# Impacts of Restoration: Assessing Resource Selection by Reintroduced Plains Bison in Banff National Park and their Influence on Birds

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# Abstract

Parks Canada helped to restore the biodiversity of Banff National Park by reintroducing a herd of plains bison into Banff's backcountry in 2017. Questions remain as to how bison might use the landscape and how their choice of what parts of a landscape to use might affect creatures already present there. I used remote sensing and GIS to examine how topography, the history of fire, and ecosystem type affected the odds of the Banff bison inhabiting parts of their reintroduction zone. I also used acoustic bird surveys, and vegetation structure and composition surveys to examine if changes to vegetation might influence the overall abundance and species richness of the bird population of the reintroduction zone.

Bison were most likely to inhabit areas of the reintroduction zone that were on flatter terrain, closer to water, frequently burned, and that were in a grassland/shrubland ecosystem. The percent coverage of forbs increased with increasing bison usage. The percent coverage of mosses was found to increase with increasing bison usage in forests but decreased with increasing bison usage in grassland/shrublands. The overall bird population was associated with a decrease in areas most used by bison.

These results show that the prescribed burn program in Banff National Park can create good habitat for bison and encourage them to explore the landscape. Burns will create critical habitat for disturbance-tolerant species and bison will help to maintain these disturbed patches. These results also show how birds sensitive to disturbance by bison may decline in the early stages of a reintroduction and that the lack of an effect on species richness may be because disturbance-tolerant birds need more time to find this new habitat. Expanding the bison reintroduction zone in the long run would be advantageous as managers work to restore bison as a force that encourages biodiversity within the Canadian Rockies.

# Chapter 1: Introduction

## Research Background

Global biodiversity continues to decline at an alarming rate and while progress in curbing the decline has been made, bold new methods are needed to prevent any further loss (United Nations Environment Program, 2020). Maintaining what biodiversity we do have left through actions like preserving critical habitat for endangered species and restoring the keystone species that once helped to maintain that habitat can form a key component in halting the loss of worldwide biodiversity (Menz et al., 2013; Maehr et al., 2001). There are many examples of such restorations occurring around in North America, with the reintroduction of ecosystem engineers like beavers, grey wolves, and plains bison (Truett et al., 2001; Wilmers et al., 2003; Hood & Bayley, 2008). These species provide benefits to the environments they inhabit far beyond their just being present within them and can greatly enhance areas that they're restored to (Truett et al., 2001; Wilmers et al., 2003; Hood & Bayley, 2008).

Plains bison (*Bison bison bison*) were once widespread across North America, with a range that extended as far west as the American Rockies to modern-day Washington D.C. (COSEWIC, 2013). The overhunting of the plains bison in the 18th and 19th century to feed the demands of both the fur trade and burgeoning settler population, as well as deliberate extermination by governments to disempower Indigenous Nations, led to a nearly complete extirpation across their former range, with numbers dropping potentially as low as 88 animals across the entirety of North America in 1888 (COSEWIC, 2013; Kolipinski et al., 2014; Taschereau, 2020). Conservation efforts in the late 19th century helped to conserve the species from a population of about one thousand, and in the last one hundred years land managers have changed focus from simply preserving the species to reintroducing plains bison across North America (Hornaday, 1889; Kolipinski et al., 2014). The Banff National Park plains bison reintroduction is a recent and unique example of these efforts as it is a reintroduction of plains bison into a subalpine environment on the edge of the species' range as it existed three hundred years ago (Skinner & Kaisen, 1947).

The Committee on the Status of Endangered Wildlife In Canada has assessed plains bison as Threatened in Canada, though the species is not listed under the Species at Risk Act (COSEWIC, 2013). Plains bison are important symbols of plains First Nations and Métis culture and restoring the species has great symbolic and practical value for Nations looking to assert their rights to their lands (Kolipinski et al., 2014). Bison conservationists helped to preserve the species through breeding programs and protected areas in the 20th century, and there are now calls to increase the number of herds and the areas in which they roam (Buffalo Treaty, 2014; Duckett, 2022). Bison have become such an important symbol of successful conservation that they were made the national mammal of the United States of America in 2016 (National Park Service, 2017).

Many plains bison herds today are typically small, managed on small (< 10000 acres) areas and are unable to roam freely (Aune et al., 2017). Bison that are raised for meat production are not subject to natural selection, and their conservation value has been questioned (Aune et al., 2017). This is of particular concern when we consider that roughly ninety five percent of the current plains bison population exists in herds raised for meat production (Boyd & Gates, 2006). Gross and Wang (2005) found that an effective population size of 1000 plains bison was needed in a herd to have the best odds of maintaining genetic variation in the long term. Herds will benefit from containing more than one thousand individuals, as an effective population size estimate does not account for factors like uneven sex ratios or variation in reproductive success (Caballero, 1994).

Large ($N$> 1000) herds present on large landscapes (> 10000 acres) subject to natural selection are of high conservation value, as these characteristics more closely resemble the conditions that plains bison would have historically been subjected to (Aune et al., 2017). As of 2017 there were only two plains bison conservation herds with populations greater than one thousand individuals (Aune et al., 2017).

Because plains bison modify the environments that they exist within through grazing, the effects of a reintroduction into an ecosystem should be carefully monitored (Nickell et al., 2018). Understanding these effects may provide benefits for future reintroductions of other large herbivores into montane environments (Steenweg et al., 2016). The impacts of plains bison are not homogenous in distribution and bison choice for where they will spend time on the landscape by abiotic factors like the fire history, slope of the landscape or the distance of a grazing patch to the nearest water source, as well as biotic factors such as interactions with other grazing species (Allred et al., 2011; Pearson et al., 1995). Understanding where and how plains bison choose to use the landscape can have important implications. For example, changes to vegetation structure from cattle grazing at different intensities has been shown to impact bird species that are habitat dependent on vegetation structures (Davis et al., 2019).

Bird populations are sensitive to changes in the ecosystems they inhabit (Gregory & Van Strien, 2010). Two examples of these within Banff National Park are the Olive-sided Flycatcher (*Contopus cooperi*) and the Common Nighthawk (*Chordeiles minor*), both of which are listed as at-risk species (COSEWIC, 2018; Environment Canada, 2016). A mix of closed-canopy forests and disturbed, open patches within those forests form critical habitat for both species (COSEWIC, 2018; Environment Canada, 2016). Habitat loss due to a lack of natural disturbance on the landscape has been noted as a threat for both species and restoring historical disturbance regimes will form part of their successful recovery in the future (COSEWIC, 2018; Environment Canada, 2016).

Whitehorn et al. (2013) noted that dry forests in the Northern Rockies region are expected to expand to higher elevations because of climate change, reducing habitat for bird species dependent on open habitats. Plains bison were known to have historically ‘held back’ aspen forests in conjunction with disturbances like fire in the parkland region of Alberta by consuming sapling shoots and through usage intensity like trampling, horning trees, and wallowing (Campbell et al., 1994). The presence of large herds of bison, along with the restoration of the fire regime to the landscape, may help to mitigate forest expansion in the Rockies and maintain a heterogenous mix of open, disturbed habitats alongside old growth, closed canopy ones. In January of 2017 Parks Canada introduced a herd of 16 plains bison into

Banff National Park to, in part, help restore these processes that had been absent from the landscape since bison were extirpated in the 19th century. These plains bison were introduced from the prairie pothole ecoregion of Elk Island National Park and there are questions as to how they will adapt to a more mountainous environment (cite elk island). For example, what parts of the landscape will be used most often by bison and how might creatures sensitive to disturbance, such as songbirds, respond to the presence of these large ecosystem engineers?

## Reintroduction Area

### *Climate and Vegetation*

The plains bison reintroduction area is a 1200 km$^2$ region located in the Northeast section of Banff National Park, Improvement District Number Nine, Alberta, Canada (Banff National Park, 2020a). It is centred around the Panther and Dormer River Valleys and extends from 51° 44' 39.84" N, 115° 55' 46.56" W to 51° 21' 10.08" N 115° 33' 32.04" (Banff National Park, 2020a). The reintroduction area is located entirely within the subalpine and alpine ecoregions of the park, which range from dense forests at low elevations to barren rock and ice as elevation increases (Banff National Park, 2020b). Banff National Park is classified as a continental, no dry season, regular subarctic climate (Dfc) under the Koppen classification system and its vegetative communities are influenced by cool summers, cold winters, and an arid 472.3 mm of precipitation per year (Peel et al., 2007, Environment Canada, 2020).

The subalpine ecoregion, which starts between 1300 - 2300 meters in elevation, can be subdivided into the lower and upper subalpine (Alberta Parks, 2014). Both ecoregions contain isolated stands of Subalpine Fir and Engelmann Spruce trees in between open meadows (Gadd, 2009). Trees are shorter and the tree stands sparser as elevation increases through the upper subalpine until the treeline is reached, past where no trees can grow, and marking the start of the alpine ecoregion (Gadd, 2009). The forested stands in the subalpine have slowly been expanding in the last century as open meadows are encroached upon by woody vegetation (Stockdale et al., 2019). The absence of grazing by bison and other large ungulates, as well as fire control efforts over the preceding century largely explain these changes (Kay & White, 2001). Miller & Halpbern (1998), for instance, found that the effect of grazing on reducing tree establishment in the subalpine was only significant at high grazing intensities. It follows that the loss of large herbivores and increasing fire control efforts in the last century has promoted the expansion of woody vegetation in this ecoregion (Miller & Halpbern, 1998; Coogan et al., 2021). Subalpine ecosystems are sensitive to smaller-scale disturbance, and so when keystone species like bison are reintroduced, they may produce strong local changes in areas in which they roam. (King & Brewster, 1978).

The alpine ecoregion is the land above the treeline which starts between 1900 - 3650 meters and ranges from open meadows at lower elevations to rock and ice at higher elevations (Alberta Parks, 2014; Gadd, 2009). Vegetation in the alpine has been shown to be highly nutritious and forms an important part of the summer diet in ungulates like bighorn sheep (Johnston et al., 1968). Alpine plants grow rapidly to maximise the short growing season, with grasses forming a more nutritious early summer food source in June, and sedges and dicots forming a more nutritious late summer food source in July and August (Chapin et al., 1975). Morgantini & Hudson (1989) found that migratory elk herds living on the Eastern Rockies of Alberta would migrate seasonally to alpine areas that contained this more nutritious forage. More specifically, in the Panther and Red Deer River drainages of Banff National Park these migratory patterns were reflected in the movements of several elk herds (Morgantini, 1988). While it is important to note that not all elk were migratory, and that the movements of those that were may have been motivated by other factors, the nutritional value of those alpine plants may still act as motivation for ungulate herds to climb into the alpine (Morgantini, 1988). In Montana, bison herds were found to exhibit a similar migratory pattern, moving to the upper slopes of the mountain environment in the summer and the valley bottoms in the winter (Van Vuren, 2001). If herds do make the climb, there is a small window to consume these plants and thus competition to access these areas may be high between extant and reintroduced ungulates, as prior work has demonstrated moderate overlap in bison and elk diets and high overlap in bison and Dall sheep diets (Jung et al., 2015).

## *Fire Regime*

Most North American ecosystems, including those in grasslands and mountains, evolved with fire as a natural part of their ecology (Wright & Bailey, 1982). With the arrival of humans in the Banff area roughly 13,000 years ago, the fire regime was maintained and augmented by Indigenous peoples, who regularly set fires that helped to maintain a more heterogeneous patchwork of ecosystems in mountain landscapes (Anderson & Barbour, 2003; Landals, 2008). Part of the motivation for Indigenous burning also extended to hunting opportunities as herbivores like plains bison, elk, and deer would be attracted to the nutritious and rapidly regrowing plants (Arthur, 1974; Hind, 1971: Vol. 2-107). Decades of fire control by European settlers across the continent have led to dense forests expanding across the landscape that are at greater risk of disease and catastrophic fires (Wright & Bailey; 1982, Steel et al., 2015).

The subalpine ecoregions of the Eastern Slope Rocky Mountains have been governed by a 90-year fire cycle since a shift into a warmer and wetter climate occurred circa 1730 (Johnson & Larsen, 1991; Rogeau & Armstrong, 2017; Coogan et al., 2021). These cycles can vary in different regions of the Rockies, however, as fire return intervals are also influenced by factors like elevation and slope aspect, with lower elevations and warmer southern and eastern facing slopes typically experiencing shorter fire return intervals (Rogeau & Armstrong, 2017). Studies on fire in grassland regions have reported that fires occurred less often on slopes and led to increasing forest coverage when compared to lower elevations/gradients (Collins & Calabrese, 2012). Though it has been suggested that slopes above valleys with a higher burning potential may share that potential due to the tendency of fire to spread upslope (Kay et al., 1999). Knowing where, when, and how intensely a fire burns in a region is an important part of understanding plant community dynamics and, likewise, how forage availability may differ following a burn (Busby, 2020). Previous work has shown that woody vegetation decreased, herbaceous plants increased, and forage available to elk herds in Banff National Park was significantly higher following prescribed burns (Sachro et al, 2005).

Stahelin (1943) found that it typically took between 50 and 100 years for a subalpine forest to recover to a pre-disturbance state after a fire. However, he also noted that this would occur only under certain conditions where enough seeds from the original stands survived the fire, and that regeneration to communities more resembling aspen parkland or grassland ecosystems were also possible over similar time scales (Stahelin, 1943). Reed et al. (1999) reported that nine years after a fire, the net primary productivity and leaf area index of younger, recovering lodgepole pine stands in Yellowstone National Park had reached levels nearly equivalent to what they were prior to the burn, and thus some vegetation types within an ecosystem may recover more rapidly than others. In the boreal forests and taiga of the Northern Prairies and Northwest Territories, similar studies of net primary productivity have shown recovery times of about 15-20 years following a fire (Amiro et al., 2000). It follows that in an ecosystem as sensitive to local change as the subalpine, it is of critical importance to understand how ecosystems recover from fire and how they may interact with other disturbances like those caused by bison to influence their post-recovery stable state (King & Brewster, 1978; Collins & Calabrese, 2012).

For instance, old forests tend to have dense canopies that reduce the ability of understory to grow due to lower amounts of solar radiation penetrating through the trees above (Simonson et al., 2014; De Grandpré et al., 2000). Disturbances from forces like fire or bison open these canopies and allow for vigorous short-term regrowth of the understory, creating habitat for species that would not have inhabited those spaces before (Simonson et al., 2014; De Grandpré et al., 2000). Fire itself may be critical in allowing bison to consume plants in very densely vegetated areas as a study by Tarleton & Lamb (2020) found bison in Riding Mountain National Park were reluctant to enter areas with tall, dense shrubs if those areas had not been burned. This opening up of these spaces leads grazers like bison to return to those burned patches to consume this regrowth, often consuming or trampling young trees and preventing the forest from re-establishing itself and creating more open patches of land (Miller & Halpbern (1998); (Kay & White, 2001).

Many of the subalpine forests in Banff National Park have historically been a part of a 90 to 100-year fire cycle that was characterized by several shorter, low-intensity burns set by Indigenous peoples to encourage good grazing for game species in addition to less frequent lightning-sparked fires (Parks Canada, 2021). The region within which the bison herd is located has been identified as an area for "extensive" fire management, where fires will be managed for ecological benefits due to the low visitation this section of the park receives (Parks Canada, 2021).

## Plains Bison Conservation

Plains bison are perhaps one of the most iconic and enduring examples of conservation in North America. For many Indigenous Nations, plains bison form part of the understanding of how the world was formed, with teachings across many Indigenous cultures of humanity being descendants of the bison and that bison were the only reason humans were able to sustain themselves and survive (Zontek, 2007). Indigenous oral histories often reflect the archaeological record and provide insight into how significant and ancient the relationship of these Nations is with the bison (Zontek, 2007). As this relationship grew, so too did Indigenous understandings of bison ecology, how they impacted the plants and animals that existed around them, and how to sustainably harvest the species (Zontek, 2007). A perspective shared widely throughout the Blackfoot Nation is that of the plains bison being a non-human relation, and that people would return the gift of being able to harvest the animals for their meat through reciprocal actions like deliberate burning of fields to create higher quality forage (Oetelaar, 2014). This relationship began to be challenged with the beginning of the fur trade, as Eurocentric perspectives on bison as resources for profit and distinct from humans were introduced to Indigenous communities (Oetelaar, 2014).

Plains bison were first recorded by Europeans in the late 1500s, with later explorers in the early 1800s reporting herds of tens of thousands of animals roaming across the great plains (Hornaday, 1889, Ambrose, 2003). Pre-European contact estimates of the population of plains bison in North America range from thirty million to as many as one hundred million and this number is estimated to have declined to the low millions following the end of the American Civil War (Shaw, 1995; Barrett & Markowitz, 2004). This decline was spurred on by the introduction of the horse to the great plains in the 1700s as Indigenous hunters became more efficient, allowing Indigenous Nations to expand both their populations and their ability to trade with Europeans (Cunfer & Weiser, 2016). Pressure on plains bison populations only increased through the 19th century as demand from settlers and the fur trade industry increased (Taschereau, 2020). In a final effort to disempower the Indigenous peoples of the plains, understanding both the importance of plains bison to their way of life and the tremendous decline bison populations were experiencing, colonial governments heavily incentivized white hunters to kill as many plains bison as possible, with estimates of three thousand hides per day taken between 1872 and 1874 in the US alone (Hämäläinen, 2019).

In the early 1870s, a small herd of bison was conserved by two men of the Pend d'Orielle Nation, Atatitsa and Latatitsa, who worked alongside Salish First Nations to maintain the species after noticing the population decline over decades of hunting in the Eastern Rockies (Tascherau, 2020). The land the herd was kept on was seized and broken up by the US government in 1904, and the herd's caretakers sought out a new home for the plains bison (Tascherau, 2020). The herd was purchased by the Canadian government and brought from their reservation in Montana and into Elk Island National Park in an act heavily motivated by a growing desire to conserve what few bison were left (Tascherau, 2020). However, bringing the herd under government control recontextualized the plains bison from Indigenous into Eurocentric ideas of conservation (Zontek, 2007). The Elk Island herd grew over the following decades and soon the Canadian government began to transfer plains bison out of the park and into other conservation areas, including the transfer of sixteen plains bison into Banff National Park in 2017 (Zontek, 2007; Tascherau, 2020).

Modern day bison conservation is often carried out in a partnership between governments and Indigenous nations, and the species is also cultivated by ranch owners, though bison raised by ranchers are not subject to the forces of natural selection as they are on conservation land (Aune et al., 2017; Zontek, 2007). Despite this, the area in North America in which plains bison exist today is less than 1 percent of what it was at its maximum extent, highlighting the needs not only to continue to conserve the species, but also to expand their current range through reintroduction projects (Sanderson et al., 2008). Currently, the priority for plains bison conservation is to establish herds with populations above one thousand that can roam without borders on large parcels of land (Aune et al., 2017). Providing the ability for a large herd of plains bison to roam unrestricted over a landscape of 1200 $km^2$ in a mountain environment will be a key step in achieving that goal (Parks Canada, 2013). Plains bison represent a species that is ecologically, symbolically, and economically important for settlers, and one that is intricately tied to identity, history, and healing for Indigenous peoples (Kolipinski et al., 2014; Haggerty et al, 2018). Working to restore the species to large parts of its former range where they may roam unhindered is not merely of ecological interest to Banff National Park, but also speaks to the historical and cultural ties of those who have lived and continue to live within its borders (Kolipinski et al., 2014; Parks Canada, 2013).

## Research Context

The 2010 Banff National Park Management Plan called for an assessment of the feasibility of reintroducing plains bison to the park as a long-term conservation goal (Parks Canada, 2010). Indigenous oral histories as well as archaeological evidence tell us that plains bison were present in the park for at least part of the year and likely would have greatly impacted the ecosystems around them (Kay & White, 2001). Restoring the species to the park would bring back an animal of great cultural, historical, and biological significance to Banff. Preliminary work included development of a habitat suitability index that identified a potential 1200 $km^2$ reintroduction area within the park borders (Steenweg et al., 2016). The reintroduction process has not been performed strictly through a purely western scientific approach; rather, it has benefited from the knowledge and experience of Indigenous leaders who continue to be instrumental in ensuring the project's success (Taschereau, 2020).

In January 2017, Banff National Park began a 5-year pilot project to assess the viability of a plains bison herd within the reintroduction area (Heuer, 2019). Elders from Treaty 6 and Treaty 7 Nations held a communal ceremony to prepare the bison for their journey into their new home (Taschereau, 2020). Following the ceremony, sixteen plains bison were brought from Elk Island National Park and placed into a holding pasture in the Panther-Dormer valley (Heuer, 2019). In July 2018, the pasture was opened, and the herd was released into the reintroduction area, and as of 2022 are free roaming with a population of 88 (Heuer, 2019; Ellis, 2022). A hazing zone was established around the reintroduction area to act as a buffer for plains bison to be turned around should they roam too close to unprotected provincial lands or less suitable areas of the park (Heuer, 2019). This zone is defined by a set of wildlife fences that stretch across the mountain valleys and rivers at the borders of the reintroduction zone (Laskin et al., 2020). These fences are frequently checked by Parks staff for any damage and can be reconfigured to allow for easier transit for other wildlife when the herd is far away from the fence itself (Laskin et al., 2020). The pilot project concluded in 2022, showing that Banff National Park was a landscape within which bison could successfully exist and recommended that bison continue to remain on the landscape under the close monitoring of park staff (Banff National Park, 2022).

The report on the plains bison reintroduction noted that the herd experienced a 33% growth rate per year with a natural mortality rate below 1% per year and that even at a more conservative 20% growth rate the bison herd would reach more than two hundred animals within the next 8 years (Banff National Park, 2022). This growth rate and the potential to sustain large numbers of animals on the landscape is not unprecedented as Steenweg et al. (2016) predicted that the reintroduction zone could support between 600 and 1000 plains. With so many animals potentially occupying the landscape in the years to come it is important to build an understanding of what drives bison to spend time on different parts of the landscape and predict how they might modify those places they use most frequently and manage bison so that they enhance and restore habitats and provide ecological benefits for other species.

As part of the reintroduction’s ongoing ecological monitoring component, songbird populations within the reintroduction area were sampled for three years prior to the reintroduction and sampling is ongoing (Heuer, 2019). Assessing the impacts of the bison reintroduction on other species as well as on abiotic factors such as stream quality were also tracked as part of the five-year pilot project (Heuer, 2019)

My research first investigated whether a patch was burned, how frequently that patch was burned, slope steepness, distance to water, and ecosystem type would affect resource selection by the Banff bison herd. My research also continued the bird monitoring program started by Parks Canada for the pilot project (Heuer, 2019) and built upon it by assessing how vegetation structure, and vegetation composition may influence the total abundance and diversity of bird populations at different usage intensities.

## Research Purpose

The purpose of this research was to develop an understanding of what factors influence plains bison resource selection and how different usage intensities from that selection impacts the total abundance and diversity of bird species through changes to vegetation structure. This research helped to provide managers in Banff National Park and in other jurisdictions insight as to what factors influence plains bison to select for some parts of the landscape over others, and what the effects the plains bison are having on bird and vegetation communities within sites they use at varying intensities.

## Research Objectives

1. Determine how slope, fire history, habitat type and distance to the nearest waterbody influence plains bison resource selection.
2. Determine whether increasing levels of bison usage influence vegetation structure, vegetation composition, and bird communities dependent on that vegetation structure.

## Research Predictions

I predict that bison will show a preference for habitats that have been burned, that they will not be limited by slope and distance to water, and that they will show a preference for grasslands and shrublands over forests. I also predict that increasing bison usage will be associated with a decline in understory height, vegetation density, and grass coverage and be associated with an increase in the percent coverage of forbs and non-vegetated material.

## Literature Cited

Alberta Parks. (2014). *Natural Regions & Subregions of Alberta: A Framework for Alberta's Parks.* https://www.albertaparks.ca/media/6256258/natural-regions-subregions-of-alberta-a-framework-for-albertas-parks-booklet.pdf

Allred, B. W., Fuhlendorf, S. D., & Hamilton R. G. (2011). The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. *Ecosphere*, *2*(3), 26–17. https://doi.org/10.1890/ES10-00152.1

Ambrose, S. T., (2003). *The Lewis and Clark Companion.* Henry Holt & Co.
Amiro, B. D., Chen, J. M., & Liu, J. Net primary productivity following forest fire for Canadian ecoregions. *Canadian Journal of Forest Research. 30*(6): 939-947. https://doi-org.uml.idm.oclc.org/10.1139/x00-025

Anderson, M. K., & Barbour, M. G. (2003). Simulated indigenous management: A new model for ecological restoration in National Parks. *Ecological Restoration*, *21*, 269–277. https://doi-org.uml.idm.oclc.org/10.3368/er.21.4.269

Arthur, G. (1974). *Introduction to the Ecology of Early Historic Communal Bison Hunting Among the Northern Plains Indians.* University of Ottawa Press. https://doi-org.uml.idm.oclc.org/10.2307/j.ctv16qcg

Aune, K., Jørgensen, D. & Gates, C. (2017). *Bison bison* (errata version published in 2018). *The IUCN Red List of Threatened Species 2017*: e.T2815A123789863. https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T2815A45156541.en.

Banff National Park. (2022) *Report on the Plains Bison Reintroduction Pilot, 2017 - 2022.* https://parks.canada.ca/pn-np/ab/banff/info/gestion-management/bison/rapport-reintroduction-report

Banff National Park. (2020, October 16). *Ecosystems and Habitat*. Banff National Park Webpage. https://www.pc.gc.ca/en/pn-np/ab/banff/nature/environnement-environment/ecosystemes-ecosystems

Banff National Park. (2020, September 16). *Frequently Asked Questions (Where is the Reintroduction Zone?)*. Banff Bison Blog. https://www.pc.gc.ca/en/pn-np/ab/banff/info/gestion-management/bison/faq

Barrett, C. A., Markowitz, H., (2004) Resource Use: Pre-contact. *American Indian Culture*, *2*, 611–614.

Boyd, D. P., & Gates, C. C. (2006). A brief review of the status of plains bison in North America. *Journal of the West*, *45*(2), 15 - 21. https://www.buffalofieldcampaign.org/legal/esacitations/boydreviewstatus.pdf

Buffalo Treaty. (September 24, 2014). *Buffalo Treaty*. The Buffalo: A Treaty Of Cooperation, Renewal and Restoration. https://www.buffalotreaty.com/treaty

Busby, S. U., Moffett, K. B., & Holz, A. (2020). High-severity and short-interval wildfires limit forest recovery in the Central Cascade Range. *Ecosphere*, *11*(9). https://doi.org/10.1002/ecs2.3247

Caballero, A. (1994). Developments in the prediction of effective population size. *Heredity 73*, 657–679. https://doi.org/10.1038/hdy.1994.174

Campbell, C. I., Campbell, C. B., & McAndrews, J. (1994). Bison extirpation may have caused aspen expansion in western Canada. *Ecography 17*, 360-362. https://doi.org/10.1111/j.1600-0587.1994.tb00113.x

Chapin, F. S., Van Cleve, K., & Tieszen, L. L. (1975). Seasonal Nutrient Dynamics of Tundra Vegetation at Barrow, Alaska. *Arctic and Alpine Research*, *7*(3), 209-226, 10.1080/00040851.1975.12003828

Collins, S., & Calabrese, L. (2012). Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *Journal of Vegetation Science*, *23*(3), 563-575.

http://www.jstor.org/stable/23251087

Coogan, S. C. ., Daniels, L. D., Boychuk, D., Burton, P. J., Flannigan, M. D., Gauthier, S., Kafka, V., Park, J. S., & Wotton, B. M. (2021). Fifty years of wildland fire science in Canada. *Canadian Journal of Forest Research*, *51*(2), 283–302. https://doi.org/10.1139/cjfr-2020-0314

COSEWIC. (2013). COSEWIC assessment and status report on the Plains Bison Bison bison bison and the Wood Bison Bison bison athabascae in Canada. *Committee on the Status of Endangered Wildlife in Canada*. Ottawa. xv + 109 pp. (www.registrelep-sararegistry.gc.ca/default_e.cfm).

