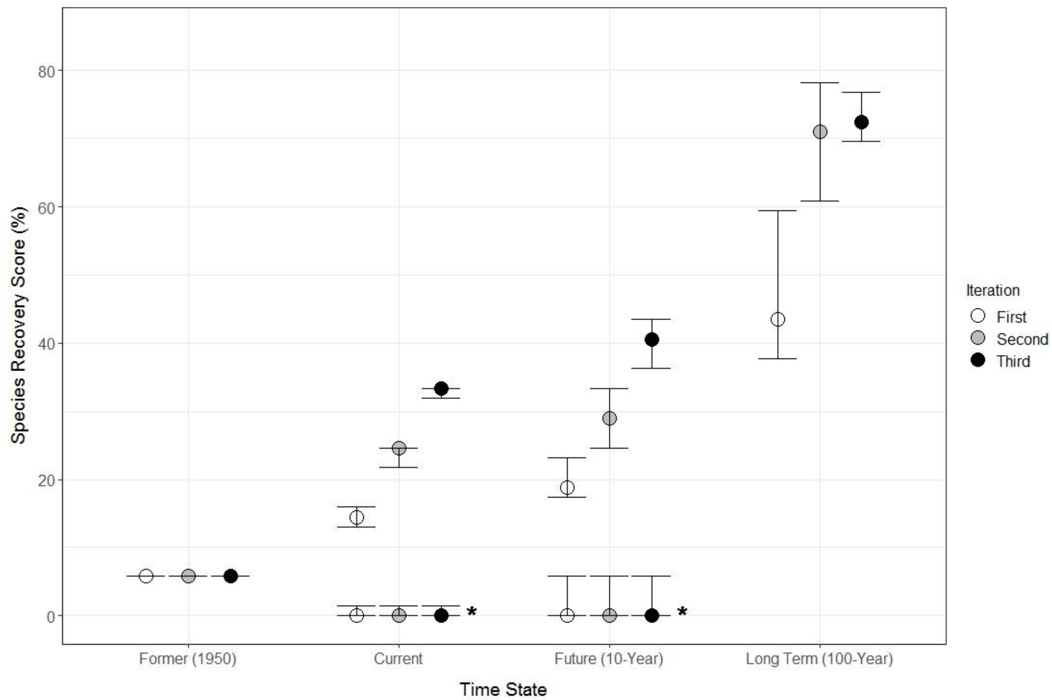

Figure 2.2: Graphical representation of the first, second, and Third Iteration bison herd species recovery scores at the six time states. The central point represents the best estimate of the species recovery score (percent recovery out of a possible 100%) at the time state. The upper and lower bounds represent the 95% confidence intervals of the species recovery score. Groups marked by an asterisk are the counterfactual (without conservation efforts) scenarios.