COSEWIC. (2018). COSEWIC assessment and status report on the Olive-sided Flycatcher Contopus cooperi in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. ix + 52 pp. (http://www.registrelep-sararegistry.gc.ca/default.asp?lang=en&n=24F7211B-1).

Cunfer, G., Weiser, B. (2016). *Bison and People on the North American Great Plains: A Deep Environmental History*. Texas A&M University Press.

Davis, K. P., Augustine, D. J., Monroe, A. P., Derner, J. D., & Aldridge, C. L., (2020). Adaptive rangeland management benefits grassland birds utilizing opposing vegetation structure in the shortgrass steppe. *Ecological Applications 30*(1) :e02020. 10.1002/eap.2020

De Grandpré, L., Morissette, J. and Gauthier, S. (2000). Long-term post-fire changes in the northeastern boreal forest of Quebec. *Journal of Vegetation Science, 11*: 791-800. https://doi-org.uml.idm.oclc.org/10.2307/3236549

Duckett, M. (2022, October 3). Bison returning to the Prairies. *Yellowstone to Yukon Initiative.* https://y2y.net/blog/bison-returning-to-the-prairies/

Ellis, C. (2022, August 26). *Sixteen bison calves born to Banff herd this year.* Rocky Mountain Outlook. https://www.rmotoday.com/banff/sixteen-bison-calves-born-to-banff-herd-this-year-5724640

Environment Canada. (2016). Recovery Strategy for the Olive-sided Flycatcher (Contopus cooperi) in Canada. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa. vii + 52 pp.

Environment Canada. (2020, September 17). *Canadian Climate Normals 1971-2000 Station Data (Banff, Alberta).* https://climate.weather.gc.ca/climate_normals/results_e.html?searchType=stnProv&lstProvince=AB&txtCentralLatMin=0&txtCentralLatSec=0&txtCentralLongMin=0&txtCentralLongSec=0&stnID=2364&dispBack=0

Gadd, B. (2009). *Handbook of the Canadian Rockies (2nd ed.)* Corax Press.

Gregory, R.D., & Van Strien, A. (2010). Wild Bird Indicators: Using Composite Population Trends of Birds as Measures of Environmental Health. *Ornithological Science, 9*(1), 3-22. https://doi.org/10.2326/osj.9.3

Gross, J. E., & Wang, G. (2005). *Effects of population control strategies on retention of genetic diversity in National Park Service bison (Bison bison) herds.* United State Geological Survey.

Haggerty, J., Rink, E., McAnally, R., & Bird, E. (2018). Restoration and the Affective Ecologies of Healing: Buffalo and the Fort Peck Tribes. *Conservation and Society, 16*(1), 21-29. doi: 10.4103/cs.cs_16_90

Hämäläinen, P. (2019). *Lakota America*. Yale University Press

Heuer, K. (2019). *Plains bison reintroduction in Banff National Park pilot project 2017-2022: 2018 progress report.* Parks Canada. http://www.publications.gc.ca/site/eng/9.891745/publication.html

Hind, H.Y. (1971) *Narrative of the Canadian Red River exploring expedition of 1857 and the Assiniboine and Saskatchewan exploring expeditions of 1858* (Reprint of 1860 ed., Vol. 2). Charles E. Turtle Co.

Hornaday, W. (1889). *The extermination of the American bison: with a sketch of its discovery and life history*. U.S. Government Printing Office.

Johnson, T. N., Kennedy, P. L., DelCurto, T., & Taylor, R. V. (2011). Bird community responses to cattle stocking rates in a Pacific Northwest bunchgrass prairie. *Agriculture, Ecosystems & Environment, 144*(1), 338–346. https://doi.org/10.1016/j.agee.2011.10.003

Johnson, E. A., & Larsen, C. P. S. (1991). Climatically Induced Change in Fire Frequency in the Southern Canadian Rockies. *Ecology, 72*(1), 194–201. https://doi.org/10.2307/1938914

Jung, T., Stotyn, S., & Czetwertynski, S. (2015). Dietary Overlap and Potential Competition in a Dynamic Ungulate Community in Northwestern Canada. *The Journal of Wildlife Management, 79*(8), 1277-1285. http://www.jstor.org/stable/24764386

Kay, C. E., White, C., & Patton, B. (1999). *Long-term ecosystem states and processes in Banff National Park and the central Canadian Rockies* (Occasional Paper). Banff National Park, Resource Conservation.

Kay, C. E., & White, C. A. (2001). Reintroduction of bison into the Rocky Mountain parks of Canada: historical and archaeological evidence. *Crossing Boundaries in Park Management*, 143-151.

King, R., & Brewster, G. (1978). The Impact of Environmental Stress on Subalpine Pedogenesis, Banff National Park, Alberta, Canada. *Arctic and Alpine Research, 10*(2), 295-312. doi:10.2307/1550762

Kolipinski, M., Borish, S., Scott, A., Kozlowski, K., & Ghosh, S. (2014). Bison: Yesterday, Today, and Tomorrow. *Natural Areas Journal*, *34*(3), 365-375. http://www.jstor.org/stable/43914546

Landals, A. (2008). *The Lake Minnewanka Site: Patterns in Late Pleistocene Use of the Alberta Rocky Mountains* [Doctoral dissertation, University of Calgary]. PRISM.

Laskin, D. N., Watt, D., Whittington, J., & Heuer, K. (2020). Designing a fence that enables free passage of wildlife while containing reintroduced bison: a multispecies evaluation. *Wildlife Biology, 2020*(4), 1-14. https://doi.org/10.2981/wlb.00751

Lott, D. F. (2002). *American Bison: A Natural History*. University of California Press.

Maehr, D., Noss, R., Larkin, J., & Sunquist, M. (2001). Large Mammal Restoration: Ecological And Sociological Challenges In The 21St Century. Island Press.

Menz, M. H., Dixon, K. W., & Hobbs., R. J. (2013). Hurdles and Opportunities for Landscape-Scale Restoration. *Science (American Association for the Advancement of Science)*, *339*(6119), 526–527. https://doi.org/10.1126/science.1228334

Miller, E. A., & Halpern, C. B. (1998). Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. *Journal of Vegetation Science*, *9*(2), 265-282.

Morgantini, L. (1988). Behavioural adaptive strategies of wapiti (Cervus elaphus) in the Canadian Rocky Mountains [Doctoral dissertation, University of Alberta]. Education & Research Archive.\

Morgantini, L., & Hudson, R. (1989). Nutritional Significance of Wapiti (Cervus elaphus) Migrations to Alpine Ranges in Western Alberta, Canada. *Arctic and Alpine Research*, *21*(3), 288-295. doi:10.2307/1551568

National Park Service. (2017, November 2). *Bison Bellows: America's New National Mammal.* National Park Service Website. https://www.nps.gov/articles/bison-bellows-5-12-16.htm#:~:text=Afterpercent20fourpercent20yearspercent20ofpercent20outreach,makingpercent20thepercent20bisonpercent20ourpercent20national

Nickell, Z., Varriano, S., Plemmons, E., & Moran, M. D. (2018). Ecosystem engineering by bison (Bison bison) wallowing increases arthropod community heterogeneity in space and time. *Ecosphere, 9*(9) e02436. https://doi.org/10.1002/ecs2.2436

Oetelaar, G. A. (2014). Worldviews and human–animal relations: Critical perspectives on bison–human relations among the Euro-Canadians and Blackfoot. *Critique of Anthropology, 34*(1), 94–112. https://doi.org/10.1177/0308275X13510187

Parks Canada. (2021). *Fire management plan 2020: Banff, Yoho, and Kootenay National Parks.* https://publications.gc.ca/collections/collection_2021/pc/R64-586-2020-eng.pdf

Parks Canada. (2013). *PLAN FOR REINTRODUCTION OF PLAINS BISON IN BANFF NATIONAL PARK.* http://www.parkscanadahistory.com/publications/banff/plains-bison-reintro-e-2013.pdf

Parks Canada. (2010). *Banff National Park Management Plan*. https://www.pc.gc.ca/en/pn-np/ab/banff/info/gestion-management

Pearson, S. M., Turner, M. G., Wallace, L. L., & Romme, W. H. (1995). Winter Habitat Use by Large Ungulates Following Fire in Northern Yellowstone National Park. *Ecological Applications, 5*(3), 744–755. https://doi.org/10.2307/1941982

Peel, M., Finlayson, B., Mcmahon, T. (2007). Updated World Map of the Koppen-Geiger Climate Classification. *Hydrology and Earth System Sciences Discussions. 4*. 10.5194/hess-11-1633-2007.

Powell, A. (2006). Effects Of Prescribed Burns And Bison (BOS BISON) Grazing On Breeding Bird Abundances In Tallgrass Prairie. *The Auk, 123*(1), 183–197. https://doi.org/10.1642/0004-8038(2006)123[0183:EOPBAB]2.0.CO;2

Reed, R. A., Finley, M. E., Romme, W. H., Turner, M.G. (1999) Aboveground net primary production and leaf area index in early postfire vegetation in Yellowstone National Park. *Ecosystems*, *2*, 88–94. Doi: 10.1007/s100219900061

Rogeau, M. P., & Armstrong, G. W. (2017). Quantifying the effect of elevation and aspect on fire return intervals in the Canadian Rocky Mountains. *Forest Ecology and Management*, *384*, 248–261. https://doi.org/10.1016/j.foreco.2016.10.035

Sachro, L. L., Strong, W. L., & Gates, C. C. (2005). Prescribed burning effects on summer elk forage availability in the subalpine zone, Banff National Park, Canada. *Journal of Environmental Management*, *77*(3), 183-193.

Sanderson, E.W., Redforda, K. H., Weber, B., Aune, K., Baldes, D., Berger J., Carter, D., Curtin, C., Derr, J., Dobrott, S., Fearn, E., Fleener, C., Forrest, S., Gerlach, C., Gates, C.C., Gross, J.E., Gogan, P., Grassel, S., Hilty, J. A., Jensen, M., Kunkel, K., Lammers, D., List, R., Minkowski, K., Olson, T., Pague, C., Robertson, P. B., Stephenson, B. (2008). The ecological future of the north American Bison: Conceiving long-term, large-scale conservation of wildlife. *Conservation Biology*, *22*, 252–266. doi: 10.1111/j.1523-1739.2008.00899.x

Simonson, Allen, H. D., & Coomes, D. A. (2014). Overstorey and topographic effects on understories:

Evidence for linkage from cork oak (*Quercus suber*) forests in southern Spain. *Forest Ecology and Management, 328*, 35–44. https://doi.org/10.1016/j.foreco.2014.05.009

Skinner, M. F. & Kaisen, O. C. (1947). The Fossil Bison of Alaska and Preliminary Revision of the Genus. *Bulletin of the American Museum of Natural History, 89*, 127–256.

Stahelin, R. (1943), Factors Influencing the Natural Restocking of High Altitude Burns by Coniferous Trees in the Central Rocky Mountains. *Ecology, 24*, 19-30. https://doi.org/10.2307/1929857

Steel, Z. L., Safford, H. D., & Viers, J. H. (2015). The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere, 6*, 1–23. https://doi-org.uml.idm.oclc.org/10.1890/ES14-00224.1

Steenweg, R., Hebblewhite, M., Gummer, D., Low, B., & Hunt, B. (2016). Assessing Potential Habitat and Carrying Capacity for Reintroduction of Plains Bison (Bison bison bison) in Banff National Park. *PLoS ONE, 11*(2), 1–22. https://doi-org.uml.idm.oclc.org/10.1371/journal.pone.0150065

Stockdale, C.A., Macdonald, S.E., & Higgs, E. (2019). Forest closure and encroachment at the grassland interface: a century-scale analysis using oblique repeat photography. *Ecosphere, 10*(6). https://doi.org/10.1002/ecs2.2774

Sutherland, C. R. (2018). Remembering and Igniting Fires: Prescribed Burns as Memory Work. *RCC Perspectives*, *3*, 19–26. http://www.jstor.org/stable/26511169

Tarleton, P. & Lamb, E. G. (2020). Modification of Plant Communities by Bison in Riding Mountain National Park. *Écoscience (Sainte-Foy), 28*(1), 67–80. https://doi.org/10.1080/11956860.2020.1850622

Taschereau, M. D. (2020). “Last of the buffalo”: bison extermination, early conservation, and visual records of settler colonization in the North American west. *Settler Colonial Studies, 10*(1), 126–147. https://doi.org/10.1080/2201473X.2019.1677134

United Nations Environment Program. (2020) Global Biodiversity Outlook

5. https://www.cbd.int/gbo/gbo5/publication/gbo-5-en.pdf

White, C. (1985). Wildland Fire in Banff National Park, 1880 - 1980. *National Parks Branch: Occasional Paper No. 3.* https://www.researchgate.net/publication/306065367_White_C_A_Wildland_Fires_in_Banff_National_Park_1880-1980_National_Parks_Branch_Occasional_Paper_3_Ottawa_Parks_Canada_1985

Whitehorne, I., Alaine, C., Véronique, C., Newbury, A., Middleton, H., & Krebs, E. (2013). *Bird Conservation Strategy for Bird Conservation Region 10 Pacific and Yukon Region: Northern Rockies*. Environment Canada. https://www.canada.ca/en/environment-climate-change/services/migratory-bird-conservation/regions-strategies/description-region-10/pacific-yukon.html#_Toc355602851

Wright, H.A., Bailey, A.W. (1982). *Fire Ecology: United States and Southern Canada.* John Wiley and Sons, New York, NY. 978-0-471-09033-5

Van Vuren, D. H. (2001). Spatial relations of American bison Bison bison and domestic cattle in a montane environment. *Animal Biodiversity and Conservation, 24*(1).

Zontek, K. (2007). *Buffalo Nation: American Indian Efforts to Restore the Bison*. University of Nebraska Press.

# Chapter 2: Investigating how Fire, Landscape Type and Topography Influence Site Selection in a Reintroduced Plains Bison Population in Banff National Park

## Abstract

Plains bison and fire are the two major disturbances that governed the ecology of the Great Plains over the last 13000 years. These forces worked together to hold back forests and expand grasslands across the historical range of plains bison in North America, including the Canadian Rockies. The reintroduction of fire through Parks Canada's prescribed burning program and the reintroduction of plains bison to the ecosystem of Banff National Park offer an opportunity to see both disturbance regimes influence the landscape once more. Using GPS collar data obtained from thirteen members of the Banff bison herd, remote sensing and generalized estimating equations I examined how whether a patch was burned, how often it was burned, topography, and land classification affected resource selection by the reintroduced herd of plains bison in Banff National Park. Bison spent significantly more time in patches that had burned more than ten times since 1909, and patches that were in areas classified as a grassland or shrubland. Bison selected sites located within eight hundred meters of a waterbody and on slopes below 11°. Fire remains an important force for governing where and how bison will spend their time on the landscape and can create excellent grazing conditions for them. Continuing the prescribed fire program in the bison reintroduction zone will be critical in encouraging the bison to select for habitat in new areas and create a more heterogenous habitat across the landscape.

# Introduction

Over the last thirteen thousand years the Great Plains of North America have been governed by two forces: fire and disturbance by large ungulates (Axelrod, 1985). These forces created a diverse landscape which increased in biodiversity through changes to the structure and composition of plant communities (Fuhlendorf, 2009). Both fire and disturbances from animals like bison are necessary to help maintain a diverse and stable grassland ecosystem (Collins & Calabrese, 2012). Borman (2005) suggested that unregulated grazing paradoxically contributed to the conversion of Ponderosa Pine Grasslands to dense, homogenous stands across the Western United States as grazers reduced the fuel load of herbaceous plants in the understory of a forest, leading to less frequent fires. Karp et al. (2018) provided evidence that grassland expansion over the late Miocene was driven in large part by increased fire frequency and provided the conditions that grasslands, and the plants that make them up, evolved within. A long-term study by Koerner & Collins (2014) into the effects of fire, grazing and drought in grasslands in North America and South Africa found that fire and grazing were the most significant drivers of plant community composition and productivity.

Grazers can alter how deeply plants extend their roots into the soil to absorb water and can induce changes to plant communities at local scales (O'Keefe & Nippert, 2017). Frank & Evans (1997) noted that grazing by large ungulates increased nitrogen cycling rates within grasslands and helped to make more nitrogen available for plants in those ecosystems. Around the end of the Pleistocene period roughly twenty-five thousand years ago the ancestors of modern-day bison (*Bison antiquus* & *Bison occidentalis*) became some of the only species of large herbivores present in North America, with their descendants in the form of plains bison being the most dominant grazer in the Great Plains and eastern Rocky Mountains around the time of European contact with the plains three hundred years ago (Larson, 1940; Guthrie, 1970; Daubenmire, 1985; Anderson, 2006). Bison induced changes to the environments they grazed in through the direct consumption of plants and the deposition of phosphorus and nitrogen through their bodily waste (Frank & McNaughton, 1992). Plains bison had a significant impact on how the ecosystems on the Great Plains and Western Rockies functioned as herds preferentially grazed areas that had been recently burned, creating a more heterogeneous landscape (Babin et al., 2011; Knapp et al., 1999).

These patterns of site selection could also be influenced by fire, topography, or distance to water, further leading to increased habitat heterogeneity. Grazers like cattle have been found to preferably use low lying, flatter patches when compared to steeper, upland ones (Raynor et al., 2017). Flatter areas require less energy expenditure from grazers, leading to more efficient gains from grazing, however grazers may be willing to climb up steep topography if the forage at the top is of a very high nutritional value (Senft et al., 1987).

Kohl et al. (2011) reported that bison are not as limited by the distance to a water source as cattle are, with bison showing a willingness to move up to ten kilometres from a water source when compared to cattle which never moved further than three kilometres away from one. Bison have been shown to select for patches near permanent water bodies like lakes or large rivers that flow throughout the winter but are willing to move further away from water than cattle are (Kohl et al., 2011). Access to water may provide additional benefits to bison besides simply having access to an essential part of life. For instance, Wallis de Vries & Schippers (1994) found that water may be a significant source of essential minerals to cattle and other animals that made use of watering holes and rivers. Water is, however, not a critical part in cooling off bison in hot weather, as they typically do so by evaporating water from their lungs as they wallow and inhale dry, dusty air (Lott, 2002). The distribution of water itself has not been found to be limiting to bison, nor has the size of a particular river or lake been found to influence their selection of sites (Babin et al., 2011). The Banff bison are originally from Elk Island National Park, where there is only standing water, thus the year they spent learning to cross and interact with moving water in the holding paddock was a of critical importance and they do not appear to be limited by moving waterbodies within the reintroduction zone (Heuer, 2019).

Vinton et al. (1993) found that recent burning also influenced site selection by bison, with frequently burned areas containing much larger patches that had been grazed by bison (13.6 $m^2$) compared to those within infrequently burned areas (1.9 $m^2$).The relationship between bison and fire was well understood by Indigenous peoples who regularly set fire to grasslands to create good grazing grounds for bison (Sutherland, 2018; Hoffman, 2021). These burned patches would help to attract the bison to the new growth within those burned areas in the following year, increasing the odds that the people would be able to find and hunt the herd (Brink, 2008). This type of fire management also occurred within mountainous regions, with Indigenous people setting frequent, low intensity burns in valley bottoms to maintain travel routes, to foster culturally significant plants, to create good habitat for game, and for aesthetic reasons (White, 1985; Christianson, 2019; Lake & Christianson, 2020). This type of land management as well as the relationship between humans and bison began to change with the entrance of a new group of people into the Canadian Rockies.

The first Europeans to verifiably enter the Canadian Rockies were Hudson's Bay Company surveyor Peter Fidler's party in 1792 when they met with the Ktunaxa at the Gap of the Oldman River in the Livingstone Mountain Range of Southeastern Alberta (Gadd, 2009; Yanicki, 2014). This was soon followed up by the establishment of Rocky Mountain House in the foothills along the North Saskatchewan River by the North West Company in 1799 to support the growing fur trade with Indigenous peoples in the region (Parks Canada, 2022a). Eight years later, in 1807, North West Company fur trader David Thompson crossed the Continental Divide via the Howse Pass, establishing Kootenay House in modern-day British Columbia (Thompson, 1915; Gadd, 2009). European presence in the mountains in these early years was limited to the fur trade brigades travelling through the passes with trade goods or overwintering at their forts, though their presence was felt beyond their travel routes and into the surrounding Montane valleys and foothills as great numbers of plains bison were hunted each year to make the pemmican that fuelled the voyageurs on their long journeys (Colpitts, 2014). It would not be until the Palliser expedition in 1857 that the British government showed any interest in settling Western Canada, and there would be no serious considerations of exactly how such a task would be accomplished until the arrival of the Canadian Pacific Railway surveyors in the 1870s (Berton, 1970; Haig, 1983).

At this point, a period of rapid change hit the bison populations of Western Canada, with hunting pressure, competition with European ungulates and habitat conversion increasing as more of the land to the east of the Rockies was settled as the railway worked its way across the country (Taschereau, 2019). Canada's bison population declined throughout the 1870s and the last free-roaming herd was spotted in 1881, marking the end of their influence in the Canadian Rockies (Colpitts, 2002). In 1883 the Canadian Pacific Railway arrived in the Bow Valley and, with the discovery of a pair of thermal springs at the base of Sulphur Mountain, the Government of Canada would establish a twenty-six $km^2$ protected area around the springs that would later be expanded and named Banff National Park (Parks Canada, 2022b).

The entrance of settlers into the area of modern-day Banff did not only change the land physically through the building of infrastructure and homes, but they also changed the cycles that had formerly governed the mountain landscape. Fire was seen as an undesirable and destructive force by European settlers who implemented fire control programs in both prairie and mountain ecosystems to prevent fires (Norgaard, 2019). These included areas meant to conserve biodiversity such as Banff National Park where, despite fires having long been a part of the landscape, park officials attempted to prevent fires from occurring for safety and aesthetic reasons (White, 1985). Fire control in Banff National Park continued throughout the 1900s until the 1980s, with very few major fires occurring in the park compared to the historical average (Coogan et al., 2021).

Throughout the 1900s the influence of both bison and fire were absent from Banff National Park. Early conservation efforts for bison took place in Banff National Park with a small herd of bison in a paddock at the base of Cascade Mountain in 1897 that lasted until 1997 when it was closed as part of a larger project to remove barriers to the movement of mammals like wolves and cougars in the Bow valley (Markewicz, 2017). Park philosophies around fire began to change as well, and in 1983 Banff National Park conducted its first prescribed burn, with a more regular prescribed burn program taking hold since the 1990s (Coogan et al., 2021). These former policies continue to be felt in the loss of ecosystems and species that depend on frequent disturbance by fire and in 2020 Parks Canada released an updated fire management plan for Banff, Kootenay and Yoho National Parks which emphasizes the use of fire as a critical tool for conservation (Parks Canada, 2021b).

Prescribed burns were used to prepare and maintain the land for a reintroduced bison herd that was airlifted to the park's backcountry in 2017 (Parks Canada, 2019). Unlike the 1897 herd that lived beneath Cascade Mountain in Banff, the reintroduced herd can freely roam around a 1200 $km^2$ section of the park's backcountry (Parks Canada, 2020a). As it has been well over a century since Banff National Park held a free roaming bison herd, questions exist as to how this historical relationship between fire and resource selection will continue and play out in Banff National Park. Understanding where and how bison interact with burned patches of the landscape, and the role topographic factors like slope steepness or the distance to the nearest water source factors into those decisions will be a key part in helping managers determine where and how to conduct prescribed burns in the future.

I used GPS collar data from thirteen members of the Banff bison herd, remote sensing and generalized estimating equations to examine the question of whether reintroduced bison in Banff National Park select resources in burned patches within the reintroduction zone. Specifically, I examined how burn frequency, slope steepness, whether an area is classified as a grassland/shrubland or a forest, and the distance to the nearest source of water affects resource selection by bison in Banff National Park. I predicted that bison would show a preference for areas that had been burned, that burn frequency would not be a significant factor in their choice, that they would preferentially inhabit grasslands/shrublands over forests, and that they would be willing to occupy areas far from water and on steeper slopes.

## Methods

### Study Area

The study area was restricted to the 1200 $km^2$ reintroduction core zone and hazing zone and did not account for movement by bison outside the border of Banff National Park. To date four animals have made their way out of the park for a few weeks before being relocated or destroyed (Ellis, 2021). As the bison have not visited the entire reintroduction area, analysis will be further restricted to areas within the borders of the utilization distributions produced by the bison GPS collar data. For the utilization distribution produced by the kernel density estimate, this extent is from 51° 28' 34.05" N, 115° 59' 3.26" W to 51° 47' 30.98" N, -115° 36' 37.39" W.

### Home Range Estimate

GPS data from collars worn by thirteen members of the herd (five males and eight females) since the free roaming release were used to estimate the home range and of the bison herd. These collars are either a Vectronic Vertex Plus or a Vectronic Vertex Lite, with most members wearing a Vertex Plus. In either case, both types of collars are equipped with VHF and Iridium GPS uplinks that provide location data every two hours, 24 hours per day (Vectronic Aerospace, 2023a; Vectronic Aerospace, 2023b). Tagging and collaring of the bison herd is done in September each year, with Parks Canada staff members operating on horseback (Parks Canada, 2020b). They have found that this minimizes stress on the herd and should not impact habitat selection, with members of the herd often choosing to remain in the same field they had been darted in for a few days afterwards (Parks Canada, 2020b)  To estimate the home range of the herd, I generated a model based on a utilization distribution generated from these GPS data. I explored two methods for generating my utilization distribution: a Brownian bridge movement model and a kernel density estimate.

The Brownian bridge movement model method was attempted first as they can better estimate movement paths of mobile species, account for error associated with the individual GPS points and accounts for autocorrelation by assuming individual points are not independent in contrast to a kernel density estimate (Horne et al., 2007). The Banff bison herd are a mobile species whose movements are constrained by mountain valleys, and thus I thought this model would produce a more accurate home range size estimate. The Brownian bridge movement model was created using the adehabitatHR package in R (Calenge, 2006; R Core Team, 2021).

Kernel density estimates are a common estimation of home range size; however, they can be susceptible to type II errors with smaller datasets and may not include habitat that an animal is otherwise using (Fieberg & Börger, 2012). The converse can also occur, with large datasets leading to type I errors by including habitat that is not being utilized by the animal (Fieberg & Börger, 2012). Despite these drawbacks, kernel density estimates are still useful tools for estimations of home range and can provide accurate estimations of home range (Lichti & Swihart, 2011). The adehabitat HR package in R was used to create a kernel density estimate (Calenge, 2006; R Core Team, 2021). The kernel density estimate was estimated to the 95 percent probability contour using the default 'href' bandwidth.

Upon comparing the utilization distribution produced by the Brownian bridge movement model and the kernel density estimate, I found that both methods produced nearly identical home range estimates for the Banff bison herd, and Brownian bridge movement models had technical challenges not found with kernel density estimates. For conciseness, I only show results from kernel density estimates here.

### Resource Selection Functions

Resource selection functions provide a way of estimating the probability of resource use of an animal or group of animals proportionate to the amount of that resource available in the environment (Boyce et al., 2002). To produce a resource selection function based on my data, I first generated 98,521 random points within the boundaries of the kernel density estimate utilization distribution via the AMT package in R (Signer et al., 2019). I then compared these points with 98,521 GPS points subsampled from tracking points from thirteen satellite-collared members of the bison herd between July 29, 2018, and October 10, 2021, with October 10, 2021 being the date nearest to when these analyses were performed. When a GPS point completely overlapped with one of the randomly generated points the first "random" point was discarded, and a new random point was generated. This continued until there were an equal number of random points and GPS points. These points were then overlaid atop layers of topographic and ecosystem data to compare where an animal was present during this period vs where it was not. In doing so I was better able to estimate how the Banff bison were selectively using resources within the reintroduction zone.