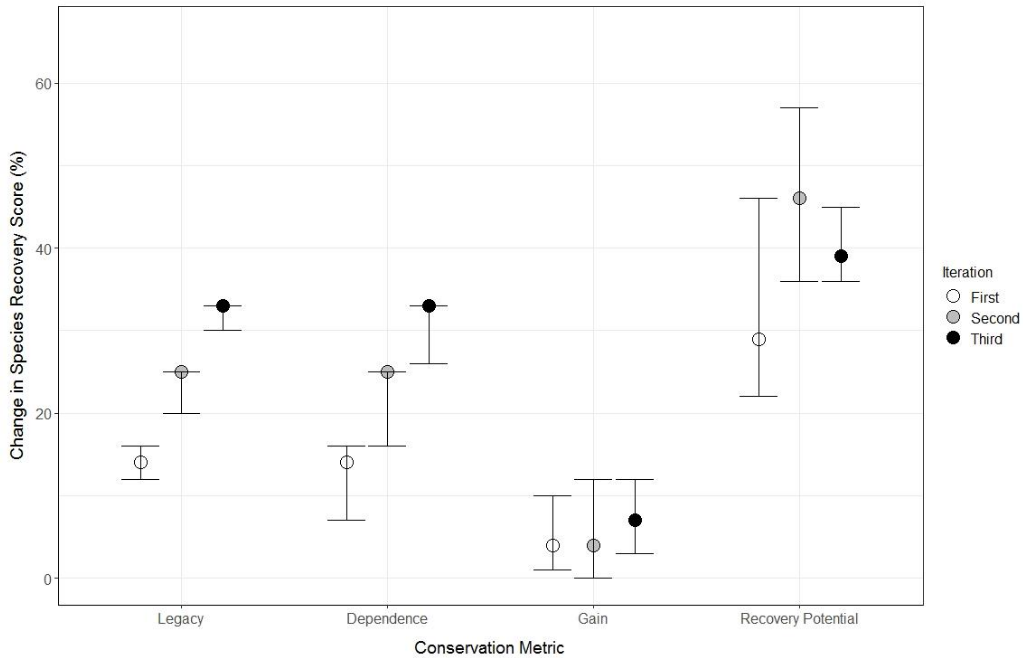

Figure 2.3: Graphical representation of the first, second, and Third Iteration GSA conservation metrics. The central point represents the best estimate of the percent change in species recovery score for the conservation metric. The upper bounds are the upper limit of the 95% confidence intervals for the species recovery score assessed at the later time state minus the lower limit of the 95% confidence intervals for the species recovery score at the current time state. The lower bounds are the lower limit of the 95% confidence intervals for the Green Scores assessed at the later time state minus the upper limit of the 95% confidence intervals for the species recovery score at the current time state.

CHAPTER IV

SYNTHESIS AND RECOMMENDATIONS

This research showed for the first time a clear picture of the status of the American bison (*Bison bison* subspp.) herds through a comprehensive and widely distributed survey. I used information gathered from this survey to test the sensitivity of the novel International Union for Conservation of Nature (IUCN) Green Status Assessment (GSA) based on the inclusion or exclusion of bison herds based on criteria set in the most recent Red List Assessment (RLA), and found meaningful results (Aune et al. 2017; Akçakaya et al. 2019; IUCN 2019; Grace 2020). Through these two pieces of scholarship I gained insight into the continuum of bison situations across North America that is valuable to the bison community and has the potential to inform future small and large-scale management decisions.

I surveyed approximately 10% of the total number of bison herds in North America, but at least 25% of the total number of bison. My survey distribution methods and network of contacts likely resulted in capturing most if not all of the large bison herds containing >1,000 individuals in North America. Through partnership with the Mexican National Bison Working group, the first ever inventory of Mexico's bison herds was completed. Using a Multiple Correspondence Analysis (MCA) with this data, I found that when visualizing management sectors in relation to herd and range size as well as management intensity, a clear linear path between the centroids of the private, non-profit, federal, and state or provincial management sectors is evident (Greenacre & Blasius 2006; Abdi & Valentin 2007). This linear path indicates a larger herd and range size as the x-axis increases and less intensive management as the y-axis increases, with the exception of the influence of "NA" responses. This linear path also visually shows for the first time the placement of bison herds along the continuum of bison situations. This continuum has created the possibility of divergent evolutionary pathways, with some bison potentially deviating from being "wild" and instead trending towards domestication. However, the 95% confidence ellipse around the centroid for the federal sector intersects both the non-profit and state or provincial, indicating that the federal management sector is not significantly different from the state or provincial or the non-profit management sectors (Audigier et al. 2017; Strauss & Maltitz 2017).

My results from the Freeman-Halton-Fisher exact tests of independence agree with my MCA findings. In five of the nine RLA criteria presented by Aune et al. (2017) that were surveyed, the state or provincial management sector had the highest proportion of herds meeting the criteria of any management sector. The federal management sector had the highest proportion of herds meeting RLA criteria in the other four out of nine surveyed. Non-profit, zoo, and private herds did not have the highest proportion of herds meeting RLA criteria in any of the nine surveyed. This suggests that proportionally state/provincial and federal herds are adhering to Aune et al.'s (2017) RLA criteria most closely. Conversely, zoo herds had the lowest proportion of herds meeting RLA criteria in seven out of the nine surveyed. Private herds had the lowest proportion of herds meeting RLA criteria in two out of the nine surveyed. This suggests that, proportionally, zoo and private herds are adhering to

Aune et al.'s (2017) RLA criteria the least closely, supporting previous research (Sanderson et al. 2008; Redford et al. 2011; Aune et al. 2017). Non-profit herds did not have the highest or lowest proportion of herds adhering to any of the nine criteria, suggesting intermediacy between state or provincial and federal herds and zoo and private herds.

My three GSA iterations reflect the varying levels of recovery based on which bison are considered for assessment. Unsurprisingly, the GSA scores increased significantly from the First Iteration to the Third Iteration for both the current and future with conservation time states due to the inclusion of more bison herds and larger number of individuals. However, in the long-term aspiration time state the Second Iteration and the Third Iteration were significantly greater than the First Iteration, but not significantly different from one another. For the Third Iteration, I found that every spatial unit could reach present or viable within 100 years, which is due to an overall greater numerical recovery across the original range of bison than the First Iteration or the Second Iteration. However, due to the lower management restrictions and lower reported frequency of ecological functions in the private sector from Chapter Two, I estimated that fewer spatial units would reach the functional state than the Second Iteration because the majority of bison would be held in private herds not observing all four ecological functions. The change in ecological recovery scores between the Second and Third Iterations present a fundamental challenge for bison recovery. Numerical recovery and distribution may be obtained in greater numbers if any management intensity, range size, or herd size is considered "wild" for assessment purposes, but it may come at the cost of ecological recovery of the species (Gates et al. 2010).

My first objective was to update and summarize the status of bison herds in North America by their various management sectors. I accomplished this through a widely distributed survey of bison managers on the continent, and evaluation of the proportional adherence of herds in these management sectors to criteria presented in the most recent RLA. My second objective was to test the variation in species recovery scores of this tool when herds are included or excluded. I accomplished this through three nested iterations of the IUCN GSA using based on progressively relaxed definitions of the criteria for “wild” presented in the most recent RLA (Aune et al. 2017). While I accomplished my objectives, obstacles were encountered during research.

Collecting information regarding every bison herd was not possible as some bison managers were not reachable through the methods provided, and some were simply not willing to participate. Additionally, the majority of data collection occurred during the COVID-19 global pandemic, creating unique challenges for contacting bison managers. Specifically, the pandemic resulted in a very low response rate from the tribal management sector, which prevented us from reliably analyzing their proportional adherence to Aune et al.’s (2017) RLA criteria and analyze how it differs from others. Future research should focus on where the tribal management sector fits within the others.

A complete, robust dataset of all American bison herds in each management sector may have yielded different results. I recognize the limitations in my data to address criteria 2.4 (intraspecific genetic variation), 2.5 (cattle gene introgression), 3.1 (reproduction selection), and 4.1 (legal protection) of Aune et al.'s (2017) RLA. I would have also potentially obtained two clusters from my MCA instead of three: one containing very small to medium herd and range sizes with captive to intensive management, and one containing medium to very large herd and range sizes with light management. Additionally, the centroid of the zoo management sector could potentially locate within the bottom-left corner of the MCA plot along the clear linear path between the other management sectors indicating the smallest herd and range size and most intensive management. Lastly, a complete dataset of bison herds would remove the overlap in 95% confidence ellipses around the centroids for the federal and non-profit management sectors, if not also the federal and state or provincial management sectors.

The IUCN GSA is a novel and powerful standardized conservation assessment tool but is not free from its complications. The one-size-fits-all criteria and protocols in this assessment do not account for the unique current management situations many bison exist within and their conservation history (Akçakaya et al. 2019; Grace 2020; IUCN 2020). Bison experience more range restriction than most wildlife species, a fundamental difference that severely limits the inclusion of herds in assessments (Boyd 2003; Boyd & Gates 2006; Gates et al. 2010). Also, the majority of their conservation in the state or provincial and federal sectors took place prior to 1950, but the GSA criteria rigidly requires 1950 to be the earliest possible time of the former state (IUCN 2020; Grace et al. 2021). By mandating an earliest former state of 1950, the GSA underestimates the true conservation legacy of bison. I suggest that future discussions of the GSA involve adaptive decision making by relaxing the range restriction criteria and the date of the former state to accommodate the unique situation of bison without losing the standardization of the assessment.

Despite some minor discrepancies with my data collection and the IUCN GSA protocol, I achieved research that creates a baseline dataset for American bison in the 21st Century, which can be adopted, updated, and used by major bison conservation organizations. This data will inform the next RLA, which will be completed by 2023. (G. Wilson pers comm 2020). The information gathered from this research can also assist GSA and other similar assessments for species with diverse continuums of management situations similar to bison. This research was an important first step for understanding the recovery of bison in North America that will lead to future conservation directions.

In summary, the bison community now has a clearer picture of the continuum of situations American bison herds exist within. Empirical evidence shows us that some significant differences exist between management sectors, but not in their belief that their herds contribute to bison conservation. Each sector has its own strengths and weaknesses towards future conservation visions such as the Vermejo statement of 2008 and Bison 1 Million initiative, but no sector alone can achieve these visions (Sanderson et al. 2008). Current shared stewardship practices have shown the potential for cooperation and collaboration among management sectors to advance these visions of bison conservation into the future. I advocate for the expansion of these current local shared stewardship project and establishment of new ones where appropriate (Ranglack & Du Toit 2016; Young 2019; *Department of the Interior Bison Conservation Initiative* 2020). In order to do this, we may need to revisit and change my mindset towards which bison count and do not count towards conservation (Freese et al. 2007; Sanderson et al. 2008; Redford et al. 2011). We may also need to embrace new strategies and ideas such as local stewardship of public resources (Ranglack & Du Toit 2016). In doing so, we may be able to create herds that both adhere to RLA and GSA criteria and have the greatest strengths of each management sector, ending the plateau in conservation that we have experienced in the past five decades and propelling us to new heights that were once thought to be impossible.