### Slope, Water, Vegetation and Fire Data

I obtained shapefiles for slope grade data from Natural Resources Canada's digital surface model via the Government of Canada's geospatial extraction tool (Natural Resources Canada, 2017); water bodies from the Alberta base watershed dataset (Alberta Environment and Parks, 2018); burns from Banff National Park's fire history database (Parks Canada, 2021a); and the Vegetation Resources Inventory Land Classification from Banff National Parks' Vegetation Resources Inventory dataset (Parks Canada, 2021c). These data were analysed using QGIS version 3.16 "Hannover" (Graser, 2020).

I first loaded shapefiles for each dataset into QGIS and extracted only data from the study area via the use of the Intersection geoprocessing function (QGIS, 2021). Vegetation Resources Inventory data were reclassified in QGIS by use of its editing feature into Grassland/Shrubland, Forested or Non-Vegetated based on the British Columbia Land Cover Classification Scheme designation listed for each vegetation polygon within the study area (Ministry of Sustainable Resource Management, 2002). Areas where shrubs or herbs made up more than fifty percent of the area were given 'Grassland/Shrubland' designations. Areas where trees made up seventy five percent or more of the area were given 'Forest' designations. Areas that were made up of bedrock, talus, river or lake sediments, moraines, lakes, rivers, and icefields were given 'Non-Vegetated' designations.

Banff National Park's fire database contains data for wildfires in the study area from between 1909 and 2020 (Parks Canada, 2021a). I first created a layer that contained every fire within the reintroduction zone over the last 111 years and assigned each part of the reintroduction zone either a 'burned' or 'unburned' value. I then used the Join Attributes (Summary) function in QGIS to build a GIS layer that counted the number of overlaps between each burn that had occurred in the study area between 1909 and 2020 (QGIS, 2021). This new layer provided an estimate of burn frequency over the last 111 years by counting the number of burns a particular patch had experienced since 1909.

How near a patch of land is to water can be an important consideration for what sort of places bison select for when roaming across a landscape. I included only rivers that flowed year-round in the analysis to avoid counting ephemeral streams that were not accessible to the bison for more than a few months of the year. Previous studies have shown that the distribution and availability of permanent standing water sources across the landscape is of greater importance than the size of those water sources; therefore, I decided to count any permanent body of standing water in the reintroduction zone regardless of its size (Reynolds, 2003; Babin et al., 2011; Kohl, 2012; Bauman, 2023).

Waterbody data were transformed into a heatmap that showed the distance of each coordinate on the map to the nearest waterbody via the use of the distance() function in the philentropy package in R (Drost, 2018). Data were then saved as new shapefiles in QGIS and were loaded into R to be analysed along with the Heatmap and Resource Selection Function data in the habitat utilization models.

## Habitat Utilization Models

Variables for fire frequency, the slope grade of each coordinate in the reintroduction zone, vegetation resources inventory and the distance to nearby rivers were created in R. Data for each variable were re-projected onto the World Geodetic System 1984 Coordinate Reference System. Data that were not already in raster form were rasterized using the raster() function in the raster package (Hijmans, 2021). Rasters were then layered over one another using the stack() function in the utils package in R (Bengtsson, 2003).

Generalized estimating equations (GEEs) that utilize empirical standard errors can provide accurate parameter estimates for resource selection functions with sufficiently large sample sizes (Koper & Manseau, 2012). This can be done even if the underlying correlation structure for the GEE is unknown, which it will be since the correlation structure between the GPS points and the random points will be different (Koper & Manseau, 2012). GEEs estimate marginal parameters rather than conditional ones, this means that the results they provide must be considered at the population scale rather than the individual one (Koper & Manseau, 2012).

I created a set of generalized estimating equations using the geepack package in R for the Kernel density estimate (Halekoh et al., 2006). I first compared model fit between the ‘exchangeable’, and ‘independence’ correlation structures offered by geepack using a Quasilikelihood under the Independence model Criterion (QIC) rank comparison (Halekoh et al., 2006). While I could not know the underlying correlation structure, it was still useful to compare different structures to see which fits the model the best (Koper & Manseau, 2012). The ‘exchangeable’ correlation structure provided the best fit.

Models were fitted with binomial distributions and data from each variable were centred prior to analysis via the scale() function in R (R core team, 2021). Whether or not a point was considered ‘used’ was set as the response variable. Slope, Vegetation Resource Inventory Land Classification, Time Since a Burn, whether a plot of land was Burned or Unburned, whether the fire was Natural or Prescribed and the Distance to the Nearest River were all independent variables. I converted results from each model into odds ratios.

## Results

Bison showed a preference for burned patches over unburned patches (Table 1, Figure 1). Bison showed a preference for patches that had been burned more than ten times (Table 1, Figure 2). Bison selected for areas that were one hundred meters closer to waterbodies when compared to randomly generated points (Table 1, Figure 3). Bison selected for areas that were on slopes 5 percent shallower when compared to randomly generated points (Table 1, Figure 4). Bison visited grassland and shrubland habitat five times as often than they did forests and fifty times more often than they did non-vegetated areas (Table 1, Figure 5).

**Table 1. Odds ratios estimates for binomial fitted generalized estimating equations describing the odds of the Banff bison herd occupying a patch that has been burned instead of an unburned patch, the number of times the patch had been burned, the percentage of slope in that patch, the distance of that patch from the nearest waterbody, and whether it was classified as either a grassland/shrubland patch or as a non-vegetated patch instead of a forested patch.**

| Factor | Estimate | Std. Error | Wald Estimate | p-value |
|---|---|---|---|---|
| Burned Patch (vs. Unburned) | 1.65 | 0.005 | 7166.0 | < 0.0001 |
| Fire Frequency (# of fires between 1909-2020) | 1.87 | 0.006 | 9377.7 | < 0.0001 |
| Distance to Nearest Waterbody | 0.67 | 0.007 | 3137.0 | < 0.0001 |
| Slope (Degrees) | 0.90 | 0.008 | 19118.0 | < 0.0001 |
| Land Classification - Grassland / Shrubland | 5.33 | 0.012 | 20287.9 | < 0.0001 |
| Land Classification - non-vegetated | 0.80 | 0.034 | 46.8 | < 0.0001 |

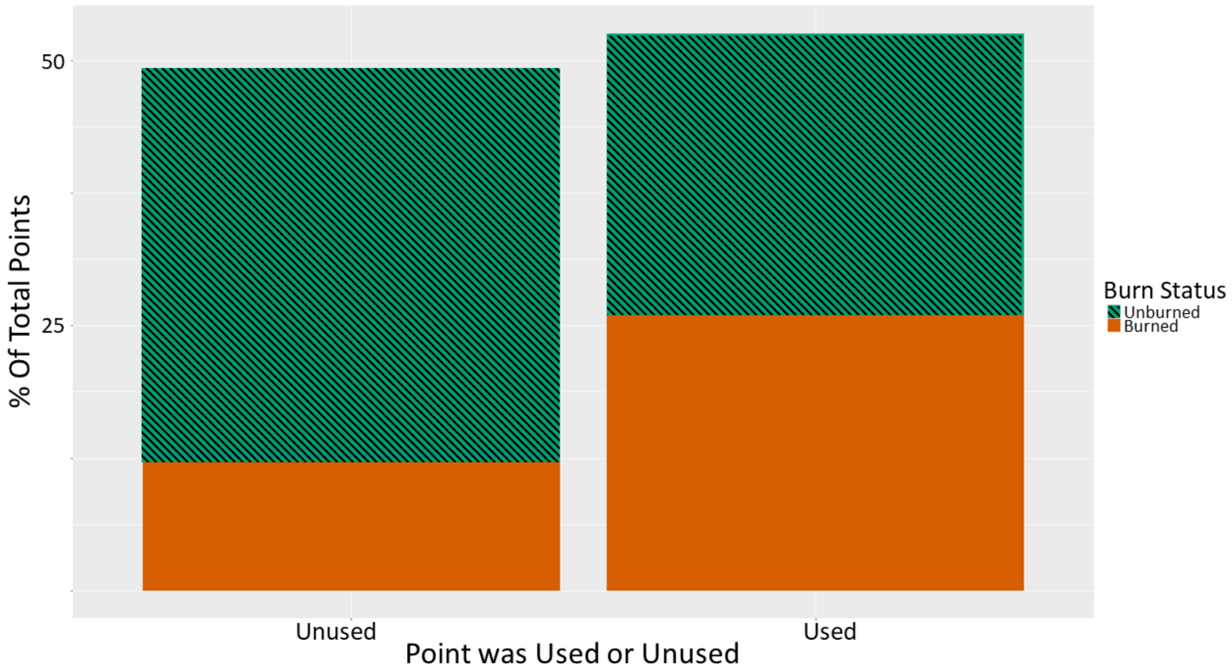

**Figure 1. Bar graph showing distribution of used and available points compared to whether a patch was burned between 1909 and 2020. One half of the used points are in patches that have burned while three quarters sof the unused points are in patches that have not burned.**

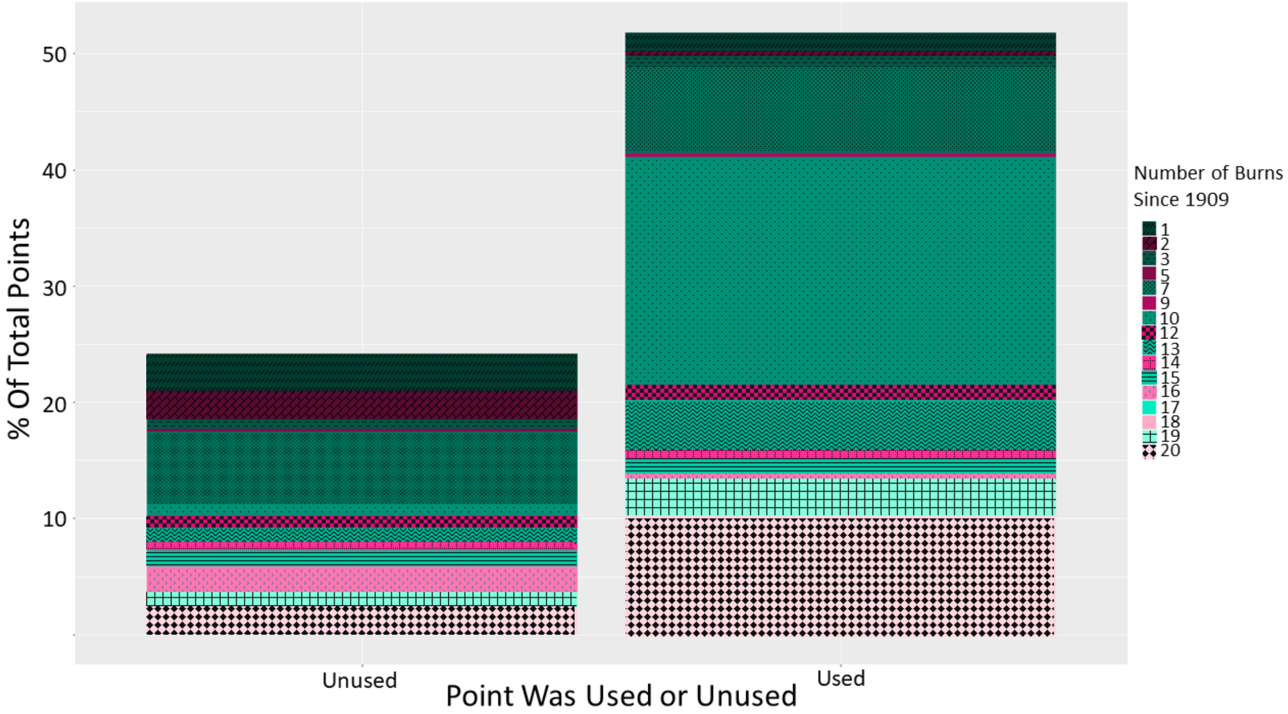

**Figure 2. Bar graph showing the percentage of used and available points for patches burned at different frequencies. Patches burned more than ten times make up three quarters of the points that were used by bison.**

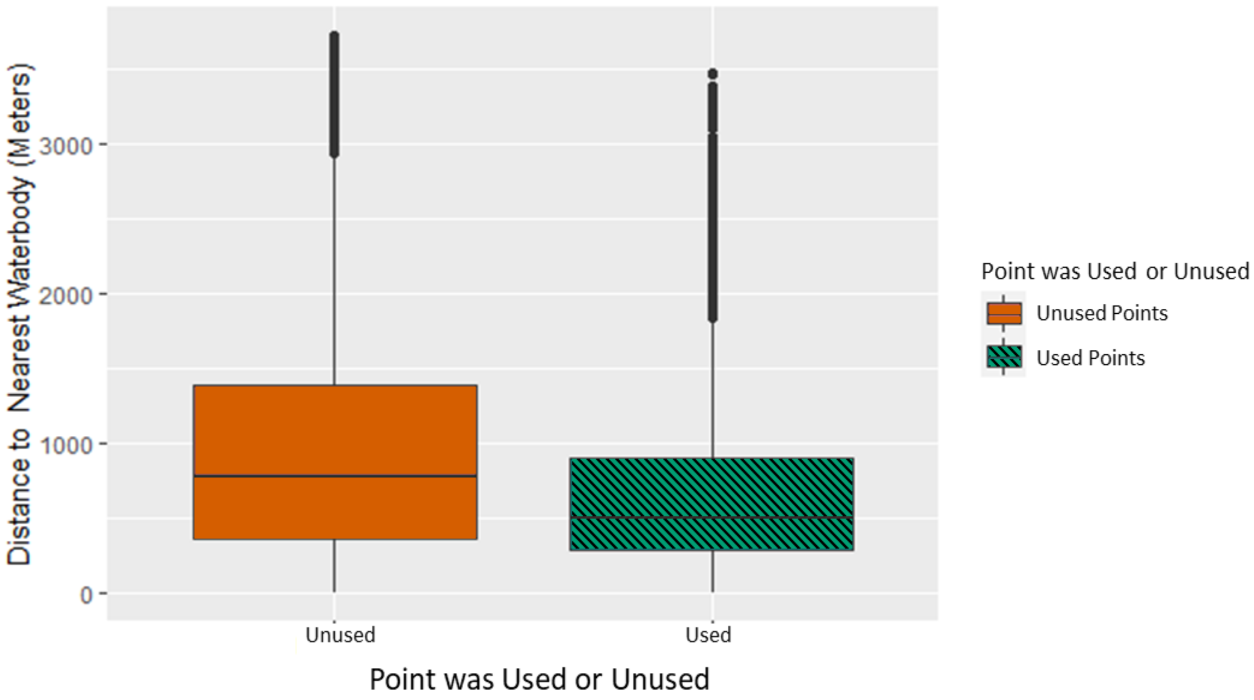

**Figure 3. Boxplots showing distribution of used and available points compared to the distance to the nearest waterbody. Used points occupied a tighter range of distances from water when compared to unused points. The lower boundary of the used points boxplot is one hundred meters closer to water when compared to the lower boundary for the unused points boxplot.**

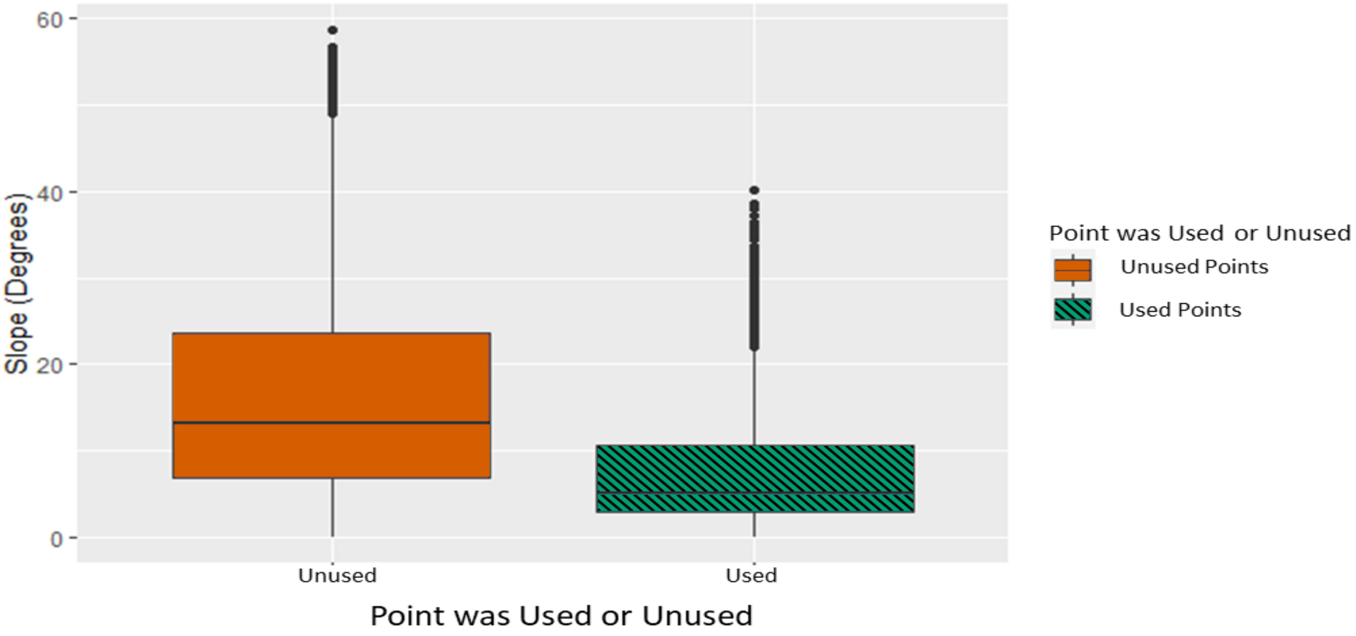

**Figure 4. Boxplots showing distribution of used and available points compared to the slope of the landscape. Used points occupied a tighter range of slopes compared to unused points. The lower boundary of the used points boxplot occupied slopes 5 percent less steep when compared to the lower boundary for the unused points boxplot.**

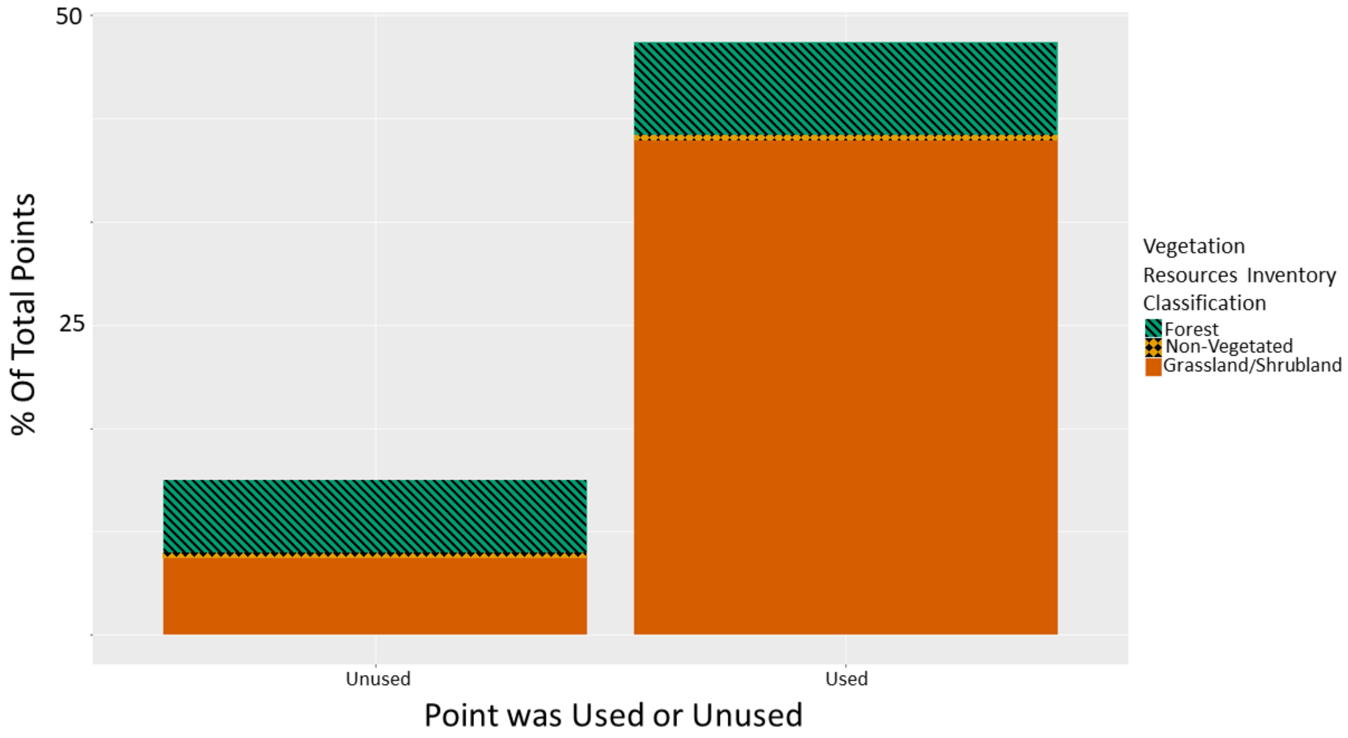

**Figure 5. The number of used and unused points in each land classification. There are seven times as many used points occupied patches classified as grassland/shrubland then there are unused points. The number of used and unused points in forests and non-vegetated areas is roughly equal.**

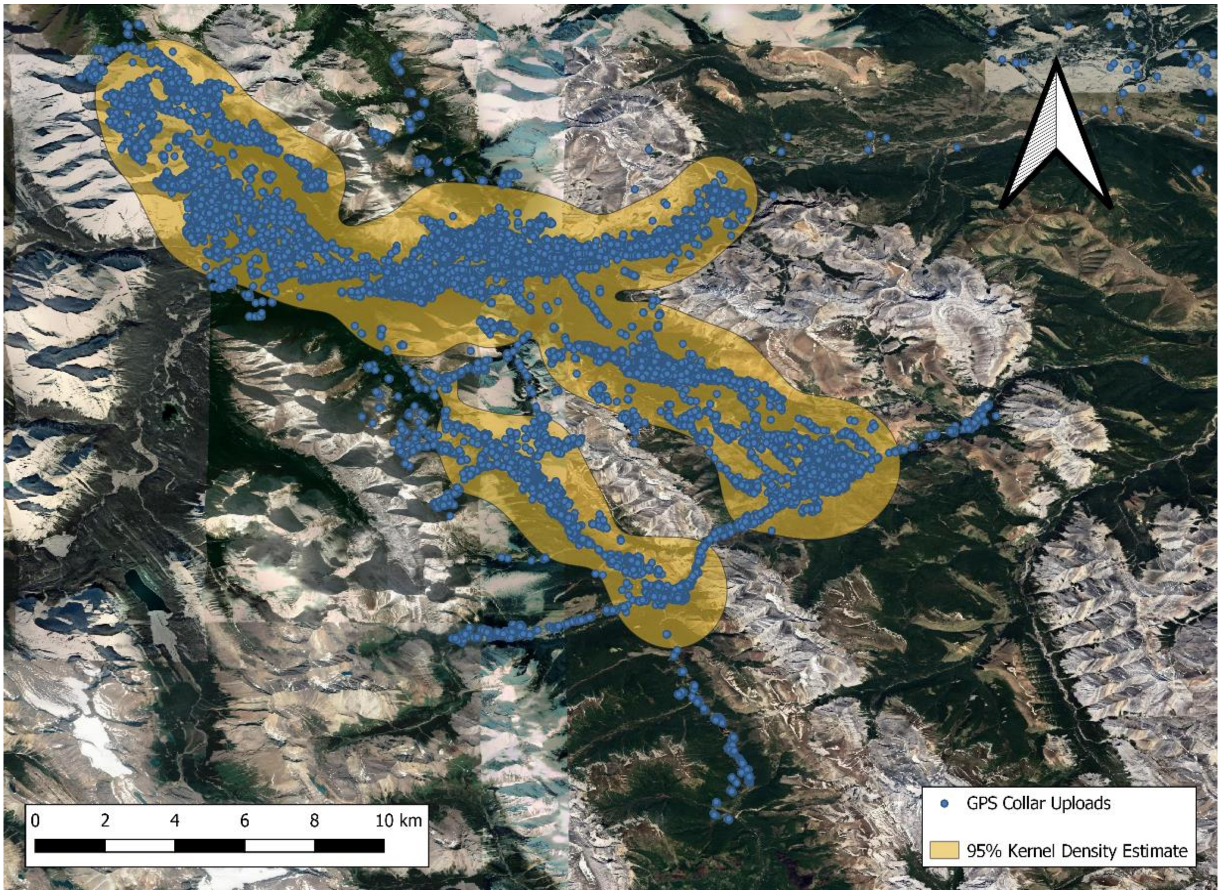

**Figure 6. Map showing the 95-percent kernel density estimate over the study area. The estimate covers the valleys within the reintroduction zone. GPS collar uploads in the Northeast corner of the map outside of the Rocky Mountains were from two escaped bulls and were not included in the estimate.**

## Discussion

I investigated the question of how burn frequency, slope steepness, ecosystem type, and the distance to the nearest water source influenced resource selection by reintroduced plains Bison in Banff National Park. The Banff reintroduction is one of the only reintroductions of plains bison into a mountainous environment, and the only existing attempt at reintroducing plains bison into the Canadian Rockies. Understanding how the ruggedness of the Canadian Rockies might influence resource selection by these bison would be helpful in informing and potentially identifying other sites for reintroductions elsewhere in the Rockies. The Banff herd strongly selected for frequently burned patches that were within eight hundred meters of a water source, on slopes below 11°, and that were in grassland/shrubland habitats.

### *The Influence of Fire*

The history of fire on a landscape is often a major factor in determining where and for how long bison will spend their time on a patch of land (Vinton et al., 1993). For the Banff bison herd, areas that have been subjected to frequent fires seem to hold a great appeal. For thousands of years prior to European contact, traditional Indigenous land management methods were what governed the Canadian Rockies and the Great Plains as well as the bison herds that roamed them (Brink, 2008; Colgan et al., 2021). These methods included the use of fire to proactively create good habitat for bison on the Great Plains and encourage them to return to a burned spot in the following years to make hunting easier (Brink, 2008). Indigenous applications of fire were closely tied to season, with some burns occurring in the spring so that hunts in the fall could harvest meat during colder times of the year where it had a lower chance of spoiling (Eisenberg et al.; Roos et al., 2018). Fall fires were also set to create good grazing grounds for the next spring, producing much higher intensity burns than the spring fires would (Eisenberg et al., 2019). High intensity fall fires would historically have resulted in reduced woody plants following a burn, with post-burn grazing by the bison making woody recolonization difficult as they consumed the young shoots of trees like aspen (Eisenberg et al., 2019).

Burns that occur in grasslands can result in an increase in plant productivity and create highly palatable forage for animals like bison in the years following a burn (Verrall & Pickering, 2019; Raynor et al., 2015). The quality of forage in forest patches in the years immediately after a burn may be higher due to the proliferation of fresh new growth that is easier to access with the reduction in understory (Sachro et al., 2005). Work by Proffitt et al. (2015) found that forage quality in burned forests was highest in the years immediately after a burn and declined as time went on.