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Appendix A. Fifty-three questions asked to bison herd managers via an online survey.

Question number	Survey Question	Survey Answer
1	Which species or subspecies of bison is present in this herd? Select one answer.	Plains bison
		Wood bison
		European bison
		Wood and Plains bison hybrid
		Unknown
		I prefer not to answer
2	What was the approximate population size of this herd before calving in 2019? Select one answer.	Other (input number)
		1-10 individuals
		11-50 individuals
		51-100 individuals
		101-200 individuals
		201-400 individuals
		401-1000 individuals
		1001-5000 individuals
		More than 5000 individuals
		Unknown
		I prefer not to answer
3	What is the population trend (number of individuals in the herd) over the last 5 years? Select one answer.	Increasing
		Decreasing
		Stable
		This herd has only recently been established
		Unknown
		I prefer not to answer
4	What is a realistic but optimistic population size within in the next 15 years? Select one answer.	Other (input number)
		1-10 individuals
		11-50 individuals
		51-100 individuals
		101-200 individuals
		201-400 individuals
		401-1000 individuals

		1001-5000 individuals
		More than 5000 individuals
		Unknown
		I prefer not to answer
5	Approximately what is the ratio of breeding males to breeding females in this herd? Select one answer.	2+ breeding males: 1 breeding female
		1 breeding male: 1 breeding female
		1 breeding male: 2 breeding females
		1 breeding male: 3-5 breeding females
		1 breeding male: 6-10 breeding females
		1 breeding male: 11-20 breeding females
		1 breeding male: 21-50 breeding females
		1 breeding male: 50+ breeding females
		Unknown
		I prefer not to answer
6	What is the legal status of the herd? Select all that apply.	Non-profit
		Private
		Federal
		Tribal
		State/Provincial
		Zoo
		Other (input text)
		Unknown
		I prefer not to answer
7	What roles do you believe this herd fulfills? Select all that apply.	Ecosystem and landscape restoration
		Cultural use
		Tourism
		Bison conservation
		Meat production
		Education and outreach
		Public hunting
		Private hunting
		Other (input text)
		I prefer not to answer

8	Would you like to include the location of this herd within the specified subecoregion on the final published map? This information will be aggregated within the subecoregion only; the exact location and population size of this herd will not be visible to the public.	Yes, I would like to include this herd's subecoregion location on the publicly available map
		No, I would not like to include this herd's subecoregion location on the publicly available map
9	Please click on the subecoregion that contains the majority of the herd's available range. This will not become public information unless you previously specified that you are willing to share the location of this herd at the subecoregion level as part of a final published map.	Other (select ecoregion)
10	Please click on the approximate location of this herd. This will not become public information.	Other (select location)
11	If you are unable to use the map provided, please include an address that is near the approximate location of this herd. This will not become public information.	Other (input text)
12	Which units are you most comfortable using regarding range size? Select one answer.	Acres
		Hectares
		Square miles
		Square kilometers
13	What is the total size of the available range to this herd in acres, including deeded and leased properties? Select one answer.	Other (input number)
		0-12 acres
		13-49 acres
		50-124 acres
		125-494 acres
		495-1,236 acres
		1,237-2,471 acres
		2,472-4,996 acres
		4,997-12,355 acres
		12,356-24,710 acres
		49,998-499,993 acres
		24,711-49,997 acres
		More than 499,993 acres
		Unknown
14	What is the total size of the available range to this herd in hectares, including deeded and leased properties? Select one answer.	Other (input number)
		0-5 hectares

		6-20 hectares
		21-50 hectares
		51-200 hectares
		201-500 hectares
		501-1000 hectares
		1001-2022 hectares
		2023-5000 hectares
		5001-10,000 hectares
		20,234-202,340 hectares
		10,001-20,233 hectares
		More than 202,342 hectares
		Unknown
15	What is the total size of the available range to this herd in square miles, including deeded and leased properties? Select one answer.	Other (input number)
		0-0.02 square miles
		0.03-0.08 square miles
		0.09-0.19 square miles
		0.20-0.77 square miles
		0.78-1.93 square miles
		1.94-3.86 square miles
		3.87-7.81 square miles
		7.82-19.31 square miles
		19.32-38.61 square miles
		78.13-781.24 square miles
		38.62-78.12 square miles
		More than 781.24 square miles
16	What is the total size of the available range to this herd in square kilometers, including deeded and leased properties? Select one answer.	Other (input number)
		0-0.05 square kilometers
		0.06-0.20 square kilometers
		0.21-0.50 square kilometers
		0.51-2.00 square kilometers
		2.01-5.00 square kilometers
		5.01-10.00 square kilometers
		10.01-20.22 square kilometers

		20.23-50.00 square kilometers
		50.01-100.00 square kilometers
		202.34-2,023.40 square kilometers
		100.01-202.33 square kilometers
		More than 2,023.42 square kilometers
		Unknown
17	What is a realistic but optimistic objective total range size in acres available to this herd in the next 15 years, including deeded and leased properties? Select one answer.	Other (input number)
		0-12 acres
		13-49 acres
		50-124 acres
		125-494 acres
		495-1,236 acres
		1,237-2,471 acres
		2,472-4,996 acres
		4,997-12,355 acres
		12,356-24,710 acres
		49,998-499,993 acres
		24,711-49,997 acres
		More than 499,993 acres
		Unknown
18	What is a realistic but optimistic objective total range size in hectares available to this herd in the next 15 years, including deeded and leased properties? Select one answer.	0-5 hectares
		6-20 hectares
		21-50 hectares
		51-200 hectares
		201-500 hectares
		501-1000 hectares
		1001-2022 hectares
		2023-5000 hectares
		5001-10,000 hectares
		20,234-202,340 hectares
		10,001-20,233 hectares
		More than 202,342 hectares

		Unknown
19	What is a realistic but optimistic objective total range size in square miles available to this herd in the next 15 years, including deeded and leased properties?	Other (input number)
		0-0.02 square miles
		0.03-0.08 square miles
		0.09-0.19 square miles
		0.20-0.77 square miles
		0.78-1.93 square miles
		1.94-3.86 square miles
		3.87-7.81 square miles
		7.82-19.31 square miles
		19.32-38.61 square miles
		78.13-781.24 square miles
		38.62-78.12 square miles
		More than 781.24 square miles
		Unknown
20	What is a realistic but optimistic objective total range size in square kilometers available to this herd in the next 15 years, including deeded and leased properties? Select one answer.	Other (input number)
		0-0.05 square kilometers
		0.06-0.20 square kilometers
		0.21-0.50 square kilometers
		0.51-2.00 square kilometers
		2.01-5.00 square kilometers
		5.01-10.00 square kilometers
		10.01-20.22 square kilometers
		20.23-50.00 square kilometers
		50.01-100.00 square kilometers
		202.34-2,023.40 square kilometers
		100.01-202.33 square kilometers
		More than 2,023.42 square kilometers
		Unknown
21	What are common sources of bison deaths in this herd? Select all that apply.	Non-human predation (wolf, bears, other animal predation)
		Human predation (hunting, culls, harvest for meat production)

		Disease
		Resouce limitation caused by seasons and/or weather
		Other (input text)
		None of these
		Unknown
		I prefer not to answer
22	Which of the following functions have been observed in this herd? Select all that apply.	Patchy grazing (some areas are heavily grazed by bison, others are not)
		Wallow pits
		Whole bison carcasses allowed to decompose on the landscape where the animal died
		Other (input text)
		Unknown
		I prefer not to answer
23	In the next 15 years, given the population and range size changes mentioned previously, which of the following do you anticipate proportionally more of? Select all that apply.	Non-human predation (wolf, bears, other animal predation)
		Human predation (hunting, culls, harvest for meat production)
		Disease
		Resouce limitation caused by seasons and/or weather
		Patchy grazing (some areas are heavily grazed by bison, others are not)
		Wallow pits
		Whole bison carcasses allowed to decompose on the landscape where the animal died
		Unknown
		I prefer not to answer
24	In the next 15 years, given the population and range size changes mentioned previously, which of the following do you anticipate proportionally less of? Select all that apply.	Non-human predation (wolf, bears, other animal predation)
		Human predation (hunting, culls, harvest for meat production)
		Disease
		Resouce limitation caused by seasons and/or weather

		Patchy grazing (some areas are heavily grazed by bison, others are not)
		Wallow pits
		Whole bison carcasses allowed to decompose on the landscape where the animal died
		Unknown
		I prefer not to answer
25	In the next 15 years, given the population and range size changes mentioned previously, which of the following do you anticipate proportionally the same amount of? Select all that apply.	Non-human predation (wolf, bears, other animal predation)
		Human predation (hunting, culls, harvest for meat production)
		Disease
		Resouce limitation caused by seasons and/or weather
		Patchy grazing (some areas are heavily grazed by bison, others are not)
		Wallow pits
		Whole bison carcasses allowed to decompose on the landscape where the animal died
		Unknown
		I prefer not to answer
26	Which other species share the range available to this herd? Select all that apply.	Cattle
		Sheep
		Other domestic livestock
		Other large wild herbivores (deer, elk, or similar)
		Small herbivores (prairie dog, rabbit, or similar)
		Large Predators (bear, wolf, or similar)
		Small predators (coyote, fox, or similar)
		Large scavengers (vulture or similar)
		Small scavengers (dung beetle or similar)
		Other (input text)
		I prefer not to answer
		Unknown
27	Which types of fire occur on the range available to this herd? Select one answer.	Naturally occurring field fires