Over the last three hundred years the Canadian Rockies experienced regular wildfires that would have burned across the mountains and foothills at varying intensities (Amoroso et al., 2011). Fire frequency was also variable across the landscape, as fires were caused by both occasional ignitions from lightning and more frequent ignitions from Indigenous peoples (Parks Canada, 2021b). Spring burning was a common practice for many Indigenous peoples in the montane ecoregion of Banff National Park, as these burns produced medicinal plants, maintained travel routes, and helped to create good grazing grounds for bison so they could be tracked hunted more easily (White, 2001). This management style worked in part because bison will often select for frequently burned patches over less frequently burned ones and tend to graze frequently burned patches for longer periods (Vinton et al., 1993). Vegetation regrowth in the first two years following a fire is notably more nutritious and palatable for grazers, leading them to occupy those patches more often (Nichols et al., 2021). For the vegetation community this can result in greater species richness and habitat heterogeneity at these heavily used sites, as frequent burning in combination with disturbances like grazing can keep more competitive plant species from establishing themselves and taking over (Harnett et al., 1996).

These concepts were reflected in the habitat selection by the bison herd in this study, with bison showing a strong preference for burned areas over unburned areas, and for more frequently burned areas over less frequently burned ones (Tables 1 & 2). By combining varying intensities of prescribed burns and by burning some sites more frequently than others to encourage heterogenous site selection from the ever-growing bison herd, managers may be able to restore much of the subalpine grasslands that were lost over the last few centuries. Prescribed burns should continue to be applied to the landscape to create good habitat for the bison that will help support a larger and more stable population while returning ancient natural processes to the land.

### *Topography*

The herd appeared to be more willing to occupy sites further from water than they were to travel up to ones on steeper slopes, which falls in line with previous studies that found bison are less limited by water, having been noted to roam as far as 10 km away from water sources (McHugh, 1958; Kohl et al., 2013, Allred et al., 2011). However, the Banff bison never strayed too far from water compared to these other studies, typically keeping to within a kilometer of a water source. Van Vuren (2001) noted that vertical distance to water was more limiting to bison in a mountainous environment than horizontal distance to water and so the herd is likely choosing to move between water sources along the flattest paths possible. Typically, these paths come in the form of trails alongside major rivers like the Red Deer and the Panther as they offer easier travel through flatter terrain as herds move throughout the landscape and bison may not wish to stray too far from these trails when traveling through the reintroduction zone (Parks Canada, 2018). It is also important to note that my study did not capture daily usage habits from the bison herd and only looked at broad trends in where they selected for sites on the landscape.

Previous work by Allred et al. (2011) found similar behaviour by bison in a grassland ecosystem as the herd tended to stick to flatter, lower areas on the landscape The Banff herd was sourced from bison herds in Elk Island National Park, approximately 45 minutes east of the city of Edmonton, Alberta, Canada (Heuer, 2019). Elk Island National Park is located within a ‘prairie pothole’ environment that features no standing water and very gentle slopes with little elevation change (Parks Canada, 2022c). The Banff herd is potentially exhibiting a preference for these parts of the reintroduction zone that are more like their former home. However, slopes are not necessarily a barrier to bison who are more accustomed to a mountain landscape. For example, in the Henry Mountains in Utah a reintroduced bison herd was found to be willing to traverse slopes, noting occurrences on slopes as steep as 32° (Van Vuren, 2001). Historical accounts of plains bison also detail herds being known to forage on steeper slopes (Fryxell, 1928). This may have been because in early June to Mid-July, plants located in the alpine can be highly palatable and very nutritious, providing a reason for bison to traverse steep slopes into the alpine (Johnston et al., 1968). As slopes become steeper and the difference between energy expenditure and nutritional gains becomes smaller bison are less likely to occupy those upslope areas (Senft et al., 1987). This behaviour was exhibited by the Henry Mountain bison herd which was noted to graze at higher elevations than cattle in the same ecosystem to gain access to superior forage (Van Vuren, 2001).

If bison are not sufficiently motivated by high quality forage to stray from water sources or expend the energy to move up steep slopes they will avoid doing so. There is also a learning, or re-learning, component to consider in the case of the Banff herd. Knowledge from Elders of the Stoney Nakoda First Nation tells us that Bison herds are led by Tatâga Wiye Îtawagihâ (matriarchs) who teach the herd and direct where it goes (Stoney Nakoda Nations, 2022). Because the oldest animals in the herd have only been free roaming on the land since 2018 the Banff herd may need time to truly learn the landscape and may yet be unwilling to travel into new regions of the reintroduction zone if there is uncertainty of there being a reliable source of water. This again speaks to the importance of a prescribed burning program within the reintroduction zone as by creating these burned patches in steeper areas further from water the bison herd is more likely to venture into these regions and continue to build an understanding of the landscape. This can allow the herd to spread out across the reintroduction zone and help increasing habitat heterogeneity at the landscape scale.

### *Land Classification*

The Banff bison herd selected for patches in grasslands/shrublands over forests or areas without vegetation. This is in line with other studies where bison have been known to express a strong preference for grasslands and will selectively forage in patches with higher graminoid coverage within those grasslands, though they will also consume forbs and shrubs and in open forests when superior forage is not available (Sanderson et al., 2008, Hecker et al., 2021, Keene et al., 2021). Ranglack & du Toit (2015) recommended prescribed burns continue to be used to create grazing habitat for bison in the Henry Mountains after noting that burns within the last ten years of the study contained higher quality forage than surrounding patches.

Forage availability is not the only consideration for bison since predation risk can also moderate where and how bison will spend their time on a landscape. Fortin et al. (2009) noted that bison would select for more open meadows and grasslands when in large groups and would split into smaller groups and individuals whenever they moved into forests. Most collars in this study were applied to females who may have been expressing this preference for open spaces as they travelled in groups as opposed to males who may spend time in more forested areas separately or in small groups (Post et al., 2001). Predation risk is present for the Banff herd as it is believed that one of the herd's calves were killed by wolves in 2020 (Dorozio, 2021). Wolves in Banff National Park are still learning how to hunt bison after over a century of their being absent from the landscape and as they gain experience in doing so and can more successfully hunt juvenile and mature bison; the predation risk they carry will undoubtedly affect where bison herds are likely to spend their time (Dorozio 2021).

## Conclusion

Future research directions may include a step-selection function study that examines the probability of bison moving towards or away from different biotic and abiotic landscape features, building an understanding of how the bison are making decisions as they encounter these different elements on the landscape (Fortin et al., 2005). Being able to gain a clear picture of how the herd is using the landscape will provide a useful baseline for tracking how those usage intensity might change in later decades as the herd grows. This long-term monitoring could be of use in other bison reintroductions elsewhere in the Rocky Mountains in helping to predict suitable habitat for herds of different sizes.

A 2016 habitat suitability index predicted that between 600 - 1000 bison could be supported in the reintroduction zone while as of 2022 the herd sits at 88 members (Steenweg et al., 2016, Ellis, 2022).

Because bison may change their behaviour as competition for resources like forage becomes more intense it would be wise to re-assess how they are using the landscape as the population continues to increase. Monitoring the number of predation events affecting the herd will also be important, as being able to track how often and where these are occurring may be able to provide a clear perspective on how habitat use by the herd is responding to increased predation risk.

Prescribed burns should continue to be applied to create good foraging habitat and to encourage the herd to venture into new parts of the reintroduction zone. Disturbance by fire and the subsequent usage of burned patches by bison have historically led to the expansion of grassland ecosystems in the Great Plains, but the ruggedness of the Canadian Rockies leads to a new suite of factors such as a more severe topography that can influence which sites bison select for (Kohl et al., 2013). Knowledge of how fire drives bison to select for different patches on the landscape is one that has been well understood by human beings in the Canadian Rockies since time immemorial. Western science has built a knowledge base of this relationship as well, though these studies have mostly occurred in the prairies. My study is unique in that it examines a herd that is in its first few years of being reintroduced to a mostly subalpine landscape and considers the distinct topography and fire history of the Canadian Rockies from a Western scientific perspective.

## Literature Cited

Alberta Environment and Parks. (2018). Base Watersheds [data file]. Retrieved from: https://geodiscover.alberta.ca/geoportal/rest/metadata/item/e4197d5f6b3043be8cbf9e7f8b49c4fe/html

Allred, B. W., Fuhlendorf, S. D., & Hamilton, R. G. (2011). The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. *Ecosphere, 2*(3), 1-17. https://doi.org/10.1890/ES10-00152.1

Amoroso, Daniels, L. D., Bataineh, M., & Andison, D. W. (2011). Evidence of mixed-severity fires in the foothills of the Rocky Mountains of west-central Alberta, Canada. *Forest Ecology and Management, 262*(12), 2240–2249. https://doi.org/10.1016/j.foreco.2011.08.016

Anderson, R. C. (2006). Evolution and Origin of the Central Grassland of North America: Climate, Fire, and Mammalian Grazers. *The Journal of the Torrey Botanical Society*, *133*(4), 626–647. http://www.jstor.org/stable/20063881

Axelrod, D. I. (1985). Rise of the Grassland Biome, Central North America. *Botanical Review*, *51*(2), 163–201. http://www.jstor.org/stable/4354053

Babin, J., Fortin, D., Wilmshurst, J.F. & Fortin, M. (2011). Energy gains predict the distribution of plains bison across populations and ecosystems. *Ecology*, *92*, 240-252. https://doi.org/10.1890/10-0252.1

Barnett, A. G., Koper, N., Dobson, A. J., Schmiegelow, F. K. A., & Manseau, M. (2010). Using information criteria to select the correct variance-covariance structure for longitudinal data in Ecology. *Methods in Ecology and Evolution*, 1*(1)*, 15-24.

Bauman, P. (2023, May 4). *Considerations for Winter Bison Management.* South Dakota State University Extension. https://extension.sdstate.edu/considerations-winter-bison-management

Bengtsson, H. The R.oo package - Object-Oriented Programming with References Using Standard R Code, Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), ISSN 1609-395X, Hornik, K.; Leisch, F. & Zeileis, A. (ed.), 2003

Berton, P. (1970). *The National Dream: The Great Railway, 1871-1881*. McClelland & Stewart.

Borman, M. M. (2005). Forest Stand Dynamics and Livestock Grazing in Historical Context. *Conservation Biology*, *19*(5), 1658–1662. http://www.jstor.org/stable/3591135

Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmiegelow, F. K. (2002). Evaluating resource selection functions. *Ecological modelling, 157*(2-3), 281-300. https://doi.org/10.1016/S0304-3800(02)00200-4

Brink, J. W. (2008). *Imagining Head Smashed In: Aboriginal Buffalo Hunting on the Northern Plains*. AU Press.

Bright, B. C., Hudak, A. T., Kennedy, R. E., Braaten, J. D., & Khalyani, A. H. (2019). Examining post-fire vegetation recovery with Landsat time series analysis in three western North American forest types. *Fire Ecology*, *15*(1), 1-14. https://doi.org/10.1186/s42408-018-0021-9

Brooks, M, E., Kristensen, K., Van Benthem K, J.,, Magnusson, A., Berg C, W., Nielsen, A, W., Skaug, H, J., Maechler, M., Bolker, B, N.(2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378-400.

Calenge, C. (2006). The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 1035.

Christianson, A. (2019, March 05). Burning Territory: Indigenous Fire Stewardship. *Landscapes in Motion*. https://www.landscapesinmotion.ca/updates-1/2019/2/26/burning-territory-indigenous-fire-stewardship#_edn2

Collins, S. L., & Calabrese, L. B. (2012). Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *Journal of Vegetation Science*, *23*(3), 563–575. http://www.jstor.org/stable/23251087

Colpitts, G. (2002). *Game in the garden : a human history of wildlife in Western Canada to 1940*. UBC Press.

Colpitts, G. (2014). *Pemmican Empire: Food, trade, and the last bison hunts in the North American Plains, 1780–1882*. Cambridge University Press.

Coogan, S. C. ., Daniels, L. D., Boychuk, D., Burton, P. J., Flannigan, M. D., Gauthier, S., Kafka, V., Park, J. S., & Wotton, B. M. (2021). Fifty years of wildland fire science in Canada. *Canadian Journal of Forest Research*, *51*(2), 283–302. https://doi.org/10.1139/cjfr-2020-0314

Daubenmire, R. (1985). The Western Limits of the Range of the American Bison. *Ecology*, *66*(2), 622–624. https://doi.org/10.2307/1940411

Dorozio, J. (2021, July 5). *Bison baby boom: 16 new calves join Banff National Park's herd*. CBC News. https://www.cbc.ca/news/canada/calgary/banff-national-park-bison-herd-new-calves-1.6086108

Drost HG.  Philentropy: Information Theory and Distance Quantification with R.  Journal of Open Source Software (2018). doi:10.21105/joss.00765

Eisenberg, C., Anderson, C. L., Collingwood, A., Sissons, R., Dunn, C. J., Meigs, G. W., ... & Edson, C. B. (2019). Out of the ashes: ecological resilience to extreme wildfire, prescribed burns, and indigenous burning in ecosystems. *Frontiers in Ecology and Evolution*, *436*.https://doi.org/10.3389/fevo.2019.00436

Ellis, C. (2022, August 26). *Sixteen bison calves born to Banff herd this year*. Rocky Mountain Outlook. https://www.rmotoday.com/banff/sixteen-bison-calves-born-to-banff-herd-this-year-5724640

Ellis, C. (2021, August 18). Parks Canada kills bison that ventured onto provincial lands. *Rocky Mountain Outlook*. https://www.rmotoday.com/banff/parks-canada-kills-bison-that-ventured-onto-provincial-lands-4230877

EROS Archive of the LANDSAT 8 OLI/TRS Level 2 Surface Reflectance Dataset courtesy of the US Geological Survey. https://www.usgs.gov/core-science-systems/nli/landsat/landsat-surface-reflectance?qt-science_support_page_related_con=0#qt-science_support_page_related_con

Fieberg, J., & Börger, L. (2012). Could you please phrase "home range" as a question?. *Journal of mammalogy*, *93*(4), 890-902. https://doi.org/10.1644/11-MAMM-S-172.1

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, *86*(5), 1320-1330. https://doi.org/10.1890/04-0953

Fortin, D., Fortin, M. E., Beyer, H. L., Duchesne, T., Courant, S., & Dancose, K. (2009). Group-size-mediated habitat selection and group fusion–fission dynamics of bison under predation risk. *Ecology*, *90*(9), 2480-2490.

Frank, D. A., & Evans, R. D. (1997). Effects of Native Grazers on Grassland N Cycling in Yellowstone National Park. *Ecology (Durham), 78*(7), 2238–2248. https://doi.org/10.1890/0012-9658(1997)078[2238:EONGOG]2.0.CO;2

Frank, D. A., & McNaughton, S. J. (1992). The Ecology of Plants, Large Mammalian Herbivores, and Drought in Yellowstone National Park. *Ecology*, *73*(6), 2043–2058. https://doi.org/10.2307/1941454

Fryxell, F. M. (1928). The former range of the bison in the Rocky Mountains. *Journal of Mammalogy*, *9*(2), 129-139.

Fuhlendorf, S. D., Engle, D. M., Kerby, J., & Hamilton, R. (2009). Pyric Herbivory: Rewilding Landscapes through the Recoupling of Fire and Grazing. *Conservation Biology*, *23*(3), 588–598. https://doi.org/10.1111/j.1523-1739.2008.01139.x

Gadd, B. (2009). *Handbook of the Canadian Rockies (2nd ed.)* Corax Press.

Graser, A. (2020, October 27). QGIS 3.16 Hannover is released! *QGIS.org* https://blog.qgis.org/2020/10/27/qgis-3-16-hannover-is-released/

Guthrie, R. D. (1970). Bison Evolution and Zoogeography in North America During the Pleistocene. *The Quarterly Review of Biology*, *45*(1), 1–15. http://www.jstor.org/stable/2817929

Haig, B. (1983) *Following Historic Trails - James Hector Explorer.* Bruce Haig Collection https://jstor.org/stable/community.34308349.

Halekoh, U., Højsgaard, S., Yan, J. (2006). The R Package geepack for Generalized Estimating Equations. *Journal of Statistical Software*. https://www.jstatsoft.org/article/view/v015i02

Hardy, C. C., & Arno, S. F. (1996). *The use of fire in forest restoration: a general session at the Annual Meeting of the Society for Ecological Restoration.* U.S. Dept. of Agriculture, Forest Service, Intermountain Research Station.

Hartnett, D. C., Hickman, K. R., & Walter, L. E. (1996). Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. Rangeland Ecology & Management/Journal of Range Management Archives, 49(5), 413-420. http://hdl.handle.net/10150/644237

Hecker, L. J., Coogan, S. C., Nielsen, S. E., & Edwards, M. A. (2021). Latitudinal and seasonal plasticity in American bison Bison bison diets. *Mammal Review, 51*(2), 193-206. https://doi.org/10.1111/mam.12229

Heuer, K. (2019). *Plains bison reintroduction in Banff National Park pilot project 2017-2022: 2018 progress report.* Parks Canada. http://www.publications.gc.ca/site/eng/9.891745/publication.html

Hijmans, R. J. (2021). raster: Geographic Data Analysis and Modeling. R package version 3.5-2. https://CRAN.R-project.org/package=raster

Hoffman, K. M., Davis, E. L., Wickham, S. B., Schang, K., Johnson, A., Larking, T., Lauriault, P. N., Le, N. Q., Swerdfager, E., & Trant, A. J. (2021). Conservation of Earth’s biodiversity is embedded in

Indigenous fire stewardship. *Proceedings of the National Academy of Sciences - PNAS, 118*(32), 1 – 6. https://doi.org/10.1073/pnas.2105073118

Hood, G. A., & Bayley, S. E. (2008). Beaver (Castor canadensis) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. *Biological Conservation*, *141*(2), 556-567. https://doi.org/10.1016/j.biocon.2007.12.003

Johnston, A., Bezeau, L., & Smoliak, S. (1968). Chemical Composition and in Vitro Digestibility of Alpine Tundra Plants. *The Journal of Wildlife Management, 32*(4), 773-777. doi:10.2307/3799553

Jung, T. S. (2020). Investigating local concerns regarding large mammal restoration: group size in a growing population of reintroduced bison (Bison bison). *Global Ecology and Conservation, 24*, e01303. https://doi.org/10.1016/j.gecco.2020.e01303

Karp, A. T., Behrensmeyer, A. K., & Freeman, K. H. (2018). Grassland fire ecology has roots in the late Miocene. *Proceedings of the National Academy of Sciences - PNAS, 115*(48), 12130–12135. https://doi.org/10.1073/pnas.1809758115

Keene, K. A., Gulsby, W. D., Colter, A. G., Miller, D. A., Johannsen, K. L., Miller, K. V., & Martin, J. A. (2021). Short-term effects of loblolly pine thinning intensity on coverage of preferred white-tailed deer forage plants. *Canadian Journal of Forest Research, 51*(4), 604-610.

Knapp, A. K., Blair, J. M., Briggs, J. M., Collins, S. L., Hartnett, D. C., Johnson, L. C., & Towne, E. G. (1999). The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *BioScience*, *49*(1), 39-50. https://doi.org/10.1525/bisi.1999.49.1.39

Koerner, S. E., & Collins, S. L. (2014). Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. *Ecology*, *95*(1), 98–109. http://www.jstor.org/stable/23597274

Kohl, M. T., Krausman, P. R., Kunkel, K., & Williams, D. M. (2013). Bison versus cattle: are they ecologically synonymous? *Rangeland Ecology & Management, 66*(6), 721-731. https://doi.org/10.2111/REM-D-12-00113.1

Kohl, M. T. (2012). *Bison Conservation in the Northern Great Plains* (153) [Master's Thesis, University of Montana]. ScholarWorks. https://scholarworks.umt.edu/etd/153

Koper, N., & Manseau, M. (2012). A guide to developing resource selection functions from telemetry data using generalized estimating equations and generalized linear mixed models. Rangifer, 195-204. DOI:10.7557/2.32.2.2269

Lake, F.K., Christianson, A.C. (2020). Indigenous Fire Stewardship. In: Manzello, S.L. (eds) Encyclopedia of Wildfires and Wildland-Urban Interface (WUI) Fires. Springer, Cham. https://doi.org/10.1007/978-3-319-52090-2_225

Larson, F. (1940). The Role of the Bison in Maintaining the Short Grass Plains. *Ecology*, *21*(2), 113–121. https://doi.org/10.2307/1930479

Lichti, N. I., & Swihart, R. K. (2011). Estimating utilization distributions with kernel versus local convex hull methods. *The Journal of Wildlife Management*, *75*(2), 413-422. https://doi.org/10.1002/jwmg.48

Lott, D. F. (2002). *American Bison: A Natural History*. University of California Press.

Markewicz, L. (2017). *Like Distant Thunder*. Parks Canada.

Mchugh, T. (1958). Social behavior of the American buffalo (Bison bison bison). *Zoologia*, *43*, 1-40. https://www.biodiversitylibrary.org/page/51124024#page/13/mode/1up

Ministry of Sustainable Resource Management. (2002). *Vegetation Resources Inventory: The B.C. Land Cover Classification Scheme*. https://www2.gov.bc.ca/assets/gov/environment/natural-resource-stewardship/nr-laws-policy/risc/landcover-02.pdf

Natural Resources Canada. (2017). Geospatial Data Extraction - [data file]. Retrieved from maps.canada.ca/czs/index-en.html

Nichols, R. A., Demarais, S., Strickland, B. K., & Lashley, M. A. (2021). Alter fire timing to recouple forage nutrients with herbivore nutrient demands. *Forest Ecology and Management*, *500*, 119646. https://doi.org/10.1016/j.foreco.2021.119646

Norgaard, K. M. (2019). Smokey Bear and Fire Suppression as Colonial Violence. In *Salmon and Acorns Feed Our People : Colonialism, Nature, and Social Action.* (pp. 72 - 128). Rutgers University Press.

O'Keefe, K. & Nippert, J. B. (2017). Grazing by bison is a stronger driver of plant ecohydrology in tallgrass prairie than fire history. *Plant and Soil*, *411*(1/2), 423–436. https://doi.org/10.1007/s11104-016-3048-1

Parks Canada. (2018). *Backcountry Trails in Banff National Park* [Brochure]. https://www.pc.gc.ca/en/pn-np/ab/banff/visit/brochures

Parks Canada. (2019, July 15). *Bison Reintroduction Project – EPISODE 3: Burning for Bison – Banff National Park* [video]. Youtube. https://www.youtube.com/watch?v=ZyH5hh5rXpY

Parks Canada. (2020a, October 27). *Plains bison reintroduction.* Parks Canada. https://www.pc.gc.ca/en/pn-np/ab/banff/info/gestion-management/bison

Parks Canada. (2020b, October 26), *Bison Blog: Radio Collaring Wild Bison*. Parks Canada. https://parks.canada.ca/pn-np/ab/banff/info/gestion-management/bison/blog

Parks Canada. (2021a). Banff National Park Fire Database [Microsoft Access Datafile]. Banff: Parks Canada.

Parks Canada. (2021b). *Fire management plan 2020: Banff, Yoho, and Kootenay National Parks.* https://publications.gc.ca/collections/collection_2021/pc/R64-586-2020-eng.pdf

Parks Canada. (2021c). Banff National Park Vegetation Resources Inventory Database [Microsoft Access Datafile]. Banff: Parks Canada.

Parks Canada. (2022a). *Site management: Rocky Mountain House National Historic Site*. https://parks.canada.ca/lhn-nhs/ab/rockymountain/info/plan

Parks Canada. (2022b). *Cave and Basin National Historic Site of Canada Management Plan, 2020.* https://parks.canada.ca/lhn-nhs/ab/caveandbasin/info/gestion-management-2020

Parks Canada (2022c). *Lakes, Rivers and Wetlands, Elk Island National Park*. https://parks.canada.ca/pn-np/ab/elkisland/nature/ecologique-ecological/eau-water

Post, D. M., Armbrust, T. S., Horne, E. A., & Goheen, J. R. (2001). Sexual segregation results in differences in content and quality of bison (Bos bison) diets. *Journal of Mammalogy, 82*(2), 407-413.

Proffitt, DeVoe, J., Barker, K., Durham, R., Hayes, T., Hebblewhite, M., Jourdonnais, C., Ramsey, P., & Shamhart, J. (2019). A century of changing fire management alters ungulate forage in a wildfire-dominated landscape. *Forestry (London)*, *92*(5), 523–537. https://doi.org/10.1093/forestry/cpz017

QGIS.org, 2021. QGIS Geographic Information System. QGIS Association. http://www.qgis.org

R Core Team (2021). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ranglack, D. H., & Du Toit, J. T. (2015). Habitat selection by free-ranging bison in a mixed grazing system on public land. *Rangeland Ecology & Management, 68*(4), 349-353.

Raynor, E. J., Gersie, S. P., Stephenson, M. B., Clark, P. E., Spiegal, S. A., Boughton, R. K., ... & Augustine, D. J. (2021). Cattle grazing distribution patterns related to topography across diverse rangeland ecosystems of North America. *Rangeland Ecology & Management, 75*, 91-103. https://doi.org/10.1016/j.rama.2020.12.002

Raynor, E. J., Joern, A., & Briggs, J. M. (2015). Bison foraging responds to fire frequency in nutritionally heterogeneous grassland. *Ecology*, *96*(6), 1586-1597. https://doi.org/10.1890/14-2027.1

Reeves, B. O. K. (1978). Bison Killing in the Southwestern Alberta Rockies. *Plains Anthropologist, 23*(82), 63–78. https://doi.org/10.1080/2052546.1978.11908902

Reynolds, H.W., C.C. Gates, and R.D. Glaholt. 2003. Bison (*Bison bison*). In Feldhamer, G.A., B.C. Thompson, and J.A. Chapman (eds.). *Wild Mammals of North America: Biology, Management, and Conservation. 2nd Edition*. (pp. 1009 – 1060). The Johns Hopkins University Press, Baltimore and London.

Roos, C. I., Zedeño, M. N., Hollenback, K. L., & Erlick, M. M. (2018). Indigenous impacts on North American Great Plains fire regimes of the past millennium. *Proceedings of the National Academy of Sciences*, *115*(32), 8143-8148.

Sachro, L. L., Strong, W. L., & Gates, C. C. (2005). Prescribed burning effects on summer elk forage availability in the subalpine zone, Banff National Park, Canada. *Journal of Environmental Management, 77*(3), 183-193. https://doi.org/10.1016/j.jenvman.2005.04.003

Sanderson, E. W., Redford, K. H., Weber, B., Aune, K., Baldes, D., Berger, J.,  Carter, D., Curtin, C., Derr, J., Dobrott, S., Fearn, E., Fleener, C., Forrest, S., Gerlach, C., Cormack G. C., Gross, J. E., Gogan, P., Grassel, S., Hilty, J. A.,  Jensen, M., Kunkel K.,Lammers D., List, R., Minkowski, K., Olson, T., Pague, C., Robertson, P. B., & Stephenson, B. O. B. (2008). The ecological future of the North American bison: conceiving long-term, large-scale conservation of wildlife. *Conservation biology*, *22*(2), 252-266.

Senft, R., Coughenour, M., Bailey, D., Rittenhouse, L., Sala, O., & Swift, D. (1987). Large Herbivore Foraging and Ecological Hierarchies. *BioScience, 37*(11), 789-799. doi:10.2307/1310545

Steenweg, R., Hebblewhite, M., Gummer, D., Low, B., & Hunt, B. (2016). Assessing Potential Habitat and Carrying Capacity for Reintroduction of Plains Bison (Bison bison bison) in Banff National Park. *PloS One*, *11*(2), e0150065–e0150065. https://doi.org/10.1371/journal.pone.0150065

Stoney Nakoda Nations. (2022). *Enhancing the Reintroduction of Plains Bison in Banff National Park Through Cultural Monitoring and Traditional Knowledge*. https://a.storyblok.com/f/112697/x/d0b9253d5a/stoney_bison_report_final_rev2.pdf

Sutherland, C. R. (2018). Remembering and Igniting Fires: Prescribed Burns as Memory Work. *RCC Perspectives*, *3*, 19–26. http://www.jstor.org/stable/26511169

Taschereau, D. M. (2019). Human-Bison Relations as Sites of Settler Colonial Violence and Decolonial Resurgence. *Humanimalia, 10*(2), 10–41. https://doi.org/10.52537/humanimalia.9500

Thomas, J. P., Larter, N. C., & Jung, T. S. (2021). Individual-based seasonal habitat selection in a forest-dwelling population of reintroduced bison Bison bison. *Wildlife Biology, 2021*(3). https://doi.org/10.2981/wlb.00852

Thompson, D. (1915). *David Thompson's Narrative of His Explorations in Western America, 1784-1812* (Vol. 12). Champlain Society.