		Prescribed (human-caused) fires
		Both A and B
		Fires are actively suppressed
		There is not enough fuel present within the available range to support a fire
		Unknown
		I prefer not to answer
28	What types of borders or barriers restrict the movement of this herd? Select all that apply.	Full perimeter fencing
		Partial perimeter fencing
		Internal or cross fencing
		Unsuitable habitat barrier (cliffs, canyons, ocean, or similar)
		Hazing and/or herding by humans
		Heavy hunting pressure by humans
		Other (input text)
		Unknown
		I prefer not to answer
29	How frequently is this herd supplementally fed (bales of hay, grain, or similar)? Select one answer.	Only under emergency circumstances (generally rare, not annual)
		Only during round-ups or handling events
		Less than 30 days per year
		31-90 days per year
		91-365 days per year
		This herd is only supplementally fed
		This herd is never supplementally fed
		Unknown
		I prefer not to answer
30	Is this herd rounded-up or handled?	Yes
		No
		Unknown
		I prefer not to answer
31	How frequently is this herd round-upped or handled? Select one answer.	yes
		More than once per year
		Yearly
		Every 2 years

		Every 3-5 years
		Other (input text)
		This herd is not round up or handled
		Unknown
		I prefer not to answer
32	Why is this herd rounded-up or handled? Select all that apply.	Disease testing
		Genetic testing
		Sale
		Separate individuals
		Pregnancy testing
		Count
		Other (input text)
		Unknown
		I prefer not to answer
33	Is there public viewing of this herd?	Yes
		No
		Unknown
		I prefer not to answer
34	What level of public access is there to this herd? Select one answer.	No access
		Public access, limited to perimeter, but bison are sometimes viewable
		Public access limited to selected locales/times on the landscape
		Public access across most landscape (>50%) at most times (>50%)
		Full public access across landscape at all times
		Unknown
		I prefer not to answer
35	What other cultural uses does this herd provide?	Other (input text)
36	What monetary values does this herd provide? Select all that apply.	Sale of hunting permits
		Sale of live individuals to other herds
		Sale of live individuals for commercial meat and other physical (ie craft) products
		Viewing (tourism)

		Carbon credits or other environmental products
		Other (input text)
		None of these
		Unknown
		I prefer not to answer
37	Are genetics considered when management decisions are made for this herd?	Yes
		No
		Unknown
		I prefer not to answer
38	How does breeding occur? Select all that apply.	Artificial insemination
		Bull bison are selected and allowed to breed with females through human intervention
		All present breeding bull bison compete for mates without human intervention
		Other (input text)
		Unknown
		I prefer not to answer
39	Are specific age groups or sexes removed from this herd?	Yes
		No
		Unknown
		I prefer not to answer
40	Which age and sex groups are removed from this herd? Select all that apply.	Male calves (less than 1 year old)
		Female Calves (less than 1 year old)
		Male Juveniles (1-2 years old)
		Female Juveniles (1-2 years old)
		Male subadults (3-4 years old)
		Female subadults (3-4 years old)
		Prime age male adults (5-10 years old)
		Prime age female adults (5-10 years old)
		Old age male adults (11+ years old)
		Old age female adults (11+ years old)
		I prefer not to answer
		Unknown

41	Are individuals in this herd currently or have they previously been removed (through culling or other methods) because of these specific these traits? Select all that apply.	Cattle hybridization
		Smaller body size or weight
		Larger body size or weight
		Lower aggression
		More aggression
		Larger horns
		Smaller horns
		More fur
		Less fur
		Unique traits (ex. white bison, inverse horns)
		No selective removal is being done on this herd
		Other (input text)
		Unknown
		I prefer not to answer
42	Are individuals in this herd currently or have they previously been bred to acquire any of these specific traits? Select all that apply.	Cattle hybridization
		Smaller body size or weight
		Larger body size or weight
		Lower aggression
		More aggression
		Larger horns
		Smaller horns
		More fur
		Less fur
		Unique traits (ex. white bison, inverse horns)
		No selective breeding is being done on this herd
		Other (input text)
		Unknown
		I prefer not to answer
43	How frequently are breeding age bison from other populations introduced into this herd? Select one answer.	Every year