Truett, J. C., Phillips, M., Kunkel, K., & Miller, R. (2001). Managing bison to restore biodiversity. *Great Plains Research*, 123-144. https://www.jstor.org/stable/23775644

Vectronic Aerospace. (2023a). *VERTEX PLUS Collars*. https://www.vectronic-aerospace.com/vertex-plus-collar/

Vectronic Aerospace. (2023b). *VERTEX Lite Collars*. https://www.vectronic-aerospace.com/vertex-lite-collar/

Verrall, B., & Pickering, C. M. (2019). Recovery of subalpine grasslands 15 years after landscape level fires. Australian Journal of Botany, 67(5), 425-436. https://doi.org/10.1071/BT19020

Vinton, M. A., Hartnett, D. C., Finck, E. J., & Briggs, J. M. (1993). Interactive Effects of Fire, Bison (Bison bison) Grazing and Plant Community Composition in Tallgrass Prairie. *The American Midland Naturalist*, *129*(1), 10–18. https://doi.org/10.2307/2426430

Waiser, W. A., & Cunfer, G. (2016). *Bison and People on the North American Great Plains A Deep Environmental History* (First edition.). Texas A&M University Press.

White, C. (2001). Aspen, elk, and fire in the Canadian Rocky Mountains (Doctoral dissertation, University of British Columbia]. UBC Open collections. https://open.library.ubc.ca/collections/ubctheses/831/items/1.0090793

Wallis de Vries, M. F., & Schippers, P. (1994). Foraging in a landscape mosaic: selection for energy and minerals in free-ranging cattle. *Oecologia, 100*, 107-117.

White, C. (1985). Wildland Fire in Banff National Park, 1880 - 1980. *National Parks Branch: Occasional Paper No. 3.* https://www.researchgate.net/publication/306065367_White_C_A_Wildland_Fires_in_Banff_National_Park_1880-1980_National_Parks_Branch_Occasional_Paper_3_Ottawa_Parks_Canada_1985

Wilkins, K., Pejchar, L., & Garvoille, R. (2019). Ecological and social consequences of bison reintroduction in Colorado. *Conservation Science and Practice*, *1*(2). https://doi.org/10.1111/csp2.9

Wilmers, C. C., Crabtree, R. L., Smith, D. W., Murphy, K. M., & Getz, W. M. (2003). Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology*, *72*(6), 909-916. https://doi.org/10.1046/j.1365-2656.2003.00766.x

Van Vuren, D. H. (2001). Spatial relations of American bison Bison bison and domestic cattle in a montane environment. *Animal Biodiversity and Conservation*, *24*(1), 117-124.

Yanicki, G. M. (2014). *Old Man's Playing Ground* (Vol. 173). University of Ottawa Press.

Zedeno, M. N. (2017). Bison hunters and the Rocky Mountains: An evolving partnership. *Quaternary International*, *461*, 80–101. https://doi.org/10.1016/j.quaint.2017.06.043

# Chapter 3: Assessing the influence of Reintroduced Plains Bison on Bird Abundance & Diversity in Banff National Park

## Abstract

Bison modify the habitats that they live within through disturbances like grazing, tree rubbing, and wallowing. Songbirds are indicators of environmental change and are known to be sensitive to changes in vegetation structure caused by disturbances from forces like bison. I performed acoustic recordings, and vegetation structural and composition surveys in areas that were visited by bison at varying intensities and that were left unused. I analysed these data using generalized linear mixed models to determine whether bison usage significantly affected either the vegetation or bird communities present in the reintroduction zone. Vegetation density and understory height showed no response to bison usage intensity. Vegetation composition responses were varied with forbs increasing with increasing bison usage and mosses decreasing in grasslands/shrublands and increasing in forests as bison usage increased. Neither the overall abundance of birds nor species richness in the study area were affected by bison usage within the first five years of their reintroduction to the landscape. I also examined songbird species that were dependent on different types of habitats to see whether they responded to any changes in their habitats that might be caused by the bison. These were Wilson's Warblers, which utilize dense, shrubby habitats, White-crowned Sparrows, which use more sparsely shrubby and grassy habitats, and Townsend's Warblers which use closed-canopy forests. I examined Brown-headed Cowbirds as well, since they co-evolved with bison. I made predictions for future trends for five other bird species, two generalists [American Robins and Canada Jays] and three species at risk [Common Nighthawks, Evening Grosbeaks, and Olive-sided Flycatchers], present in the study area. I found that modifications to habitats by bison will likely decrease the abundance of bird species that are dependent on undisturbed, closed-canopy forests and increase the abundance of bird species that require patches of disturbed, open habitat.

# Introduction

In 2017, Parks Canada reintroduced a herd of 16 plains bison into the backcountry of Banff National Park in an effort that was motivated in part by trying to restore those natural disturbance regimes that bison would have historically caused in the Canadian Rockies (Heuer, 2019). Part of the criteria that the success of the reintroduction is being assessed upon is the potential negative or positive effects the bison are having on creatures already present within the backcountry (Heuer, 2019). Assessing the early effects of a reintroduction like this can be difficult, as similar work on a herd of plains bison reintroduced into a prairie ecosystem found few notable effects of the bison on songbirds within the first five years of the reintroduction (Herakovich et al., 2021). Still, the novelty of the Banff reintroduction occurring in the Canadian Rockies, an ecosystem that has seen few if any plains bison reintroductions on this scale, means that the early response to the reintroduction of bison in sensitive communities like plants and birds may be starkly different from the reintroductions done on prairie grasslands. Building an understanding of what and how different species respond to bison in an ecosystem like this can help provide important context for future decision-making by land managers.

Plains bison are sometimes referred to as ecosystem engineers as they modify the vegetative community of the habitats that they exist within through disturbances like grazing (Knapp et al., 1999). While bison are generalist foragers, they do exhibit a preference for graminoids over forbs (Plumb & Dodd, 1993; Keery, 2019). This preference typically results in a greater abundance of forbs in grazing sites when compared to those that remain ungrazed (Collins & Calabrese, 2012). Bison, like many other grazers, are deliberate in selecting sites that will maximize the amount of nutrients they gain while also minimizing energy expenditure to get there (Senft et al., 1987). Van Vuren (2001) found that bison are willing to expend more energy to get to high quality forage when compared with cattle in a mountainous environment. Thus, site selection is influenced not only by where the highest quantity and quality of forage exists, but also how the steepness of topography and distance from waterbodies in a landscape affect the ability of bison to get to that forage (Senft et al., 1987; Wallace et al., 1995). Site selection by bison results in a mosaic of different plant types at the landscape scale (Truett et al., 2001).

Bison can also influence the ecosystems around them through ways other than grazing such as wallowing and tree rubbing. Wallowing is a behaviour unique to bison where they create large depressions in the ground by rolling from side to side on their back (McMillan et al., 2011). Collins & Barber (1986) suggested that tallgrass prairie ecosystems subject to grazing and wallowing held higher diversity than those that did not. Wallow pits themselves have been found to have lower plant diversity in the centre, but higher plant diversity at their edges when compared to adjacent prairie (McMillan et al., 2011).

Historically, bird populations were affected by disturbances from bison largely through changes to grass height, bare ground cover, and the abundance of shrubs (Truett et al., 2001; Knopf, 1996). Wiens (1973) found that among grassland songbirds, some species showed very strong preferences for areas of very tall or very short vegetation, while others appeared to have no preference. The importance of having a landscape with high heterogeneity in vegetation structure was noted in a study by Fuhlendorf et al. (2006) where species such as Henslow's Sparrows (*Ammodramus henslowii*) and Upland Sandpipers (*Bartramia longicauda*) preferred disturbed patches on the landscape with shorter vegetation. Generalist birds which generally are not limited by what vegetation is present on the landscape for vegetation types, have been found to be relatively unaffected by disturbances to vegetation structure when compared to those that are more selective (Richardson et al., 2014). Davis (1974) concluded that thirty-two of the forty-six bird species identified in a study in south-eastern New Mexico would be eliminated from the area if the woody habitat on which they were dependent were to be removed. However, in an environment where a lack of disturbance is leading to an increasingly homogenized woody ecosystem like in the subalpine of the Canadian Rockies, bird species may benefit from the heterogeneity brought by these disturbances (Patterson & Best, 1996; Stockdale et al., 2019). Circa three hundred years ago, the subalpine ecoregion of the Canadian Rockies experienced more frequent disturbances from forces like wildfires (White, 1985). The frequency and severity of fire as well as bison grazing new growth in burned patches would have led to a more heterogenous habitat with a greater mix of open and closed canopy forests and grasslands (White, 1985; Vinton et al., 1993). Birds may also learn about and respond to vegetation structural changes from other members of their community as information on habitats, such as where optimal breeding grounds exist, can be disseminated through social interactions (Betts et al., 2008)

Grazing intensity is a factor in how birds respond to these structural changes in vegetation. A study of cattle grazing in grasslands found no impact of low grazing intensities on birds' abilities to nest successfully (Lusk, 2009). Overgrazing is a notable concern in grassland ecosystems, as high stocking rates of cattle have been found to negatively impact some species of birds in bunchgrass prairies while providing no beneficial effects for other birds in the ecosystem (Johnson et al., 2011). In a study of the effects of different cattle stocking rates in pastures on grassland songbirds, a heterogeneous landscape was found to be created when a mixture of high and low intensity stocking rates was applied to pastures, and likewise bird abundances were both positively and negatively affected depending on their preferred habitat type in the pasture (Sliwinski & Koper, 2015). Grazing by plains bison traditionally mimics this heterogeneity as some sites are intensely grazed over and over while bison take advantage of palatable regrowth while others are left undisturbed, this more heterogenous habitat may in turn provide space for a greater diversity in birds across the landscape (Senft et al., 1987; Truett et al., 2001). Climate also plays an important role in these effects, as years of above or below normal precipitation can alter how rapidly vegetation recovers from being grazed and likewise the response of birds in these grazed areas (Sliwinski & Koper, 2015). Increased habitat heterogeneity is beneficial to birds as it is linked to changes in vertical vegetation structure in an ecosystem, increasing the habitat available for different species as vertical structure becomes increasingly heterogeneous (Tews et al., 2004).

How vegetation structure itself is changed by a disturbance is an important determinant of how the diversity and relative abundance of birds in disturbed areas will respond to that change. Work in Yellowstone National Park revealed that songbirds responded more strongly to changes in the vertical height of willows than to changes in their total ground cover (Baril et al., 2011). In shrub-steppe communities, vegetation structure was found to have a greater influence on where songbirds chose to live than vegetation species composition (Williams et al., 2011). This holds true across other temperate ecosystems where primarily understory height, rather than the characteristics of a particular species of vegetation, are of more relevance to bird habitat suitability (MacArthur & MacArthur, 1961). Patchiness plays an additional role in these systems, as the resulting vegetative layers provided by a meadow intermixed with patches of shrubs and trees offers a greater variety of habitats for birds to utilize (Roth, 1976). The way a disturbance affects vegetation structure is important to consider as different types of disturbances produce distinct vegetative communities. (Collins & Calabrese, 2012).

Climatic factors like rainfall and temperature are also important to consider in a mountain system, as changes in either can affect the growth rate and composition of different plants as well as the distribution and abundance of songbirds (George et al., 1992; Mahony et al., 2022). The abundance of Grasshopper Sparrows (*Ammodramus savannarum*), for example, has been shown to increase in cooler, wetter years as these sparrows potentially benefit from increased food availability or are able to seek shelter from predators in the increased amounts of vegetation provided by higher precipitation levels (Silber et al., 2023). Vegetation structure has also been shown to interact with temperature by providing wintering grassland birds with cool microclimates to seek refuge on hot days, increasing their survival rates (Perez-Ordonez et al., 2022). Both rainfall and temperature interact with the biotic and abiotic features present on a landscape, and thus it is important to keep their influence in mind when looking at changes on the landscape over time.

I examined changes in bird abundance and species richness at monitoring sites that ranged from being frequently occupied by the bison herd to having never been occupied by them. I defined different levels of occupation by the number of uploads from GPS collars worn by 13 members of the herd that were captured within 50 meters of each of my study sites. I then looked at whether the density and height of vegetation as well as the composition of different plant types was influenced by the bison using these sites at varying intensities and whether songbirds utilizing the habitat in those sites were being affected by those changes to vegetation.

## Methods

### Research Sites

The study area was restricted to the core bison reintroduction zone within Banff National Park (51° 44' 39.84" N, 115° 55' 46.56" W to 51° 21' 10.08" N 115° 33' 32.04", Figure 8), the federally-owned Ya Ha Tinda Ranch (from 51° 45’ 29.60" N, 115° 30' 23.77" W to 51° 42' 44.46" N, 115° 41' 22.37" W, Figure 8), as well as Johnson Creek (51° 15' 29.49" N, 115° 50' 17.18" W, Figure 8) and Baker Creek (51° 20' 56.32" N, 116° 3' 58.57" W, Figure 8) in Banff National Park.

Monitoring transects for the project were established in 2015, three years prior to the bison reintroduction in 2018, and bird observations at each transect have been recorded yearly since 2015 (Banff National Park Bison Project, 2019 [unpublished field protocol document]). Seven transects were established within the lower subalpine ecoregion, with six located within the bison reintroduction area and one located outside in Ya Ha Tinda Ranch (Figure 8). Each was established as either a five-point or ten-point transect with points spaced three hundred to three hundred and fifty meters apart (Figure 7). One transect, Flints-Cuthead Ridges, was dropped in 2022 after the area was burned in October of 2020. This set of transects provided me with fifty observation points that had datasets ranging from 2015 to x.

To increase the number of transects with no bison presence for my study I added one more 10-point bird monitoring transect at both Johnson Creek and at Baker creek within Banff National Park that were not explicitly built for the bison reintroduction (Figure 8). These transects are part of Banff National Park’s ongoing ecological monitoring program, are all located within the lower subalpine ecoregion and possess datasets that began between 2007 and 2010. In total I had nine transects that I sampled over two field seasons with a total of eighty sampling points (Figure 8).

I overlaid each of these eighty sampling points over shapefiles created from the park’s Vegetation Resources Inventory in QGIS that had been sorted into one of three categories: grassland/shrubland, forested, or non-vegetated (Parks Canada, 2021a; QGIS, 2021). Of these eighty points, thirty-two were grassland/shrubland, forty-eight were forested, and no points landed in non-vegetated areas.

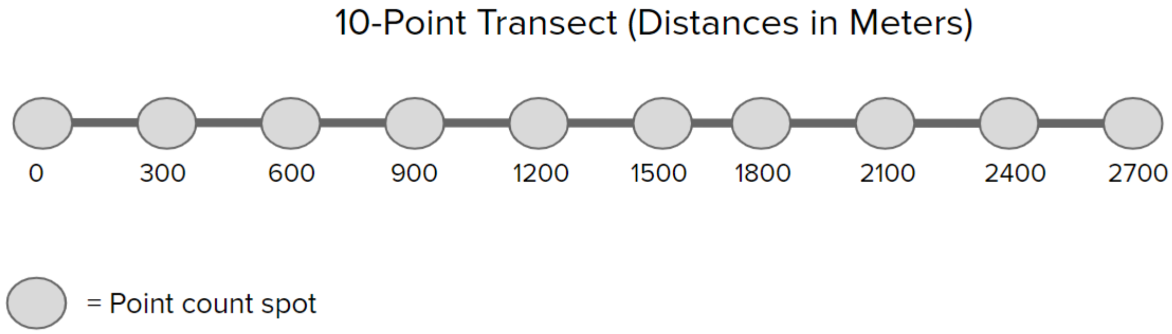

**Figure 7: Design of a 10-point transect with 300-meter spacing between each point.**

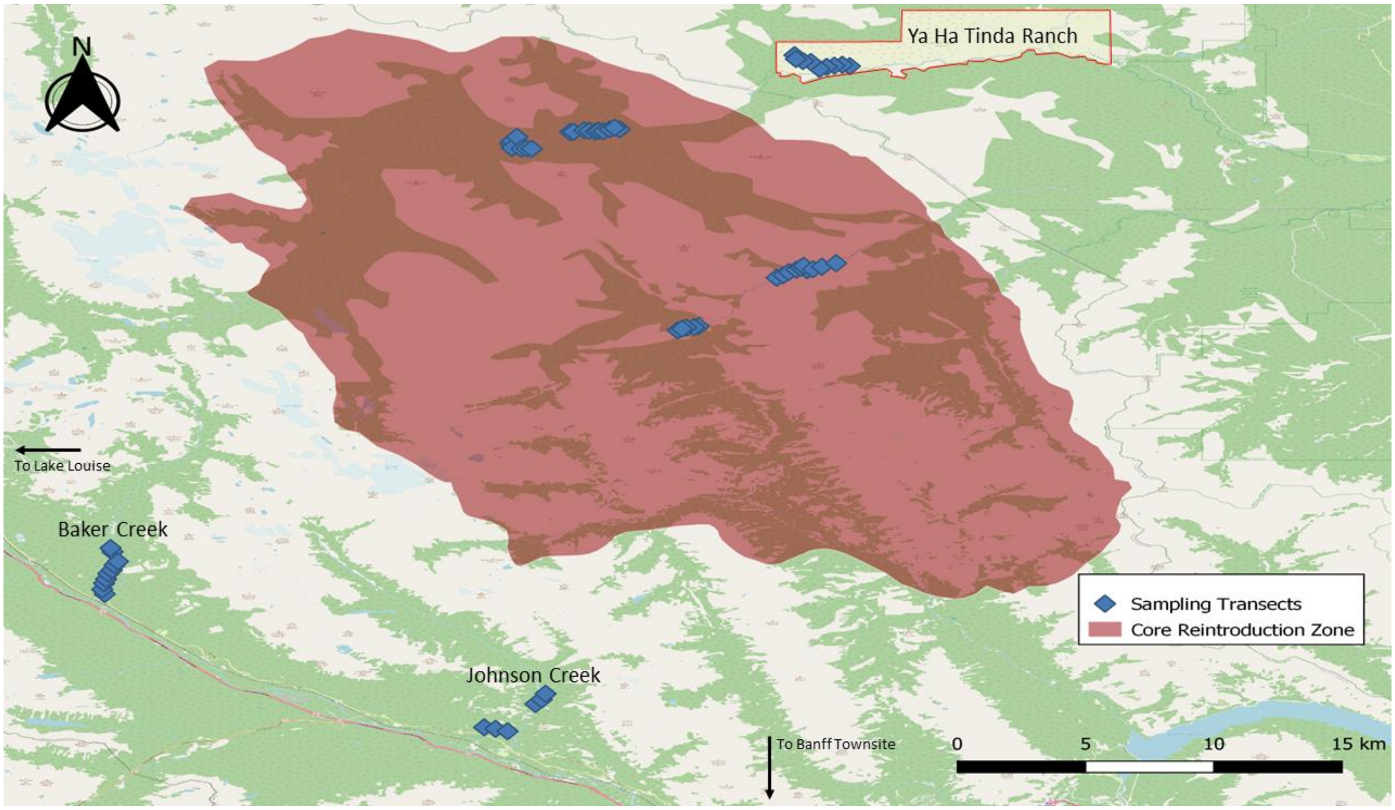

**Figure 8. Study transects in relation to the core reintroduction zone, the transects for Ya Ha Tinda Ranch, Baker Creek and Johnson Creek all fall outside of this zone and have no influence from bison.**

## Acoustic Point Counts

Audio recordings are a suitable method for estimating the relative abundances of different species in a survey, provided recording sessions are performed when birds are most vocally active (Pérez-Granados et al., 2019). Methods for the acoustic bird sampling aspect of my study followed those used by Banff National Park's environmental integrity monitoring program (Banff National Park Bison Project, 2019 [unpublished field protocol document]). Acoustic sampling was performed through a combination of automated recording units (ARUs) and in-person recording sessions. Sampling occurred between June 5th - 30th, as this is the peak breeding time for most songbirds in the region, with each transect being sampled once during this period (Environment Canada, 2018). Acoustic recordings were performed both in person and automatically using Songmeter SM Minis. ARUs have been found to be a viable alternative to point counts for sites that are visited seasonally or annually as part of a long-term monitoring strategy, particularly in rugged terrain or when skilled observers are unavailable (Venier et al., 2011; Klingbeil & Willig, 2015; Shonfield & Bayne, 2017).

In-person recordings were conducted with Songmeter SM Mini recorders placed on east-facing tripods starting half an hour before sunrise and continuing until at most 4 hours after sunrise. To minimize wind disturbance, sampling sessions were only conducted when wind speeds were below 19 km/h and were never conducted when there was precipitation or fog. Observers recorded their name, time and date, location, transect name and point number, and any other relevant comments at the start of the recording and then moved ten meters away until the end of the recording session. The 11-minute recording times are crucial, as point transect sampling with extended listening periods tends to provide a greater chance of detecting songbirds that may be difficult to detect due to a tendency to remain silent (Buckland, 2016). Multiple site visits are not feasible due to the remoteness of the study area and the logistical and time constraints imposed in travelling to the sites. Observers recorded the same information announced at the start of their recording into a logbook and then moved to the next point on their transect. Following the recording sessions, data were uploaded to the Banff National Park shared data drives.

SM Mini recorders were carried into study sites on horseback and recorders meant for overnight deployment were pre-programmed with the date and pre-set 11-minute recording times at 5:30 and 6:30 AM Mountain Daylight Time. Overnight units were mounted to trees which were then flagged for the retrieval of the recorders on the next day of fair weather. Following retrieval, dawn recordings were uploaded onto the Banff National Park shared data drives. Transcriptions and interpretations of all calls captured on the recording were performed by third party consultants that have been providing Banff National Park with this service prior to the start of my study.

## Vegetation Structural Sampling

Vegetation sampling took place in July and August following the acoustic recording sessions. To study the structure of understory vegetation, I established a series of 0.5 $m^2$ quadrats along each transect. Each set of quadrats were placed 25 and 50 meters from the centre of each point of the transect, oriented to the North, South, East, and West for a total of 8 paired quadrats nested within my larger plots (see figure 3). I used a two-meter-tall Robel pole following the practice developed by Robel et al. (1970) placed at the centre of each quadrat as this allowed me to visually estimate the density and height of vegetation present in that quadrat. Density was determined by what percentage of the pole was covered by foliage above and below one meter. Understory height was determined by measuring the point on the pole at which it was fully obscured by the surrounding foliage. A measurement of density and understory height was taken to the North, South, East, and West of the pole. If on one of these measurements the pole was fully obscured by the trunk of a tree, that observation was discarded. Finally, I visually estimated the percent cover of the different species within each quadrat to determine the percent cover of grasses, forbs, shrubs, trees, mosses, and bare ground up to 100 percent. Tree coverage was included only for completeness and occurred rarely (N = 15). For the purposes of my study bare ground included anything that was deemed to have little or no value as a food source for bison such as rocks or pine needles.

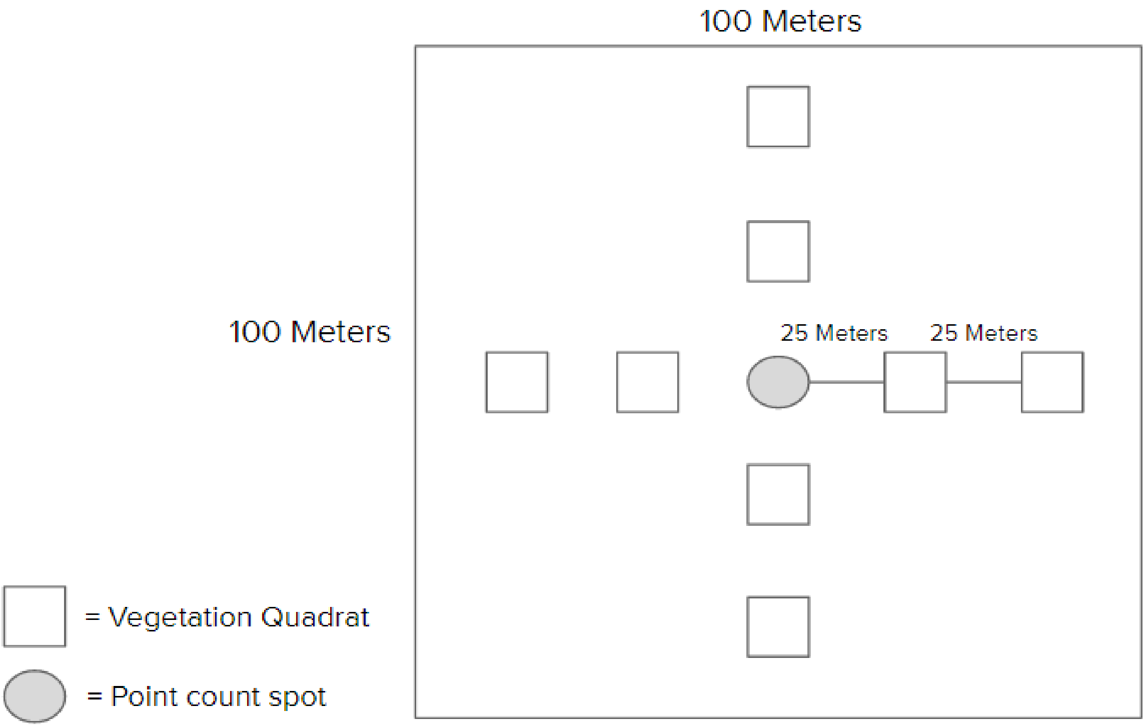

**Figure 9. Vegetation structural sampling plots, quadrats where vegetation composition and structure measurements are performed are space twenty-five meters and fifty meters out from the acoustic point count location.**

Data from the vegetation structure surveys were recorded in datasheets in the field along with the date, transect name, point number, weather, and any other pertinent comments at the time of the survey and then transcribed to Microsoft Excel spreadsheets. Data were uploaded to the Banff National Park Shared Data Drives.

## Temperature & Precipitation Data

Temperature and precipitation data were retrieved from the Government of Alberta's Alberta Climate Information Service's Historical Weather Station Data Viewer (Alberta Agriculture, Forestry and Rural Economic Development, 2022). Temperature data were gathered from four automated weather stations that form a polygon that covered roughly eighty percent of the study area. These stations were Scalp Creek (51° 47' 59.9994" N, 115° 39' 0" W), Dogrib Creek (51° 40' 12" N, 115° 30' 36" W), Scotch camp (51° 40' 0.1194" N, 115° 48' 50.3994" W), and Cuthead Lake (51° 27' 0" N, 115° 46' 0.12" W). Precipitation data were only available from two of these stations: Scalp Creek and Dogrib Creek. During the selected period the weather stations only captured precipitation in the form of rain.

Monthly average air temperatures and monthly rainfall normals for May - August from 2015 - 2022 were downloaded from the database and averaged out over the four months to create an average summer temperature (°C) and average accumulated rainfall (mm) for each year of the study. May - August were chosen to capture the months during which most of the vegetation utilized by the bird community in the park and consumed by the bison would be growing and thus affected by different weather patterns between years. These data were then added into my models as a control for the effects of any potential variation in weather patterns on the vegetation and bird communities during my study years.

## Bison Usage Index

I created an index of bison usage as a measurement for how often bison were visiting a site with a 50-meter buffer zone in QGIS around each of the acoustic survey points I had visited. I then uploaded all GPS points generated by the thirteen collared members of the bison herd between July 29, 2018, and October 10, 2021.These collars are equipped with VHF and Iridium GPS uplinks that provide location data every two hours, 24 hours per day (Vectronic Aerospace, 2023a; Vectronic Aerospace, 2023b). Tagging and collaring of the bison herd is done in September each year and is done on horseback, as this minimizes stress on the herd (Parks Canada, 2020b). By using the clip function in QGIS, I isolated each

GPS point within fifty meters of each acoustic survey point as this would provide me with a measure of how often a site was revisited by the bison. I used a count of the number of points captured within each of these 50-meter buffers as a measurement of relative bison usage at each site. I considered only using collar data during the bird breeding season, however I wanted to capture the potential cumulative effects on the landscape from the bison's use of it over the full year.

## Statistical Analysis

Songbird data from the transcribed audio recordings were uploaded into a Microsoft Excel spreadsheet and were processed into comma separated value files for analysis in R (R Core Team, 2013). Total bird abundance and diversity data at varying usage intensities were analysed using generalized linear mixed models. These models set species richness, total abundance of all species surveyed, and the total abundance for four specific species (Brown-headed Cowbird [*Molothrus ater*], White-crowned Sparrow [*Zonotrichia leucophrys*], Wilson's Warbler [*Cardellina pusilla*], and Townsend's Warbler [*Setophaga townsendi*] as response variables. Three of these species were selected to provide a cross-section of birds that use the wide variety of habitat types found throughout the reintroduction zone and thus some insights into how species dependent on said habitats may respond to increased presence of bison within them (White-Crowned Sparrow, Wilson's Warbler, and Townsend's Warbler). One species was also selected for its unique relationship with bison and how that relationship affects other birds in the ecosystem (Brown-headed Cowbird).

Since White-Crowned Sparrows exhibit a preference for open, shrubby habitat and consume seeds and insects they find on the ground, they may benefit from the presence of the bison herd as they disturb closed-canopy forests and maintain patches of open habitat following a disturbance like fire (Gadd, 2009; Vinton et al., 1993). Wilson's Warblers use willowy marshes and dense, shrubby growth in coniferous forests, they are also ground nesters and use dense shrubs and grasses to hide their nests; as such they will be negatively impacted as bison remove the dense understory that they rely upon (Gadd, 2009; Kowalczyk et al., 2021). Townsend's Warblers are found in tall, dense late-succession forests and typically nest high in the overstory and much like Wilson's Warblers will experience declines should bison prevent the re-establishment of the forests they rely upon following a fire (Gadd, 2009; Campbell et al., 1994). Brown-headed Cowbirds historically followed herds of plains bison that roamed across the Great Plains and will eat the insects that are kicked up and exposed by the movements of those herds; due to their dependence on dynamic feeding sites maintained by free-roaming bison herds, female cowbirds will lay their eggs in the nests of other birds, often having their young reared by these other birds often at the cost of their own offspring (Gadd, 2009). Because of the close association between bison and cowbirds, brood parasitism rates may be influenced by how often a site is visited since often the ranges of bison and cowbirds are intertwined (Chace & Cruz, 1998).

Bison usage, vegetation density above and below 1 meter, vegetation resources inventory classification, understory height, vegetation composition, average summer temperature, and average summer rainfall were set as fixed effects. I also set the individual identification number of each individual plot as a random effect as I wanted to generalize my results to each of the plots I was studying within the reintroduction zone. Models for each individual species were run first with only bison usage, average temperature, and average rainfall as factors. When attempting to add vegetation structure and composition data, the models for every species except White-crowned Sparrows failed to converge and were dropped to avoid the risk of overfitting. Vegetation composition data were dropped to avoid overfitting the species richness model after it failed to converge. Finally, I converted the results from each model into odds ratio estimates.

## Results

### Vegetation

Vegetation density below 1 meter increased in grassland/shrubland regions when compared to forests and was not significantly associated with bison usage, average temperature, average rainfall, or the number of years since the free-roaming release of the bison in 2018 (Table 2; Figure 10). Vegetation density above 1 meter decreased in grassland/shrubland regions when compared to forests  and was not significantly associated with bison usage, average temperature, average rainfall, or the number of years since the free-roaming release of the bison in 2018 (Table 2; Table 3; Figure 10). Understory height in grassland/shrubland regions has increased when compared to forests as well as since the free-roaming release of the bison in 2018 (Table 4; Figure 11). Understory height had no significant association with bison usage, average temperature, or average rainfall (Table 2; Table 3; Figure 10).

Percent coverage of bare ground decreased in grassland/shrubland regions when compared to forests and was not significantly associated with bison usage, average temperature, average rainfall, or the number of years since the free-roaming release of the bison in 2018 (Table 2; Table 3; Figure 10). Percent coverage of grasses increased in grassland/shrubland regions when compared to forests and were not significantly associated with bison usage, average temperature, average rainfall, or the number of years since the free-roaming release of the bison in 2018 (Table 2; Table 3; Figure 10). Percent coverage of forbs increased with increasing bison usage (Table 4; Figure 11). Percent coverage of forbs had no significant association with ecosystem type, average temperature, average rainfall, or the number of years since the free-roaming release of the bison in 2018 (Table 2; Table 3; Figure 10). Percent coverage of shrubs and trees had no significant association with bison usage, ecosystem type, average temperature, average rainfall, or the number of years since the free-roaming release of the bison in 2018 (Table 2; Table 3; Figure 10).

Percent coverage of mosses decreased with increasing bison usage in grasslands but increased with increasing bison usage in forests (Table 2; Table 3; Figure 10). Moss coverage also decreased in years with higher temperatures and higher levels of rainfall (Table 2; Table 3; Figure 10). Percent coverage of mosses had no significant association with the number of years since the free-roaming release of the bison in 2018 (Table 2; Table 3; Figure 10).

**Table 2. Generalised Linear Mixed Models for each measured vegetation variable. Percent moss model was fitted with a Poisson distribution, percent Tree model was fitted with a Gaussian distribution, and all other models were fitted with Conway-Maxwell Poisson distributions.**

| Response Variable | Model Factor | Estimate | Std. Error | z-value | p-value |
|---|---|---|---|---|---|
| *Density < 1 Meter* | | | | | |
| | Bison Usage | -0.0188 | 0.0418 | -0.447 | 0.654 |
| | Grassland/Shrubland | 0.2938 | 0.1317 | 2.219 | 0.026 |
| | Average Temperature | -0.0050 | 0.0739 | -0.617 | 0.537 |
| | Average Rainfall | -0.0129 | 0.0099 | -1.322 | 0.186 |
| | Years Since Reintroduction | -0.0001 | 0.2589 | -0.545 | 0.585 |
| *Density > 1 Meter* | | | | | |
| | Bison Usage | 0.0008 | 0.0800 | 0.015 | 0.987 |
| | Grassland/Shrubland | -0.5458 | 0.2315 | -2.308 | 0.021 |
| | Average Temperature | 0.01079 | 0.1259 | -0.357 | 0.720 |
| | Average Rainfall | -0.0004 | 0.0170 | 0.221 | 0.825 |
| | Years Since Reintroduction | -0.0002 | 0.4410 | -0.555 | 0.578 |
| *Understory height* | | | | | |
| | Bison Usage | -0.0417 | 0.0519 | -0.815 | 0.414 |
| | Grassland/Shrubland | 0.3908 | 0.3908 | 2.412 | < 0.001 |
| | Average Temperature | 0.0511 | 0.1023 | -0.085 | 0.932 |
| | Average Rainfall | 0.0063 | 0.0136 | 0.550 | 0.582 |
| | Years Since Reintroduction | -0.0002 | 0.0363 | -6.887 | < 0.001 |
| *Bare ground Coverage* | | | | | |
| | Bison Usage | 0.0067 | 0.0429 | 0.157 | 0.875 |
| | Grassland/Shrubland | -0.4173 | 0.1401 | -2.989 | 0.002 |
| | Average Temperature | 0.0452 | 0.1075 | 1.133 | 0.257 |
| | Average Rainfall | 0.0154 | 0.0139 | 0.978 | 0.328 |
| | Years Since Reintroduction | 0.0001 | 0.3928 | 0.545 | 0.585 |

| Response Variable | Model Factor | Estimate | Std. Error | z-value | p-value |
|---|---|---|---|---|---|
| *Grass Coverage* | | | | | |
| | Bison Usage | 0.0049 | 0.0443 | 0.112 | 0.911 |
| | Grassland/Shrubland | 0.4994 | 0.1518 | 3.305 | < 0.001 |
| | Average Temperature | 0.1570 | 0.1579 | 1.271 | 0.203 |
| | Average Rainfall | 0.0176 | 0.0201 | 1.304 | 0.192 |

| | | | | | |
|---|---|---|---|---|---|
| | Years Since Reintroduction | -0.0004 | 0.5883 | -0.351 | 0.725 |
| *Forb Coverage* | | | | | |
| | Bison Usage | 0.0958 | 0.0466 | 2.066 | 0.038 |
| | Grassland/Shrubland | 0.0937 | 0.0937 | 0.630 | 0.528 |
| | Average Temperature | -0.0415 | 0.1107 | -0.308 | 0.758 |
| | Average Rainfall | -0.0114 | 0.0142 | -1.097 | 0.272 |
| | Years Since Reintroduction | -0.0001 | 0.4008 | 0.247 | 0.804 |
| *Shrub Coverage* | | | | | |
| | Bison Usage | -0.0674 | 0.0674 | -1.193 | 0.233 |
| | Grassland/Shrubland | -0.1591 | 0.2091 | -0.765 | 0.444 |
| | Average Temperature | 0.1502 | 0.1821 | 0.928 | 0.354 |
| | Average Rainfall | 0.0118 | 0.0234 | 0.856 | 0.392 |
| | Years Since Reintroduction | 0.0007 | 0.6667 | -0.399 | 0.690 |
| *Tree Coverage* | | | | | |
| | Bison Usage | 0.0871 | 0.1139 | 0.779 | 0.436 |
| | Grassland/Shrubland | -0.0106 | 0.3735 | -0.021 | 0.983 |
| | Average Temperature | 0.1163 | 0.2719 | 0.993 | 0.321 |
| | Average Rainfall | 0.0188 | 0.0188 | 0.404 | 0.687 |
| | Years Since Reintroduction | -0.0002 | 0.0977 | 0.398 | 0.691 |
| *Moss Coverage* | | | | | |
| | Bison Usage | 0.3289 | 0.0734 | 4.482 | < 0.001 |
| | Grassland/Shrubland | -0.5100 | 0.1862 | -2.775 | 0.005 |
| | Average Temperature | -0.3748 | 0.0510 | -8.843 | < 0.001 |
| | Average Rainfall | -4.074 | 0.0073 | -5.677 | < 0.001 |
| | Years Since Reintroduction | -0.0005 | 0.1344 | -0.643 | 0.520 |
| | Use Index * Grassland/Shrubland | -0.3496 | 0.1069 | -3.267 | 0.001 |

**Table 3. Noted trends in vegetation structure and composition in response to bison usage intensity. + Indicates an increase, - indicates a decrease and 0 indicates no significant association.**

| Response Variable | Trend |
|---|---|
| Vegetation Density < 1 Meter | 0 |
| Vegetation Density > 1 Meter | 0 |
| Understory Height | 0 |
| Bare Ground | 0 |
| Grasses | 0 |
| Forbs | + |
| Shrubs | 0 |
| Trees | 0 |
| Mosses | - (Grassland/Shrubland)<br>+(Forest) |

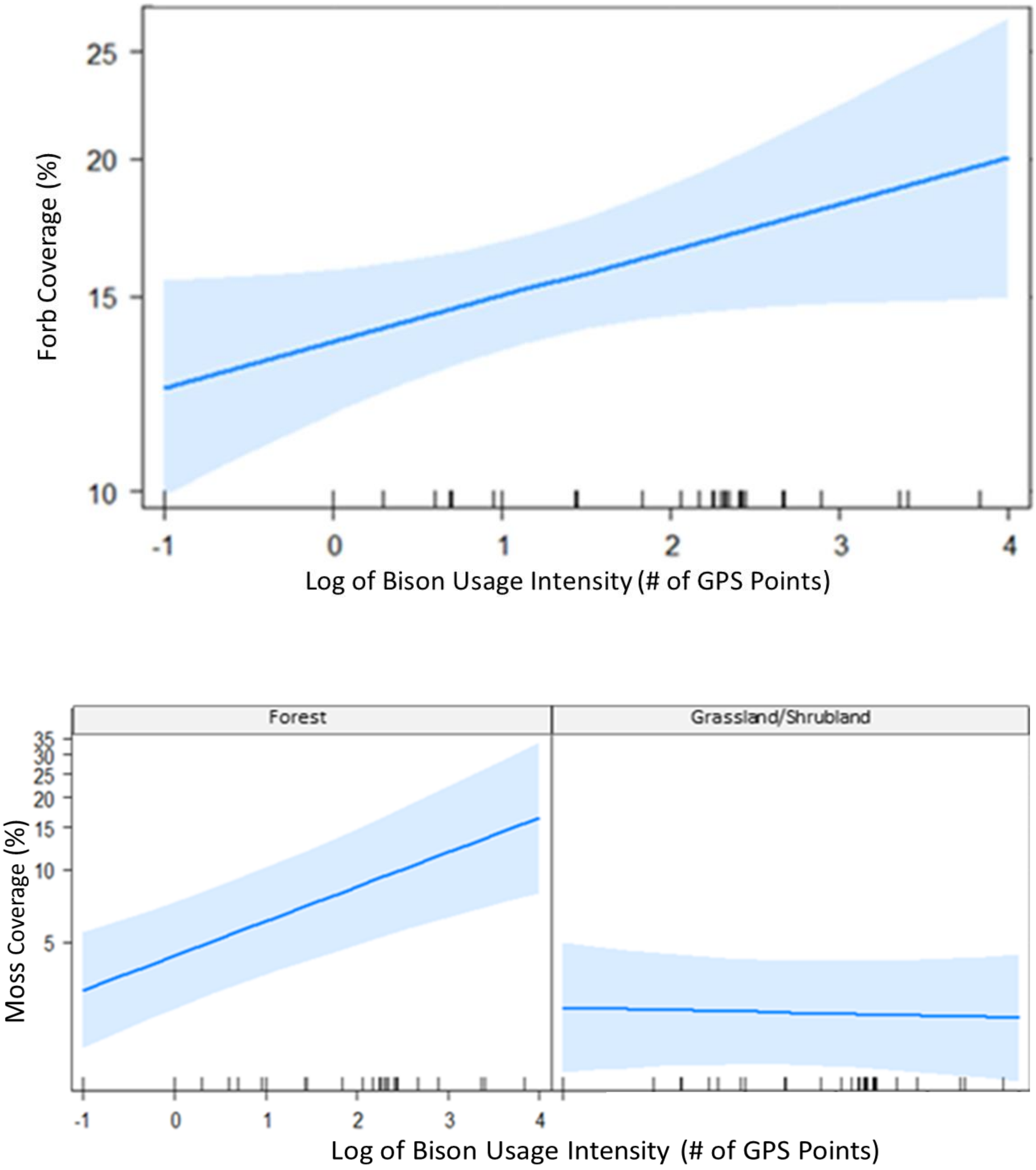

**Figure 10. Effects plots showing the relationship between bison usage intensity and the percent coverage of forbs and mosses.**

## Birds

The detection rate (the number of times a species was recorded during a sampling session) across all species decreased with increasing bison usage, decreased with increasing temperature, and has decreased since 2018 (Table 3; Figure 11). The detection rateof all species surveyed was not significantly associated with average rainfall (Table 3; Figure 11). Species richness has increased since the free-roaming release of the bison in 2018 and was not significantly associated with bison usage, average temperature, or average rainfall (Table 3; Figure 11).

When vegetation factors were accounted for, the detection rate across all species was not significantly associated with bison usage, the number of years since the free-roaming release of the bison in 2018, ecosystem type, average temperature, average rainfall, density below 1 meter, density above 1 meter, understory height, or the percent coverage of bare ground, grasses, forbs, shrubs, trees, or mosses (Table 4, Figure 12).

There was also no significant association between species richness and bison usage, the number of years since the free-roaming release of the bison in 2018, ecosystem type, average temperature, average rainfall, density below 1 meter, density above 1 meter, understory height, or the percent coverage of bare ground, trees, or mosses (Table 4, Figure 12).

Wilson’s Warblers have been detected less often since the free-roaming release of the bison in 2018 and in warmer years (Table 6; Figure 13). Wilson’s Warbler abundance was not significantly associated with bison usage or average rainfall (Table 5; Figure 13). Brown-headed Cowbirds were less likely to be detected in warmer years and were otherwise not significantly associated with bison usage, the number of years since the free-roaming release of the bison in 2018, or average rainfall (Table 6; Figure 14). White-crowned Sparrows were detected less often since the free-roaming release of the bison in 2018 and in warmer years. White-crowned Sparrow abundance was not significantly associated with bison usage or average rainfall (Table 7; Figure 15). When vegetation factors were accounted for, no variables were impacted the detection of White-crowned Sparrows (Table 8). Townsend’s Warblers were detected less often as bison usage increased and were otherwise not significantly associated with the number of years since the free-roaming release of the bison in 2018, average temperature or average rainfall (Table 9; Figure 16).

**Table 4. Generalised Linear Mixed Models of the effects of bison usage intensity, the total abundance of all species sampled and species richness. Both models were fitted with Conway-Maxwell Poisson distributions.**

| Response Variable | Model Factor | Estimate | Std. Error | z-value | p-value |
|---|---|---|---|---|---|
| *Total Abundance* | | | | | |
| | Bison Usage | -0.0328 | 0.0072 | -4.51 | < 0.001 |
| | Years Since Reintroduction | -0.0262 | 0.0068 | -3.85 | < 0.001 |
| | Average Temperature | -0.0745 | 0.0091 | -8.14 | < 0.001 |
| | Average Rainfall | -0.0006 | 0.0068 | -0.82 | 0.410 |
| *Species Richness* | | | | | |
| | Bison Usage | 0.0080 | 0.0119 | 0.675 | 0.500 |
| | Years Since Reintroduction | 0.0540 | 0.0108 | 4.993 | < 0.001 |
| | Average Temperature | 0.0215 | 0.0143 | 1.503 | 0.133 |
| | Average Rainfall | 0.0012 | 0.0013 | 0.930 | 0.352 |

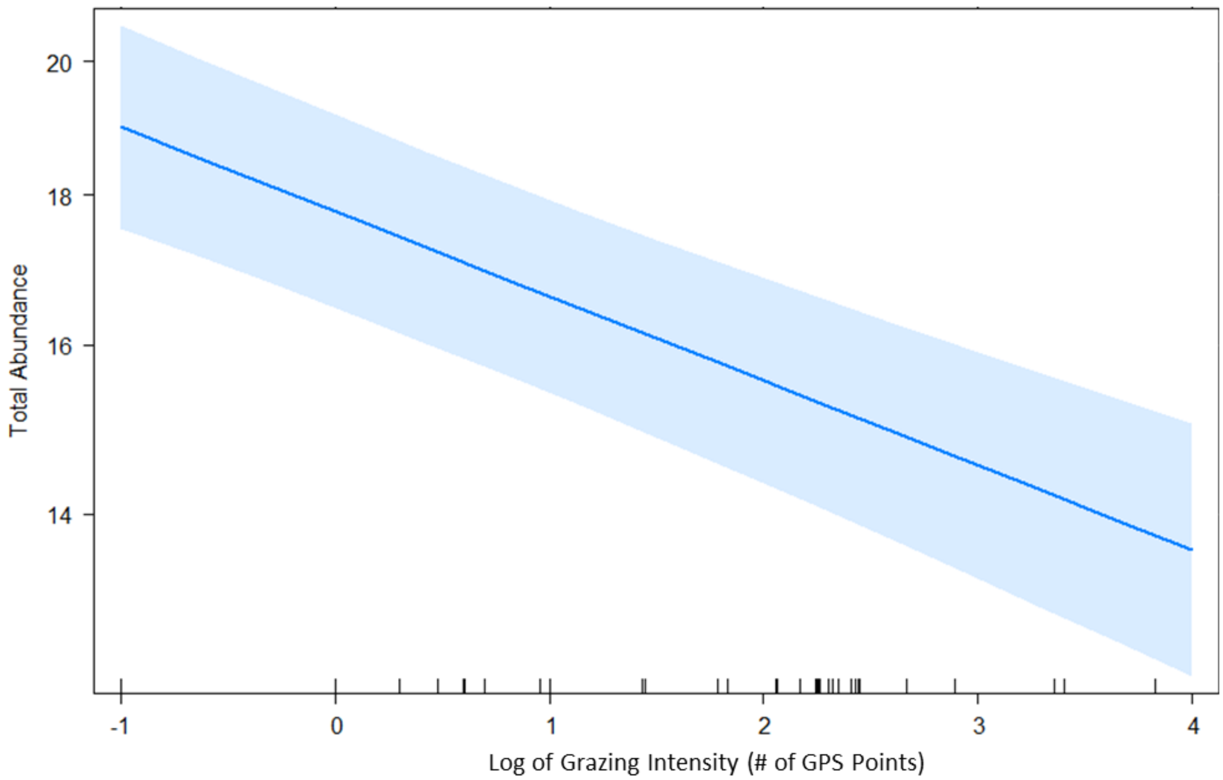

**Figure 11. Effects plots showing the relationship between bison usage intensity and the total abundance of all species surveyed.**

**Table 5. Generalised Linear Mixed Models of the effects of bison usage intensity, understory height, density, and composition on the total abundance of all species sampled and species richness. Both models were fitted with Conway-Maxwell Poisson distributions.**

| Response Variable | Model Factor | Estimate | Std. Error | z-value | p-value |
|---|---|---|---|---|---|
| *Total Abundance* | | | | | |
| | Bison Usage | -0.0162 | 0.0378 | -0.430 | 0.667 |
| | Years Since Reintroduction | -0.3454 | 0.1834 | -1.882 | 0.059 |
| | Grassland/Shrubland | 0.0265 | 0.1388 | 0.191 | 0.848 |
| | Average Temperature | -0.1720 | 0.0764 | -2.246 | 0.024 |
| | Average Rainfall | -0.0074 | 0.0207 | -0.610 | 0.541 |
| | Density < 1 Meter | -0.0012 | 0.0098 | -0.123 | 0.901 |
| | Density > 1 Meter | 0.0122 | 0.0139 | 0.880 | 0.378 |
| | Understory height | -0.0099 | 0.0105 | -0.929 | 0.353 |
| | Bare ground Coverage | 0.0350 | 0.0409 | 0.856 | 0.392 |
| | Grass Coverage | 0.0427 | 0.0409 | 1.044 | 0.296 |
| | Forb Coverage | 0.0537 | 0.0412 | 1.302 | 0.192 |
| | Shrub Coverage | 0.0428 | 0.0404 | 1.059 | 0.289 |
| | Tree Coverage | 0.0024 | 0.0016 | 1.443 | 0.149 |
| | Moss Coverage | 0.0271 | 0.0404 | 0.670 | 0.502 |
| *Species Richness* | | | | | |
| | Bison Usage | 0.0283 | 0.0316 | 0.895 | 0.371 |
| | Years Since Reintroduction | 0.0711 | 0.1149 | 0.619 | 0.536 |
| | Grassland/Shrubland | 0.0076 | 0.1087 | 0.070 | 0.944 |
| | Average Temperature | 0.0103 | 0.0356 | 0.289 | 0.772 |
| | Average Rainfall | -0.0062 | 0.0063 | -0.977 | 0.328 |
| | Density < 1 Meter | -0.0008 | 0.0068 | -0.127 | 0.899 |
| | Density > 1 Meter | -0.0062 0.9938 | 0.0066 | -0.937 | 0.349 |
| | Understory height | 0.0023 1.0023 | 0.0073 | 0.321 | 0.746 |

### *Wilson's Warbler*

**Table 6. Generalised Linear Mixed Models of the effects of bison usage intensity on the total abundance of Wilson's Warblers. Model was fitted with a Conway-Maxwell Poisson distribution.**

| Response Variable | Model Factor | Estimate | Std. Error | z-value | p-value |
|---|---|---|---|---|---|
| *Total Abundance* | | | | | |
| | Bison Usage | -0.0137 | 0.0357 | -0.386 | 0.699 |
| | Years Since Reintroduction | -0.1112 | 0.0312 | -3.557 | < 0.001 |
| | Average Temperature | -0.1318 | 0.0418 | -3.155 | 0.001 |
| | Average Rainfall | -0.0017 | 0.0030 | -0.574 | 0.566 |

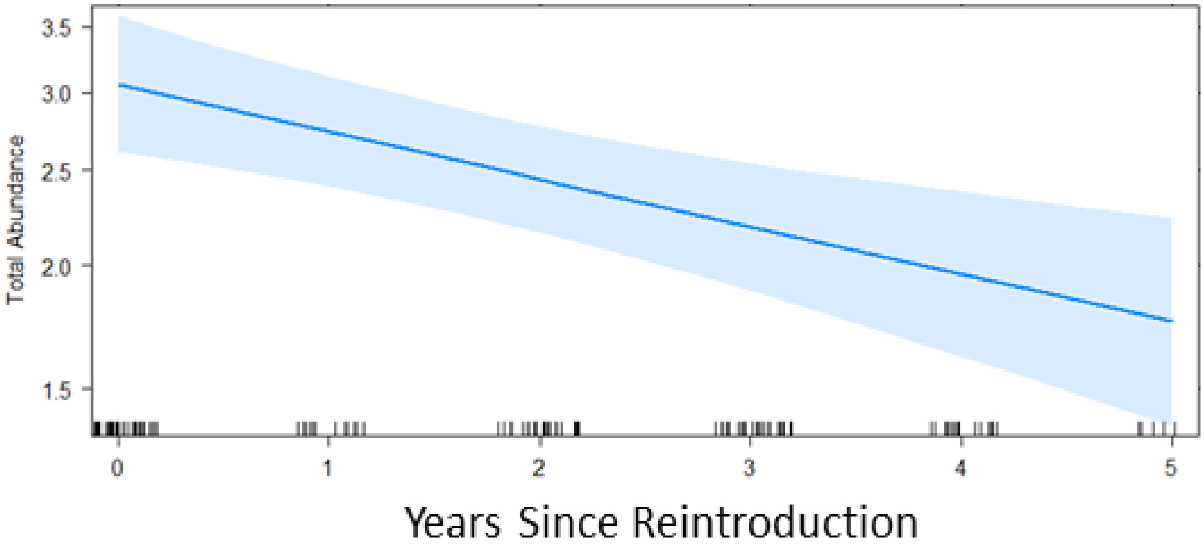

**Figure 13. Effects plot showing the relationship between the number of years that have passed since the reintroduction occurred and the abundance of Wilson's Warblers.**

*Brown-headed Cowbird*

**Table 7. Generalised Linear Mixed Models of the effects of bison usage intensity on the total abundance of Brown-headed Cowbirds. Model was fitted with a Conway-Maxwell Poisson distribution.**

| Response Variable | Model Factor | Estimate | Std. Error | z-value | p-value |
|---|---|---|---|---|---|
| *Total Abundance* | | | | | |
| | Bison Usage | 0.0421 | 0.4157 | 1.013 | 0.310 |
| | Years Since Reintroduction | -0.0583 | 0.0471 | -1.236 | 0.216 |
| | Average Temperature | -0.1262 | 0.0637 | -1.979 | 0.047 |
| | Average Rainfall | 0.0022 | 0.0052 | 0.431 | 0.666 |