		Every 2-4 years
		Every 5-10 years
		Every 10+ years
		New bison have not been introduced to this herd, but there are future plans to do so
		New bison have not been introduced to this herd, and there are no future plans to do so
		Unknown
		I prefer not to answer
44	How many breeding age bull bison are introduced into this herd each time? Select one answer.	1-3 bull bison
		4-10 bull bison
		11-25 bull bison
		25+ bull bison
		Unknown
		I prefer not to answer
		Not applicable
45	How many breeding age cow bison are introduced into this herd each time? Select one answer.	1-3 cow bison
		4-10 cow bison
		11-25 cow bison
		25+ cow bison
		Unknown
		I prefer not to answer
		Not applicable
46	Has there been genetic testing on individuals within this herd?	Yes
		No
		Unknown
		I prefer not to answer
47	Which of the following have been identified via genetic testing? Select all that apply.	Hybridization with cattle, individuals removed
		Hybridization with cattle, individuals not removed
		Rare alleles
		High genetic diversity
		Low genetic diversity
		Inbreeding depression

		Other (input text)
		This herd has not had genetic testing conducted
		Unknown
		I prefer not to answer
48	Which of the following diseases have been tested for (but not necessarily detected) in this herd? Select all that apply.	Foot and Mouth Disease
		Anthrax
		Tuberculosis
		Brucellosis
		Bovine Spongiform Encephalopathy (BSE)
		Bluetongue
		Anaplasmosis
		Johne's Disease
		Malignant Catarrhal Fever
		Bovine Viral Diarrhea
		Mycoplasma Bovis
		Pasteurella
		Other (input text)
		None of these
49	Which of the following diseases have been detected in this herd? Select all that apply.	Foot and Mouth Disease
		Anthrax
		Tuberculosis
		Brucellosis
		Bovine Spongiform Encephalopathy (BSE)
		Bluetongue
		Anaplasmosis
		Johne's Disease
		Malignant Catarrhal Fever
		Bovine Viral Diarrhea
		Mycoplasma Bovis
		Pasteurella
		Other (input text)
		None of these

50	What disease management practices are used on this herd? Select all that apply.	Testing
		Slaughter
		Vaccinations
		Parasite treatment
		Other (input text)
		None of these
		Unknown
		I prefer not to answer
51	There are three levels of species recovery. These are: 1) Present—Individuals of the species are present on the landscape. 2) Viable—In addition to being present, the herd population is large, stable, healthy, and genetically robust, resulting in very low probability of elimination or extinction. 3) Functional—in addition to being viable, the herd exhibits a full range of ecological interactions, functions and other roles in the ecosystem (such as patchy grazing, predation, and natural mortality). Which category do you believe this herd belongs to? Select one answer.	Present
		Viable
		Functional
		Unknown
		I prefer not to answer
52	Is there any additional information you would like to share about this herd that has not been captured by our survey?	Other (input text)
53	Thank you for completing this surey of American bison. If you would like to receive a copy of the summarized results of this survey, or be entered for a chance to win one of five $50 VISA gift cards, please include your email address below. The drawing will take place October 1st, 2020.	Other (input text)

Appendix B. Weighting of the surveyed RLA criteria in the MCA ordination. Weights range from 0 (no influence on positioning along axis) to 1 (complete influence on positioning along axis).

Criteria	Survey Question	Dimension 1 Weight	Dimension 2 Weight
1.1	Range size	0.842	0.671
1.1 future	Range size in ten years	0.834	0.667
1.2	Presence of fencing	0.125	0.586
2.1 and 2.2	Current herd population	0.683	0.219
2.1 and 2.2 future	Herd population in ten years	0.676	0.229
2.3	Adult sex ratio	0.087	0.319
2.4	Genetic testing	0.359	0.377
3.1	Management of breeding	0.196	0.435
3.2	Frequency of supplemental feeding	0.612	0.614
3.3	Presence of predators	0.206	0.011

Appendix C. Count and percent of responses broken down by 2017 RLA criteria for each cluster in the MCA.

Criteria	Survey Question	Survey Answer	Count of Responses	Percent of Responses in Cluster 1	Percent of Responses in Cluster 2	Percent of Responses in Cluster 3
Not applicable	Management demographic	federal	23	4.35	30.43	65.22
		state/provincial	26	7.69	26.92	65.38
		non-profit	26	23.08	53.85	23.08
		private	258	11.24	81.01	7.75
		zoo	28	67.86	32.14	0.00
		NA	0	0.00	0.00	0.00
1.1	Range size	0-5 hectares	30	70.00	30.00	0.00
		6-20 hectares	23	13.04	86.96	0.00
		21-50 hectares	38	7.89	92.11	0.00
		51-200 hectares	64	4.69	95.31	0.00
		201-500 hectares	45	4.44	95.56	0.00
		501-1000 hectares	24	0.00	100.00	0.00
		1001-2022 hectares	24	0.00	100.00	0.00
		2023-5000 hectares	14	0.00	85.71	14.29
		5001-10,000 hectares	13	7.69	46.15	46.15
		10,001-20,233 hectares	17	0.00	11.76	88.24
		20,234-202,340 hectares	25	0.00	4.00	96.00
		More than 202,342 hectares	10	0.00	0.00	100.00
		NA	34	70.59	26.47	2.94
1.1 future	Range size in ten years	0-5 hectares	18	77.78	22.22	0.00
		6-20 hectares	13	15.38	84.62	0.00
		21-50 hectares	37	10.81	89.19	0.00
		51-200 hectares	59	3.39	96.61	0.00
		201-500 hectares	47	4.26	95.74	0.00
		501-1000 hectares	30	0.00	100.00	0.00
		1001-2022 hectares	26	0.00	100.00	0.00
		2023-5000 hectares	13	0.00	92.31	7.69
		5001-10,000 hectares	10	0.00	40.00	60.00
		10,001-20,233 hectares	17	0.00	17.65	82.35

		20,234-202,340 hectares	21	0.00	0.00	100.00
		More than 202,342 hectares	12	0.00	0.00	100.00
		NA	58	56.90	36.21	6.90
1.2	Presence of fencing	no fence	60	61.67	8.33	30.00
		partial perimeter fence	8	0.00	12.50	87.50
		full perimeter fence	110	16.36	75.45	8.18
		internal fence	183	1.09	85.79	13.11
		NA	0	0.00	0.00	0.00
2.1 and 2.2	Current herd population	1-10 individuals	55	50.91	49.09	0.00
		11-50 individuals	95	10.53	87.37	2.11
		51-100 individuals	64	14.06	82.81	3.13
		101-200 individuals	47	10.64	78.72	10.64
		201-400 individuals	37	5.41	72.97	21.62
		401-1000 individuals	29	3.45	37.93	58.62
		1001-5000 individuals	29	3.45	17.24	79.31
		More than 5000 individuals	1	0.00	0.00	100.00
		NA	4	25.00	75.00	0.00
2.1 and 2.2 future	Herd population in ten years	1-10 individuals	32	62.50	37.50	0.00
		11-50 individuals	75	10.67	89.33	0.00
		51-100 individuals	45	11.11	86.67	2.22
		101-200 individuals	63	17.46	71.43	11.11
		201-400 individuals	55	3.64	87.27	9.09
		401-1000 individuals	40	7.50	45.00	47.50
		1001-5000 individuals	32	0.00	28.13	71.88
		More than 5000 individuals	2	0.00	0.00	100.00
		NA	17	47.06	47.06	5.88
2.3	Sex ratio	2+ breeding males: 1 breeding female	6	33.33	66.67	0.00
		1 breeding male: 1 breeding female	24	20.83	25.00	54.17
		1 breeding male: 2 breeding females	22	31.82	31.82	36.36
		1 breeding male: 3-5 breeding females	38	15.79	65.79	18.42

		1 breeding male: 6-10 breeding females	61	4.92	90.16	4.92
		1 breeding male: 11-20 breeding females	160	11.25	77.50	11.25
		1 breeding male: 21-50 breeding females	22	10.00	45.00	45.00
		1 breeding male: 50+ breeding females	0	0.00	0.00	0.00
		NA	28	42.86	25.00	32.14
2.4	Genetic testing	genetic testing done	128	4.69	53.13	42.19
		genetic testing not done	176	6.82	91.48	1.70
		NA	57	68.42	29.82	1.75
3.1	Management of breeding	human intervention	52	3.85	86.54	9.62
		no human intervention	255	3.53	76.08	20.39
		NA	54	85.19	12.96	1.85
3.2	Frequency of supplemental feeding	Only under emergency circumstances (generally rare, not annual)	10	0.00	70.00	30.00
		Only during round-ups or handling events	40	0.00	42.50	57.50
		Less than 30 days per year	11	0.00	100.00	0.00
		31-90 days per year	73	5.48	89.04	5.48
		91-365 days per year	136	4.41	93.38	2.21
		This herd is only supplementally fed	25	56.00	44.00	0.00
		This herd is never supplementally fed	29	3.45	10.34	86.21
		NA	37	86.49	13.51	0.00
3.3	Presence of predators	predators are present on rangeland	72	1.39	59.72	38.89
		predators are absent on rangeland	289	19.38	70.24	10.38
		NA	0	0.00	0.00	0.00