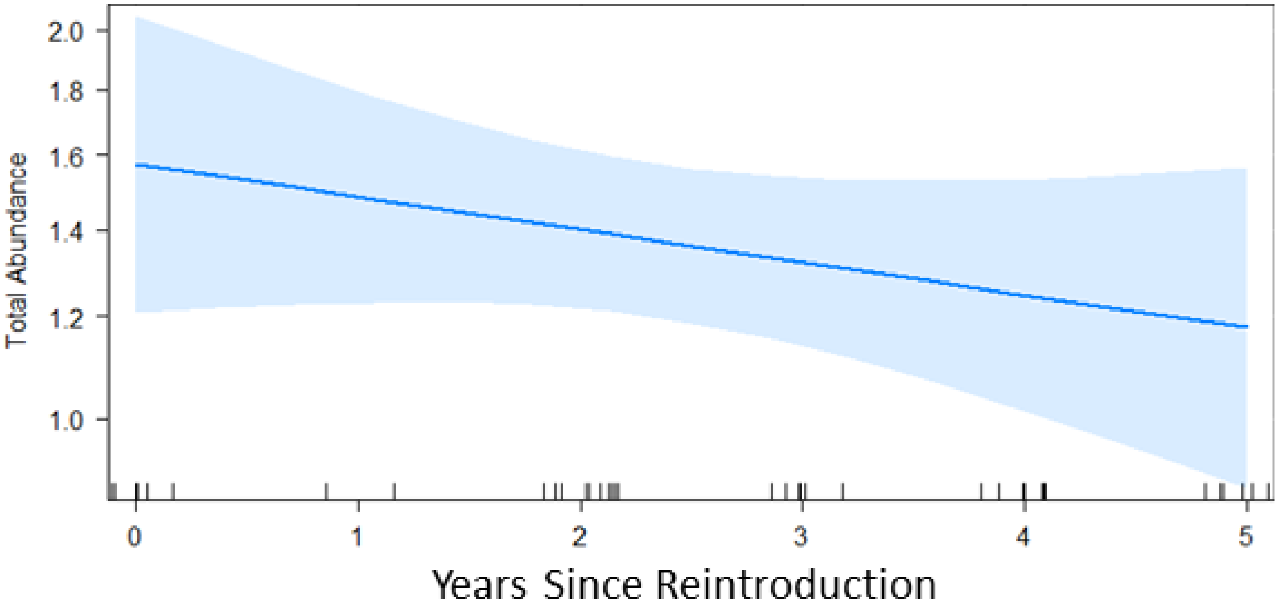

**Figure 14. Effects plot showing the relationship between the number of years since the reintroduction occurred and the abundance of Brown-headed Cowbirds.**

### *White-Crowned Sparrow*

**Table 8. Generalised Linear Mixed Models of the effects of bison usage intensity on the total abundance of White-crowned Sparrows. Model was fitted with a Conway-Maxwell Poisson distribution.**

| Response Variable | Model Factor | Estimate | Std. Error | z-value | p-value |
|---|---|---|---|---|---|
| *Total Abundance* | | | | | |
| | Bison Usage | -0.0038 | 0.0262 | -1.309 | 0.190 |
| | Years Since Reintroduction | -0.0857 | 0.0251 | -3.412 | < 0.001 |
| | Average Temperature | -0.2080 | 0.0379 | -5.485 | < 0.001 |
| | Average Rainfall | -0.0038 | 0.0025 | -1.504 | 0.132 |

**Table 9. Generalised Linear Mixed Models of the effects of bison usage intensity, understory height, density, and composition on the total abundance of White-crowned Sparrows. Model was fitted with a Conway-Maxwell Poisson distribution.**

| Response Variable | Model Factor | Estimate | Std. Error | z-value | p-value |
|---|---|---|---|---|---|
| *Total Abundance* | | | | | |
| | Bison Usage | -0.0164 | 0.0709 | -0.232 | 0.816 |
| | Grassland/Shrubland | 0.0077 | 0.3493 | 0.221 | 0.825 |
| | Years Since Reintroduction | 0.1493 | 0.1722 | 0.867 | 0.386 |
| | Density < 1 Meter | 0.0106 | 0.0229 | 0.464 | 0.643 |
| | Density > 1 Meter | -0.0059 | 0.0320 | -0.185 | 0.853 |
| | Understory height | 0.0090 | 0.0232 | 0.388 | 0.698 |
| | Bare ground Coverage | 0.0396 | 0.0626 | 0.633 | 0.526 |
| | Grass Coverage | 0.0423 | 0.0608 | 0.696 | 0.486 |
| | Forb Coverage | 0.0484 | 0.0585 | 0.828 | 0.408 |
| | Shrub Coverage | 0.0381 | 0.0575 | 0.663 | 0.508 |
| | Moss Coverage | 0.0674 | 0.0617 | 1.092 | 0.275 |
| | Tree Coverage | -0.0053 | 0.0033 | -1.575 | 0.115 |

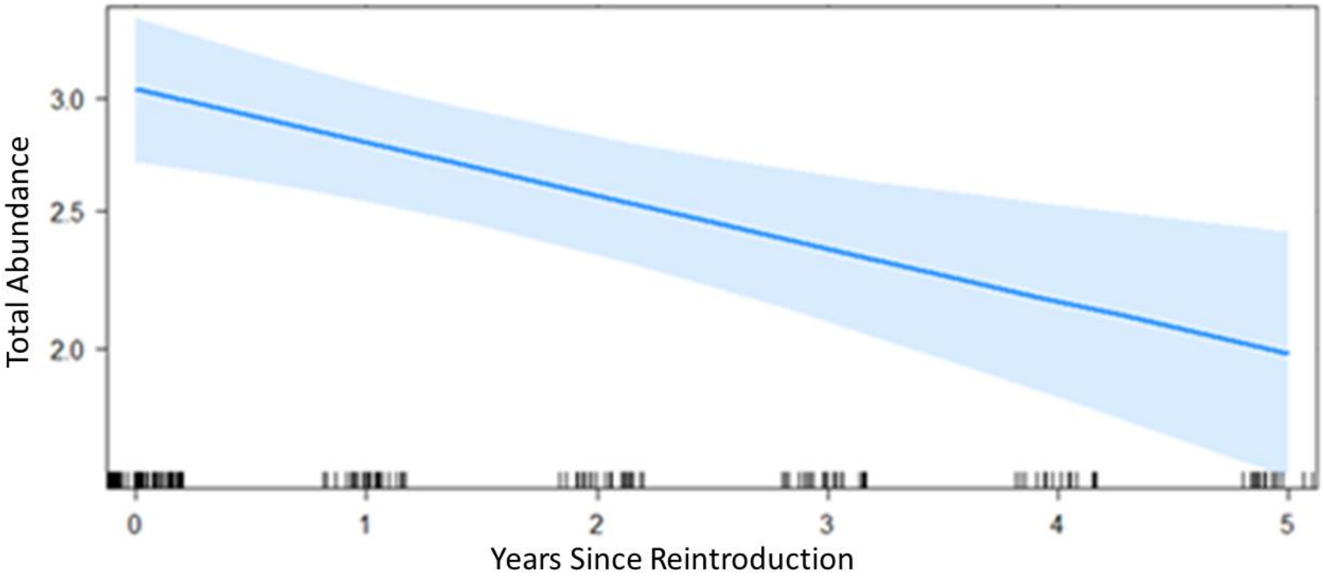

**Figure 15. Effects plot showing the relationship between the number of years since the reintroduction occurred and the abundance of White-crowned Sparrows.**

### *Townsend’s Warbler*

**Table 10. Generalised Linear Mixed Models of the effects of bison usage intensity on the total abundance of Townsend’s Warblers. Model was fitted with a Conway-Maxwell Poisson distribution.**

| Response Variable | Model Factor | Estimate | Std. Error | z-value | p-value |
|---|---|---|---|---|---|
| *Total Abundance* | | | | | |
| | Bison Usage | -0.2082 | 0.0856 | -2.432 | 0.015 |
| | Years Since Reintroduction | -0.1007 | 0.0581 | -1.733 | 0.083 |
| | Average Temperature | -0.0153 | 0.0802 | -0.192 | 0.848 |
| | Average Rainfall | 0.0138 | 0.0087 | 1.584 | 0.113 |

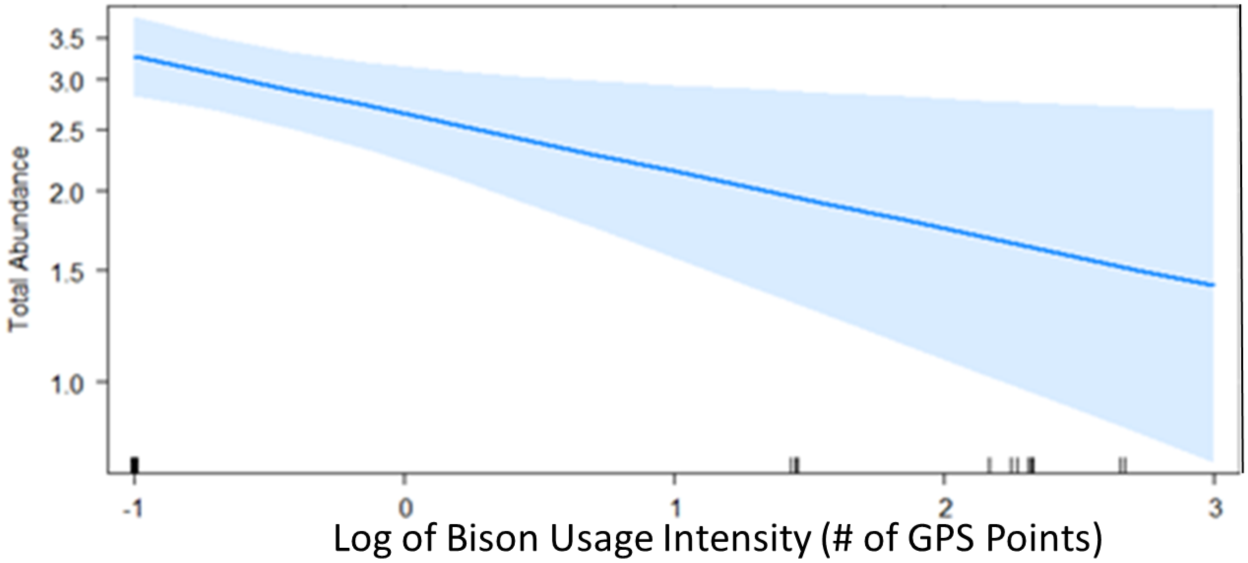

**Figure 16. Effects plot showing the relationship between bison usage intensity and the abundance of Townsend’s Warblers.**

**Table 11. Noted trends in bird abundance, species richness, the abundance of Wilson's Warblers, Brown-headed Cowbirds, White-crowned Sparrows, and Townsend's Warblers in response to bison usage intensity. + Indicates an increase, - indicates a decrease and 0 indicates no significant association.**

| Response Variable | Trend |
|---|---|
| Total Abundance | - |
| Species Richness | 0 |
| Total Abundance (With Vegetation Factors) | 0 |
| Species Richness (With Vegetation Factors) | 0 |
| Wilson's Warblers | 0 |
| Brown-headed Cowbirds | 0 |
| White-crowned Sparrows | 0 |
| Townsend's Warblers | - |

**Table 12. Noted trends between 2015 - 2022 in bird abundance of other bird species detected within the reintroduction zone. Birds with fewer than 5 observations or no significant association were omitted from this table. + Indicates an increase, - indicates a decrease.**

| Response Variable | Trend |
|---|---|
| Canada Jays | - |
| Chipping Sparrows | - |
| Mountain Bluebirds | - |
| Northern Flickers | - |
| Pine Siskins | - |
| Red Crossbills | + |
| Swainson’s Thrush | - |
| Varied Thrush | + |
| Vesper Sparrow | - |
| Warbling Vireo | - |
| Wilson’s Snipe | - |
| White-winged Crossbill | - |
| Yellow-rumped Warbler | - |

## Discussion

I addressed two questions with this study: Does bird abundance, bird species richness, vegetation structure and vegetation composition differ as bison use a site more frequently? And if so, can we attribute the differences in the bird community to changes in the vegetation community?

My results indicated that the percent coverage of forbs increased with increasing bison usage (Table 3). The percent coverage of mosses expressed a different response to increasing bison usage depending on ecosystem type, as it would decrease in grassland/shrublands and increase in forests (Table 3). I found no significant trends in the bird community in relation to increasing bison usage once vegetation factors were controlled for in my model (Table 11). When vegetation factors were excluded from my models, total abundance decreased  with increasing bison usage and the abundance of Townsend's Warblers decreased with increasing bison usage (Table 11). Thus, I have found that bison do impact both vegetation and birds living within the patches of land that they visit frequently, with the abundance of Townsend's Warblers and the overall bird community decreasing with increasing bison use. Increasing bison use was  associated with increased forb coverage well as increasing moss coverage in forests and decreasing moss coverage in grasslands/shrublands.

### *Vegetation*

Changes in vegetation structure were associated more closely with different ecosystem types rather than bison usage. The reintroduction is still in its initial stages, with the bison herd freely roaming the landscape since July 28th of 2018 and increasing to a population of eighty-eight members as of August of 2022 (Heuer, 2019; Ellis, 2022). It is likely that any effects the bison are having on the vegetation community at this stage of the reintroduction are highly localized. Still, by looking at bison reintroductions elsewhere in the world, as well as at the role bison historically played in grassland ecosystems, we may gain insights into how they will work to prevent the expansion and re-establishment of forests after fires in the coming decades.

The low population of the bison herd and the relative lack of time they have had to influence the landscape is likely why there was no noted effect of bison usage on vegetation structure in my study. This also indicates that the bison may not yet have had a significant impact on other species using the landscape such as birds or other large herbivores. Bison do not necessarily compete directly with other grazers and their presence may not diminish the quality of forage available to other grazers (Ranglack et al., 2015). Despite this, bison may still have a deleterious effect on other species in an ecosystem as they consume or otherwise disturb the plant communities they depend upon, as seen in riparian areas within in Yellowstone National Park in the US (Kauffman et al., 2023). Much of this is contingent on how many bison are present in a landscape, as when bison are not limited to small spaces at high stocking rates, they have been shown to increase the biodiversity of birds in arid grassland ecosystems (Boyce et al., 2022; Fagre et al., 2022). The population of the Banff herd is expected to continue to grow exponentially and as it does, we may start to see highly localized effects on the landscape, particularly when the herd reaches higher population densities (Fuhlendorf, & Engle, 2001; Parks Canada, 2022).

Bison do not graze randomly and instead seek out patches with high nutritive qualities, particularly those that have been burned or that have a high composition of grasses (Vinton et al., 1993). Thus, a reintroduction of bison can result in increased structural heterogeneity as they preferentially graze across a landscape and create a “patchwork” of intensively and lightly grazed areas (Henebrey, 1993). Paradoxically, intensive usage can also sometimes be associated with increases in vegetation density and height, as the edges of intensively grazed patches can see an increase in productivity when space opens for established plants to expand into (Franco & Harper, 1988). Sex ratios in a bison herd may influence how the vegetation community responds, as male and female bison roam in separate groups outside of the rut and have been shown to have different dietary preferences from one another; such as females expressing a preference for $C_4$ grasses when compared to males (Rosas et al., 2005). The Banff bison herd is comprised mostly of females to encourage population growth in these early years; thus, their usage patterns and the overall changes to vegetation structure they make at these localized scales may change in the future as the sex ratio of the herd becomes more even (Heuer, 2019; Rosas et al., 2005).

Neither vegetation density nor height were significantly influenced by temperature or rainfall amounts in the years I studied. It is possible that the small number of years examined is not a long enough time scale to examine any significant changes from these forces, particularly as it is usually studies including datasets that span decades that have associated significant changes in vegetation structure with changes in mean annual temperature and precipitation (Chen et al., 2015). Work by Shyrock et al. (2015) found that annual precipitation was an important driver in the recovery of grassland vegetation structure following a disturbance like fire; thus, as the bison herd grows, and the scale of the disturbances they cause grows in turn, climatic factors like precipitation will be of importance in determining how rapidly and to what state these plant communities recover.

Changes in vegetation have been noted to occur within as little as 6 years of a bison reintroduction (Dvorský et al., 2022). Forbs were shown to be more common with increased bison usage, and mosses had an interaction with both bison usage and ecosystem type, as they were more common with increasing bison usage in forest ecosystems and became less common with increasing bison usage in grassland/shrubland ecosystems. Bare ground, rocks, and pine needles are less common in grassland/shrubland ecosystems, while grasses are more common in grassland/shrubland ecosystems. Bison, being ecosystem engineers, can impact the plant community of the landscapes they roam within in a variety of ways, benefiting some types of plants while negatively impacting others.

Bison co-evolved with grasslands in North America and have been associated with introducing greater plant species diversity when compared to cattle (Towne et al. (2005); Karp et al. (2018); Tarleton & Lamb, 2020). As bison preferentially graze on grasses, forbs experience less competition and can expand across the grazed area, this “competitive release” was evident in my study, with forb coverage increasing with increasing bison usage (Knapp et al., 1999). Work by Elson & Harnett (2017) found that grazing by bison resulted in an increase in both the abundance and species richness of forbs in grasslands. Bison tend to consume a greater proportion of forbs in times of nutritional stress, though this may be remedied by increasing protein percentages in what grasses are present on a landscape using prescribed burns (Craine et al. 2015). The presence of wetlands within the reintroduction zone may also mediate this response as Blackburn et al (2021) found that bison in a restored grassland preferentially consumed forbs over grasses around wetlands in the late summer and fall. Forbs tend to respond to disturbances like grazing or fire on a species-specific level, thus future research may wish to examine the response of the different forb species within the reintroduction zone (Biondini et al., 1989). An increase in the coverage of forbs on the landscape also carries implications for the bird community. Forbs can benefit some birds by providing perches to sing and entice mates upon and may also function as nesting material (Patterson & Best, 1996). Forbs may also provide a diverse food source for birds that can provide food over a longer period as different forbs flower and seed throughout the year (Vickery et al., 2002; Schmidt et al., 2022). Forbs like wildflowers also help to form a more heterogeneous vegetation structure across the landscape and aid in obscuring birds and their nests from predators (Hummel et al., 2017).

While the decrease in the percent coverage of mosses within grassland/shrubland ecosystems was minimal, forests saw a marked rise in mosses as bison usage increased. This is paradoxical since most subalpine coniferous forests in the Canadian Rockies are home to long-lived feather mosses that we would expect to decline as bison disturb their habitat (Gadd, 2009; Turetsky et al., 2010). However, this may be explained by the differing microclimates within a forest, where a drier microclimate might discourage the growth of bryophytes and other plants and wetter ones might encourage that growth (Busby et al., 1978; Skre & Oechal, 1981). If these other plants are also palatable to bison or offer other advantages like cover from predators when they are traveling through forest ecosystems, then that may explain the associated increases between bison usage and mosses (Jaroszewicz et al., 2021). Bison moving through these forests will likely cause repeated disturbances to the plant communities present within them. As plant communities recover from a disturbance, they can experience significant changes in their composition; this is because the pathways of succession for plant communities are not pre-determined and can be affected by a wide variety of fixed factors such as the topography around a site and random factors like the frequency of disturbances a site experiences. (Kayes et al., 2010). As time goes on and the herd disturbs more of the land, we may start to see declines in long-lived species of forest bryophytes that may be replaced by more disturbance tolerant bryophytes (Turetsky et al., 2010; R. Belland, Personal Communication, December 22, 2022). Disturbance from the Banff herd in grasslands in the reintroduction zone may also be felt at highly localized scales; for example, bison selectively graze closer to wetlands that will naturally contain greater percentages of bryophytes than would be found in the drier sites (Blackburn et al., 2021; Kauffman et al., 2023). Mosses can form an important part of the nesting material used by different species of birds (Breil & Moyle, 1976; Andreas, 2010; Hamao et al., 2016). Some species of birds are known to consume mosses as part of their diet, though this has not been noted in species present in my research area (Gunathilaka, 2019). Mosses may also provide other services to birds, such as bathing material when the moss is saturated with water, or by forming hummocks that provide birds with perches for calling or watching for predators (Glime, 2017). Conversely, birds may also aid in dispersing moss spores and allowing them to propagate in new areas (Glime, 2017).

Bison have shown a preference for grasses in mountain grasslands, with the diet of the Henry Mountains bison herd in Utah being almost exclusively grasses (Van Vuren, 1984). While there was no significant reduction in grass coverage due to bison grazing in my study, the increase in forbs that was noted was likely due to a competitive release caused by bison preferentially grazing on grass. Grasslands subject to long-term usage by bison may show marked differences when compared to undisturbed grasslands. Veen et al. (2008) found that patches that had been grazed by bison saw increased species richness and decreased dominance of a few grass species when compared to ungrazed patches. For instance, female bison will preferentially graze on C4 grasses and can result in increased coverage and diversity of C3 grasses in the initial stages of grazing, though this effect can be moderated by colonization from forbs instead of C3 grasses into these patches (Plumb & Dodd, 1993; Jackson et al., 2010; Rosas et al., 2005).

The decline in the percent coverage of bare ground in grasslands when compared to forest ecosystems was due to the needles that fall from conifers and cover the forest floor. While some studies have reported issues with abortions rising from cattle and bison herds that consume an excessive amount of pine needles, the relative lack of barriers to movement and amount of superior forage available to the Banff bison herd should minimize this risk (Short et al., 1992). Overgrazing in some areas can rarely result in an increase in bare ground as vegetation is removed from a patch of land and should be carefully monitored in landscapes containing ungulates like bison and elk (Pengelly, 1963; Singer et al., 1998). Indigenous peoples understood this well and regularly set fires within the landscape to encourage bison to return to different hunting grounds each year and resuming this practice will likely aid in having the herd move to new areas in the reintroduction zone, possibly offering some relief to other patches that they had been using intensely (Arthur, 1974; Anderson & Barbour, 2003). Maintaining or expanding the amount of land available to the herd in addition to regular prescribed burns will be key in reducing the risk of overgrazing as the herd population increases.

Traditional knowledge from Elders of the Stoney Nakoda First Nation has highlighted the importance of willows that grow at high altitude as part of the winter forage for the plains bison in the Canadian Rockies (Stoney Nakoda Nations, 2022). Due to my study taking place entirely within valley bottoms at lower elevations this consumption may not have been captured. Additionally, a study by Kowalczyk et al. (2021) found a significant reduction in woody, shrubby vegetation after European bison had been reintroduced to an ancient forest in Poland. This study also noted that the bison were most likely to graze in areas that were in initial stages of succession rather than in late succession closed canopy forests (Kowalczyk et al., 2021). A study by Tareton and Lamb (2021) found negligible impacts of reintroduced bison in Riding Mountain National Park on the shrub community and asserted that fire was a necessary disturbance before bison could affect the proportion of shrubs, particularly established, dense stands.

Trees were rarely captured by the vegetation surveys (N = 15) and thus I am extremely cautious in my interpretation of these results. However, it is likely that any effects of the Banff bison herd would be on younger, early seral-stage forests. Bison historically were known to 'hold back' these forests following a disturbance, consuming tree saplings, and preventing their re-establishment (Campbell et al., 1994.

Plains bison reintroductions are an important part in conserving the species itself and restoring historical disturbance regimes within their former range (Allred et al., 2011). Bison are also an important aspect of many Indigenous cultures and restorations involving them are a key part in restoring Indigenous sovereignty over their land (Taschereau, 2020). A deeper understanding of how bison modify the vegetation structure and composition of landscapes they live upon will help land managers understand their importance and the benefits they can provide to other species living on the landscape through those modifications.

### *Birds*

Bison had few apparent impacts on the birds surveyed in my study. Total bird abundance was associated with a decline as bison usage increased. However, once vegetation data were added into the models, no significant effects were noted. I had originally expected changes to vegetation structure to be the main mechanism by which birds might be affected by the bison, though the bison only significantly affected the percent coverage of forbs and of mosses. This change in percent coverage of forbs and mosses seems to have had an overall negative effect on birds in the reintroduction zone, with the overall abundance of birds in the reintroduction zone showing a decline with increasing bison presence while the coverage of forbs showed an increase, and the coverage of mosses showed an increase in forests and a decrease in grasslands with increasing bison usage.

Noted changes to forb and moss coverage by bison may have significantly affected the abundances of birds living in the reintroduction zone. Increased forb coverage can often come at the expense of grass coverage as bison preferentially graze grasses over forbs. Patterson & Best (1996) suggested that some birds may express a preference for patches with a greater proportion of grasses compared to forbs and thus if the relative proportion of grasses is lowered, then the abundance of those species may decline. Still, this decline is somewhat perplexing as forbs still offer high quality seeds and nesting material and in the case of my study, I did not see a corresponding significant drop in grass coverage at sites that were used more heavily by bison (Dickson et al., 1996). A decline in bird abundance given increasing moss coverage in forests is perplexing as well, as birds have been noted as playing an important role in dispersing moss spores (Chmielewski & Eppley, 2022). Though it is also possible that too high a proportion of mosses on the forest floor may result in a lack of other vegetation that would otherwise be used for nesting or that may carry more abundant insect communities for birds to consume.

Many of the bird species that showed a decline such as the Yellow-rumped Warbler (*Setophaga coronata*), Chipping Sparrow (*Spizella passerina*), White-winged Crossbill (*Loxia leucoptera*), Warbling Vireo (*Vireo gilvus*) and Swainson’s Thrush (*Catharus ustulatus*) are species dependent on forested habitats (Table 12). While there have been fewer studies done on the effects of bison on forest birds, some studies have noted that the effects of their presence may be complex. For instance, bison fur may provide nesting material for some birds, while their tendency to rub against woody vegetation can disturb nesting sites and other critical habitat (Sanderson et al., 2008). The life-history strategy of a bird may factor into its response to disturbances from large herbivores as well, with one study in the interior mountains of British Columbia noting that forest birds that consumed insects within bark responded positively to cattle presence while aerial insectivores declined with cattle presence (Whitehorn et al., 2011). Many of these bird species have also experienced a decline over time, so it is also possible that they are declining due to a reason other than the bison. Though regardless it is possible that bison contributed to this trend since these are birds that have established themselves over the last decades in a bison-free landscape, and those that are in decline are likely sensitive to the disturbances caused by bison. In the very long term, it is likely that species which prefer the disturbed habitats that bison create will enter the reintroduction zone, leading to a more diverse set of ecosystems in the coming decades.

Past studies have noted the importance of bison in creating a heterogenous vegetation structure across a landscape as they preferentially use certain spots over others; however, these studies have been performed on herds with a higher population and that are occupying smaller spaces than Banff's herd (Knapp et al., 1999; Fagre et al., 2022). The Banff bison herd have patches within their reintroduction zone that they prefer to spend time in; the effects from this are highly localized and are likely not being captured by the monitoring program that is set up to cover a 1200 $km^2$ area. In this regard, it is possible that two things are happening. The first is that the scale of the disturbance from the bison herd is so localized that birds that are being displaced by them can easily find alternate, undisturbed sites. The second is that there may not have been sufficient time for birds that benefit from disturbances caused by the bison herd to locate these patches of suitable habitat, or that there may not be enough of this habitat that has been created to yet support a significant number of these disturbance-tolerant species.

The presence of bison on a landscape can support increased biodiversity among birds and other species as bison use different patches at varying intensities and increase habitat heterogeneity across the landscape (Fagre et al., 2022). However, in the short term the effects of this increased heterogeneity and the resulting increases in biodiversity can be less apparent, and there are questions as to whether the presence of bison on a landscape is influencing some species, as some may not be affected by the presence of bison until the herd is sufficiently large or enough time has passed for them to alter the vegetation of the landscape sufficiently (Herakovich et al., 2021). The scale and uniformity of the disturbances matter as well; as noted by Powell (2006), widespread burning and intensive usage in a grassland ecosystem led to population declines in some grassland songbirds as habitat heterogeneity declined. In a study of the impacts of a low density, moderately grazed enclosure of bison on grassland songbird, Sliwinski (2011) found that most of the focal species in the study declined with increasing bison usage, but that increasing usage also led to increased species richness.

The lack of effect the Banff herd is having on species richness is not unprecedented, as Herakovich et al. (2021) found that there was no noticeable impact of a reintroduced herd of plains bison on the species richness of grassland birds in a restored tallgrass prairie. They postulated that this may have been due to the low density of the bison herd having little impact on the vegetation structure of the study site (Herakovich et al., 2021). Researchers working with larger herds in the National Bison Range in Montana and Yellowstone National Park in Wyoming have noted an increase in grassland songbird richness as bison usage increased on the landscape, though cautioned that bison usage intensity ought to be varied enough to ensure habitat is created for the widest variety of species (Fagre et al., 2022). Monitoring the changes bird communities induced by the Banff herd over the long term will be important, as the scale of both the herd's potential population and the amount of habitat available to them may result in novel changes to bird populations not otherwise noted in reintroductions of smaller, more constrained herds (Boyce et al., 2021; Sliwinski and Koper, 2015). Bison fulfilling their historical role of creating heterogeneous habitat across the landscape that is used by the herd at different intensities will be a key part in increasing grassland songbird species richness into the future (Henebrey, 1993).

While Wilson's Warbler numbers have declined since the reintroduction occurred, it is difficult to link this change to the bison themselves. One method by which Wilson's Warblers have been known to decline is by the increased consumption and trampling of shrubs by herbivores (Baril et al. 2011). Willows and thickets in riparian zones form part of the habitat used by Wilson's Warblers and work in Yellowstone National Park has shown that large herbivores like moose can decrease the abundance of birds dependent on those habitats via consumption or trampling of the vegetation (Berger et al., 2001; Gadd, 2009). However, given the lack of any significant reduction in shrub coverage by the bison, it is unlikely that this is taking place at any meaningful scale due to the Banff herd. In fact, Wilson's Warblers have even been shown to benefit from the thinning of tree canopies and may be able to access new habitat in forests that are opened by bison following a fire (Stuart-Smith et al., 2006). Warbler nests have also been recorded as being parasitized by Brown-headed Cowbirds, though Brown-headed Cowbird numbers have not increased significantly since the start of the reintroduction (Chace & Cruz, 1998). There are other factors beyond Banff National Park that are responsible for the decline, particularly given declining trend of these and other songbirds in North America as well as the fact that Wilson's Warblers spend most of the year outside of Banff National Park (Rosenberg et al., 2019). Any notable increase or decrease in Wilson's Warblers will require far more bison and far more time to have passed before they may become apparent, and as of right now it does not appear as though the bison are significantly affecting Wilson's Warbler populations in the reintroduction zone. In the future, however, Wilson's Warblers may experience population declines if the Banff herd trample and browse on the riparian shrubs that form their habitat.

Brown-headed Cowbirds had no significant response to the bison, showing results consistent with work by Bock et al. (1993) on cattle grazing in the great plains, where Brown-headed Cowbirds showed little response to increased cattle usage. Sliwinsky (2011) found that Brown-headed Cowbird abundance increased immediately following the introduction of cattle onto a grazing enclosure but did not continue to increase with increased stocking rates. The detection frequency of Brown-headed Cowbirds was also found to be unaffected by the presence of bison at low herd densities in a study by Herakovich et al. (2021). In a similar study at the Konza Prairie Biological Station, Powell (2006) found that the abundance Brown-headed Cowbirds exhibited no response to the presence of bison or fire in their habitat. Powell (2006) considered that because Brown-headed Cowbirds can utilize a wide array of habitats across a large range when compared to other songbirds, they may be less affected by disturbances like bison and fire. Importantly, my study captured Brown-headed Cowbird abundance via acoustic recordings of bird song, which are typically performed by males and thus may not have fully captured the abundance of female cowbirds that parasitize the nests of other birds (Norman & Robertson, 1975). Brown-headed Cowbirds observed near modern bison herds will often feed in areas where plains bison are foraging and are willing to travel as far as ten kilometers from potential mates to access those feeding areas (Goguen et al., 2005). Further evidence for this ability to travel is provided by Rothstein et al. (1984), who noted ranges of 2.1 - 6.7 kilometers for Brown-headed Cowbirds to travel to horse corrals and feeders. That large range can come at a cost to Brown-headed Cowbirds, however, as their ability to effectively parasitize the nests of other birds may be mediated by the movement of the bison herds taking them further from breeding grounds (Goguen et al., 2005). It is entirely possible that the Banff bison herd will not be responsible for an increase in abundance of Brown-headed Cowbirds so much as an increase in their range, allowing them to access habitat they would not have been able to before. For instance, bison historically allowed cowbirds to exist at higher elevations and could increase the parasitism rates on songbirds that nest at those high elevations (Chace & Cruz, 1998).

Past studies have shown that White-crowned Sparrows exhibit a wide range of responses to disturbances caused by large herbivores, and in this study were shown to have decreased in the years since the reintroduction. It is difficult to say whether this was a result of the bison reintroduction, however, as when vegetation factors were included in the model there were no significant associations between White-crowned Sparrow abundance and any factor in the model. Still, work with other bison herds may offer insights into some mechanisms by which Banff's bison may have affected White-crowned sparrows in the future. Bock et al. (1993) predicted that White-crowned Sparrows in shrubby habitats would be negatively affected by increased cattle grazing due to the removal of ground cover. This ground cover would otherwise obscure the nests they build in low shrubs or on the ground itself (Gadd, 2009). White-crowned Sparrow abundance may also potentially be reduced by bison rubbing on dead trees and removing the branches that White-crowned Sparrows use to aid in their foraging (Knopf et al., 1988). Fire may serve to mitigate these effects, as work by Porzig et al. (2018) found that White-crowned Sparrows selected for early successional stage habitat. However, increased usage by bison after a burn may remove ground cover and lead to increased nest predation which was a major source of nest failure (Porzig et al., 2018).

Townsend’s Warblers are a forest species and make their nests in tall conifers and it is unsurprising that they are less associated with the open grasslands where the Banff herd is at its densest (Gadd, 2009). The tendency of bison to convert forests to grasslands holds important implications for this species and many other forest obligates. Townsend’s Warblers have been shown to respond poorly to reductions in canopy cover that can result from disturbances like bison and fire (Campbell et al., 1994; Collins & Calabrese, 2012; Sallabanks et al., 2006). Thinning of a tree stand in Oregon was found to result in twice the number of Brown-headed Cowbirds than in a non-thinned stand while Townsend’s Warblers were not present in the thinned stand but were present in the non-thinned stand (Bull et al., 1995). Townsend’s Warblers can still maintain their populations well given sufficient overstory trees left over after a disturbance like fire or logging (Stuart-Smith et al., 2006). It is likely that if major disturbances like fire open late stage, closed canopy forests within the reintroduction zone and if the bison prevent the re-establishment of those forests after they have burned, then there will be a reduction in species dependent on those forest habitats like the Townsend’s Warbler. But if the influence of bison is limited to their movements through forests and their occasional mechanical destruction of younger trees, then it is likely that species like the Townsend’s Warbler will be unaffected.

### *Predictions for the Future*

While the ecosystem in which the Banff bison have been reintroduced to is incredibly dynamic and will be subject to much change in future decades as the climate continues to warm, it is possible to predict how the populations of some bird species living within the reintroduction zone might change in the future by considering how bison disturb and transform landscapes they exist within (Böhning-Gaese et al., 2004). In doing so I assume two things: 1) the warming climate and shifting priorities for Park management means there will be more frequent wildfires in the reintroduction zone, and 2) that the bison population will continue to increase to the projected carrying capacity of between six hundred – one thousand animals (Steenweg et al., 2016).

I have selected five other species for my predictions to assess other common birds living within the reintroduction zone: (America Robin [*Turdus migratorius*], and Canada Jay [*Perisoreus canadensis*]) as well as species of special concern for Banff National Park: Common Nighthawk [*Chordeiles minor*], Evening Grosbeak [*Coccothraustes vespertinus*], and Olive-sided Flycatcher [*Contopus cooperi*].

American Robins are found most often in forested environments within the Canadian Rockies and can be found up to the treeline (Gadd, 2009). I would expect American Robins to experience a reduction in presence within the reintroduction zone if increased fire frequency and grazing by bison converts some of the reintroduction zone from forest habitat to grassland/shrubland habitat. I would also not expect any potential increase in Brown-headed Cowbird populations due to the bison to negatively affect American Robins as they are able to consistently detect and reject the eggs of Brown-headed Cowbirds laid in their own nests (Cruz et al., 2001). American Robins may benefit by the increase forage available from the insects that bison typically introduce to patches that they move into (Moran, 2014). American Robins are widespread across the reintroduction zone, and I do not predict their numbers trending in any significant way as bison provide both benefits and costs to American Robins (Table 13).

Canada Jays are common to forests in the subalpine and montane ecoregions in the Canadian Rockies (Gadd, 2009). Like American Robins, they may experience some population decline if forest habitats are converted to grasslands/shrublands while also benefiting from the increased insect abundance that bison bring. A current threat to Canada Jays is increased freeze-thaw events due to climate change in the fall and early winter that led to their food caches rotting (Sutton et al., 2019). Thus, I would attribute any future population declines in the species within the reintroduction zone to climate change rather than bison (Table 13).

Common Nighthawks are seen within open, forested areas in the Canadian Rockies (Gadd, 2009). They are also listed as threatened on the Species at Risk Act, with some potential sources of the decline being listed as habitat loss, reduced insect prey, and fire suppression (Environment Canada, 2016a). Open forests, particularly those where disturbances like burns have occurred, are preferred habitat for Common Nighthawks (Foley, 2018). They are a species that may benefit from the long-term effects of fire and bison on the landscape, as bison trample and consume forest regrowth following a fire and help to maintain open patches of habitat (De Grandpré et al., 2000; Simonson et al., 2014). Even in the absence of fire, bison may help to open forests through mechanical removal of trees, as we witnessed a male bison toppling three young lodgepole pine trees by rubbing against them during a field outing in August of 2022. I predict that the bison herd will benefit the Common Nighthawk by helping to restore critical habitat in the form of disturbed, open-canopy forests (Table 12).

Evening Grosbeaks are commonly found in the forests of the lower subalpine ecoregions of the Canadian Rockies (Gadd, 2009). They are listed as a species of special concern on the Species at Risk Act partially due to a reduction in mature mixed wood and conifer forests (Environment Canada, 2022). Evening Grosbeaks selectively use older trees as nest-building sites and typically build their nests high up and close to the tree trunk to shield the nests from the elements and from predators (Bekoff et al., 1987). The prey provided by these forests are important to Evening Grosbeaks as well as the birds show a strong preference to consuming Spruce budworms and have been shown to avoid areas where mass tree die-offs have led to a reduction in this food source (Gillihan & Byers, 2001; Mosher et al., 2019). I predict that the bison herd will negatively affect the Evening Grosbeak by disturbing the mature, old growth trees that the species rely upon for nesting and food, though the decline itself may not be very dramatic due to much old-growth forest is available to these birds in the reintroduction zone (Table 13).

Olive-sided Flycatchers are found in open coniferous woods, particularly in places that have been burned recently; the Canadian Rockies, including Banff National Park, form a sizable portion of their breeding range (Gadd, 2009; COSEWIC, 2018). As of April 2018, they have been designated a species of special concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), reflecting an improved situation from their former Threatened designation in November of 2007 (COSEWIC, 2018). Threats to the species on their breeding grounds in Canada have been identified as habitat loss or degradation due to forest harvesting and disturbance by humans as well as changes in fire regimes from climate change and fire suppression (COSEWIC, 2018). Olive-sided Flycatcher populations often require a patchwork of different ecosystem types at the landscape scale to thrive, with a mix of old-growth forests mixed with patches that have been subject to natural disturbances (Haché et al., 2014). Frequent, intense burns have been noted as a valuable tool in maintaining these open patches, though bison may also act as a supplement to this due to their ability to consume regrowth from the forest and keep those post-fire patches open and suitable for supporting high densities of Olive-sided Flycatchers (Environment Canada, 2016b). I predict that in the long-term, Olive-sided Flycatchers will benefit from the increased habitat heterogeneity bison bring to the landscape scale, particularly as they prevent forests from re-establishing after a fire and aid in maintaining conditions that support high densities of Olive-sided Flycatchers (Table 13).

**Table 13. Predicted trends in bird abundance for two common and three at-risk species in Banff National Park in response to long-term bison usage. + indicates a positive trend, - indicates a negative trend, 0 indicates no significant influence of bison on the species.**

| Species name | Predicted Trend |
|---|---|
| American Robin | 0 |
| Canada Jay | 0 |
| Common Nighthawk | + |
| Evening Grosbeak | - |
| Olive-sided Flycatcher | + |

## Conclusions

The Banff bison herd is small and has only had five years to make some sort of impact on the landscape they have been reintroduced to. Yet, my results show that the bison have made a noticeable impact on forbs, mosses and by decreasing the overall abundance of birds within the reintroduction zone and these examples may provide a window of how the reintroduction zone and those living beings within it may be changed by bison into the coming decades. The herd has been growing at a rate of 33 percent per year over the last five years of the reintroduction project and could grow to over two hundred animals within 8 years (Parks Canada, 2022). These minor changes in the ground cover of mosses and forbs, or in the potential increases in species richness may only grow in scale as more bison roam and modify the landscape. Being able to make predictions by looking at these results in conjunction with other reintroduction projects and historical and traditional knowledge may help in guiding management decisions. Generalist species like the American Robin or the Canada Jay are unlikely to be affected by the bison herd in the long-run, while species requiring close-canopy forests like the Evening Grosbeak may be negatively affected due to loss of their habitat (Table 12; Table 13). Species like the Common Nighthawk or the Olive-sided Flycatcher that rely on natural disturbances that have been absent from the park for many decades will benefit in the long run, taking advantage of the habitat heterogeneity bison help to produce after a fire (Table 12; Table 13). Monitoring changes to the bird community and the vegetation that they depend upon for habitat will continue to be of immense importance in tracking just how the bird community is shifting in response to the bison herd.

Future research could benefit from looking at small scale, localized changes in the plant and bird community at sites that bison are using particularly heavily. Identifying differences in the coverage of different species of grasses and forbs in areas that the bison use at varying intensities could give insights into how different species of plants in the Canadian Rockies respond to disturbances caused by the bison. It may also be useful to investigate what sorts of characteristics allow different plants to thrive around the bison. For example, whether a species can spread its seeds via bison consumption and deposition in fecal pats. The effects of the bison on ground nesting bird species would also be an interesting avenue of exploration, as these species are affected both directly and indirectly by actions of the bison such as trampling or exposure of their nests to predators.

The effects of bison reintroductions on the vegetation and the birds present within prairie ecosystems have been investigated before (Powell, 2006; Vinton et al., 1993; Jackson et al., 2010; Elson & Harnett, 2017). However, my work is unique in that it attempts to capture those effects in a reintroduction that is occurring on a massive scale within the subalpine ecoregion of the Canadian Rockies. As the range of the plains bison once reached the Eastern Rockies, this research can help to serve as part of the knowledge base for other Indigenous groups, conservation agencies, or governments who wish to reintroduce bison herds into the Canadian Rockies.

## Literature Cited

Alberta Agriculture, Forestry and Rural Economic Development (Alberta Climate Information Service). (September 2022). https://acis.alberta.ca

Allred, B. W., Fuhlendorf, S. D., & Hamilton R. G. (2011). The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. *Ecosphere*, *2*(3), 26–17. https://doi.org/10.1890/ES10-00152.1

Andreas, B. K. (2010). Use of bryophytes by Carolina chickadees (*Poecile carolinensis*) in nest construction. *Evansia*, *27*(1), 23-29. https://doi.org/10.1639/0747-9859-27.1.23

Arthur, G. (1974). *Introduction to the Ecology of Early Historic Communal Bison Hunting Among the Northern Plains Indians. University of Ottawa Press.* https://doi.org.uml.idm.oclc.org/10.2307/j.ctv16qcg

Banff National Park. (2020, September 16). *Frequently Asked Questions (Where is the Reintroduction Zone?)*. Banff Bison Blog. https://www.pc.gc.ca/en/pn-np/ab/banff/info/gestion-management/bison/faq

Banff National Park. (2020, October 16). *Ecosystems and Habitat*. Banff National Park Webpage. https://www.pc.gc.ca/en/pn-np/ab/banff/nature/environnement-environment/ecosystemes-ecosystems

Banff National Park Bison Project. (2019) *Field Protocol - Bird Monitoring [unpublished field protocol document]*

Baril, L., Hansen, A., Renkin, R., & Lawrence, R. (2011). Songbird response to increased willow (Salix spp.) growth in Yellowstone's northern range. *Ecological Applications*, *21*(6), 2283-2296. https://doi.org/10.1890/10-0169.1

Bekoff, M., Scott, A. C., & Conner, D. A. (1987). Nonrandom nest-site selection in Evening Grosbeaks. *The Condor*, *89*(4), 819-829. https://doi.org/10.2307/1368530

Berger, J., Stacey, P. B., Bellis, L., & Johnson, M. P. (2001). A Mammalian Predator-Prey Imbalance: Grizzly Bear and Wolf Extinction Affect Bird Neotropical Migrants. *Ecological Applications*, *11*(4), 947–960. https://doi.org/10.2307/3061004

Betts, M., Hadley, A., Rodenhouse, N., & Nocera, J. (2008). Social Information Trumps Vegetation Structure in Breeding-Site Selection by a Migrant Songbird. *Proceedings: Biological Sciences*, *275*(1648), 2257-2263. https://doi.org/10.1098/rspb.2008.0217

Biondini, M. E., Steuter, A. A., & Grygiel, C. E. (1989). Seasonal fire effects on the diversity patterns, spatial distribution and community structure of forbs in the Northern Mixed Prairie, USA. *Vegetatio*, *85*, 21-31.

Blackburn, R. C., Barber, N. A., & Jones, H. P. (2021). Reintroduced bison diet changes throughout the season in restored prairie. *Restoration Ecology*, *29*, e13161. https://doi.org/10.1111/rec.13161

Bock, C. E., Saab, V. A., Rich, T. D., & Dobkin, D. S. (1993). Effects of Livestock Grazing on Neotropical Migratory Birds in Western North America. In Finch, D. M., & Stangel P. W. (Eds.) *Status and Management of Neotropical Migratory Birds* (pp. 296-308). *United States Department Of Agriculture.*

Böhning-Gaese, K., & Lemoine, N. (2004). Importance of climate change for the ranges, communities and conservation of birds. *Advances in Ecological Research, 35*, 211-236. https://doi.org/10.1016/S0065-2504(04)35010-5

Boyce, A. J., Shamon, H., & McShea, W. J. (2022). Bison reintroduction to mixed-grass prairie is associated with increases in bird diversity and cervid occupancy in riparian areas. *Frontiers in Ecology and Evolution, 180*. https://doi.org/10.3389/fevo.2022.821822

Boyce, A., Shamon, H., Kunkel, K., & McShea, W. (2021). Grassland bird diversity and abundance in the presence of native and non-native grazers. *Bird Conservation and Ecology*, *16*(2). https://doi.org/10.5751/ACE-01944-160213

Breil, D. A., & Moyle, S. M. (1976). Bryophytes used in construction of bird nests. *Bryologist*, *95*(98). https://doi.org/10.2307/3241875

Buckland, S. (2016). *Distance Sampling : Methods and Applications*. Springer. https://doi.org/10.1007/978-3-319-19219-2

Bull, E. L., Torgersen, T. R., Blumton, A. K., McKenzie, C. M., & Wyland, D. S. (1995). *Treatment of an old-structure stand and the effect on birds, ants, and large woody debris: a case study.* Pacific Northwest Research Station, Forest Service, US Department of Agriculture. https://www.fs.usda.gov/pnw/pubs/pnw_gtr353.pdf

Busby, J. R., Bliss, L. C., & Hamilton, C. D. (1978). Microclimate control of growth rates and habitats of the boreal forest mosses, Tomenthypnum nitens and Hylocomium splendens. *Ecological Monographs, 48*(2), 95-110. https://doi.org/10.2307/2937294

Campbell, C. I., Campbell, C. B., & McAndrews, J. (1994). Bison extirpation may have caused aspen expansion in western Canada. *Ecography 17*, 360-362. https://doi.org/10.1111/j.1600-0587.1994.tb00113.x

Chace, J. F., & Cruz, A. (1998). Range of the Brown-headed Cowbird in Colorado: past and present. *The Great Basin Naturalist*, 245-249. https://www.jstor.org/stable/41713059

Chen, L., Li, H., Zhang, P., Zhao, X., Zhou, L., Liu, T., Hu, H., Bai, Y., Shen, H., & Fang, J. (2015). Climate and native grassland vegetation as drivers of the community structures of shrub-encroached grasslands in Inner Mongolia, China. *Landscape Ecology*, *30*(9), 1627–1641. https://doi.org/10.1007/s10980-014-0044-9

Chmielewski, M. W., & Eppley, S. M. (2022). Species-specific interactions in avian–bryophyte dispersal networks. *Royal Society Open Science*, *9*(1), 211230. https://doi.org/10.1098/rsos.211230

Collins, S.L., Barber, S.C. (1986). Effects of disturbance on diversity in mixed-grass prairie. *Plant Ecology*, *64*, 87–94. https://doi.org/10.1007/BF00044784

Collins, S., & Calabrese, L. (2012). Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *Journal of Vegetation Science*, *23*(3), 563-575. http://www.jstor.org/stable/23251087

COSEWIC. (2018). COSEWIC assessment and status report on the Olive-sided Flycatcher *Contopus cooperi* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. ix + 52 pp. (http://www.registrelep-sararegistry.gc.ca/default.asp?lang=en&n=24F7211B-1).

Craine, J. M., Towne, E. G., Miller, M., & Fierer, N. (2015). Climatic warming and the future of bison as grazers. *Scientific Reports*, *16738*. https://doi-org.uml.idm.oclc.org/10.1038/srep16738

Cruz, A., Cooper, L., & Richardson, C. (2001). *Behavioral defenses against brood parasitism in the American Robin (Turdus migratorius)*. City of Boulder Open Space Department, Colorado, USA, www.static.bouldercolorado.gov/docs/4177_ Cruz_Alexander_Behavioral-1-201307091311.pdf

Davis, C. A. (1974). Bird populations in a shrub-grassland area, southeastern New Mexico. *New Mexico State University Agricultural Experiment Station*, *619*, 1-29. http://contentdm.nmsu.edu/cdm/ref/collection/AgCircs/id/23408

Davis, K. P., Augustine, D. J., Monroe, A. P., Derner, J. D., & Aldridge, C. L., (2020). Adaptive rangeland management benefits grassland birds utilizing opposing vegetation structure in the shortgrass steppe. *Ecological Applications 30*(1) :e02020. 10.1002/eap.2020

De Grandpré, L., Morissette, J. and Gauthier, S. (2000). Long-term post-fire changes in the northeastern boreal forest of Quebec. *Journal of Vegetation Science*, *11*: 791-800. https://doi-org.uml.idm.oclc.org/10.2307/3236549

Dickson, J. G., Conner, R. N., & Williamson, J. H. (1993). Neotropical migratory bird communities in a developing pine plantation. In *1993 Procedings on the Annual Conference. SEAFWA*.

Dvorský, M., Mudrák, O., Dolezal, J., & Jirku, M. (2022). Reintroduction of large herbivores restored plant species richness in abandoned dry temperate grassland. *Plant Ecology*, *223*(5), 525–535. https://doi.org/10.1007/s11258-022-01225-w

Environment Canada. 2016a. Recovery Strategy for the Common Nighthawk (*Chordeiles minor*) in Canada. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa. vii + 49 pp.

Environment Canada. (2016b). Recovery Strategy for the Olive-sided Flycatcher (*Contopus cooperi*) in Canada. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa. vii + 52 pp.

Environment Canada. (2018, October 30). *Nesting Periods (B4 zone).* https://www.canada.ca/en/environment-climate-change/services/avoiding-harm-migratory-birds/general-nesting-periods/nesting-periods.html#_zoneB_calendar

Environment and Climate Change Canada. 2022. Management Plan for the Evening Grosbeak (*Coccothraustes vespertinus*) in Canada [Proposed]. Species at Risk Act Management Plan Series. Environment and Climate Change Canada, Ottawa. v + 45 pp.

Ellis, C. (2022, August 26). *Sixteen bison calves born to Banff herd this year.* Rocky Mountain Outlook. https://www.rmotoday.com/banff/sixteen-bison-calves-born-to-banff-herd-this-year-5724640

Elson, A., & Harnett, D. C. (2017). Bison Increase the Growth and Reproduction of Forbs in Tallgrass Prairie. *The American Midland Naturalist*, *178*(2), 245–259. http://www.jstor.org/stable/45434060

Esri. (2021). ArcMap (version 10.8.1) https://desktop.arcgis.com/en/arcmap/

Fagre, D. A., Janousek, W. M., & Dreitz, V. J. (2022). Bird species richness and abundance show stronger responses to bison grazing intensity than to ecosystem productivity. *Ecosphere*, *13*(12). https://doi.org/10.1002/ecs2.4299

Foley, G. (2018). *Habitat Use by Common Nighthawks (Chordeiles minor) in Canada's Boreal Forest* [Master's Thesis, University of Regina]. oURspace. http://hdl.handle.net/10294/8886

Fuhlendorf, S., & Engle, D. M. (2001). Restoring Heterogeneity on Rangelands: Ecosystem Management Based on Evolutionary Grazing Patterns. *Bioscience, 51*(8), 625–632. https://doi.org/10.1641/0006-3568(2001)051[0625:RHOREM]2.0.CO;2

Fuhlendorf, S., Harrell, W., Engle, D., Hamilton, R., Davis, C., & Leslie, D. (2006). Should Heterogeneity Be the Basis for Conservation? Grassland Bird Response to Fire and Grazing. *Ecological Applications, 16*(5), 1706-1716. https://doi.org/10.1890/1051-0761(2006)016[1706:SHBTBF]2.0.CO;2

Franco, M., & Harper, J. L. (1988). Competition and the Formation of Spatial Pattern in Spacing Gradients: An Example Using Kochia Scoparia. *Journal of Ecology*, *76*(4), 959–974. https://doi.org/10.2307/2260626

Gadd, B. (2009). *Handbook of the Canadian Rockies (2nd ed.)* Corax Press.

George, T. L., Fowler, A. C., Knight, R. L., & McEwen, L. C. (1992). Impacts of a severe drought on grassland birds in western North Dakota. *Ecological applications*, *2*(3), 275-284. https://doi.org/10.2307/1941861

Gillies, C. (2016). *Banff National Park Bison Songbird Monitoring Results [unpublished report]*

Gillihan, S. W., & B. E. Byers. (2001). Evening Grosbeak (*Coccothraustes vespertinus*). In A. F. Poole and F. B. Gill, (Eds.). *The birds of North America.* Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.599

Glime, J. (2017). Birds and Bryophytes Intersect. In J. Glime (Ed), *Bryophyte Ecology* (16-1 – 16-23). Michigan Technological University. https://digitalcommons.mtu.edu/bryophyte-ecology/

Gregory, R.D., & Van Strien, A. (2010). Wild Bird Indicators: Using Composite Population Trends of Birds as Measures of Environmental Health. *Ornithological Science*, *9*(1), 3-22. https://doi.org/10.2326/osj.9.3

Goguen, C., Curson, D., & Mathews, N. (2005). Behavioral Ecology of the Brown-Headed Cowbird (Molothrus ater) in a Bison-Grazed Landscape in New Mexico. *Ornithological Monographs*, (57), 71-83. doi:10.2307/40166815

Gunathilaka, M. D. K. L. (2019). A review of bryophytes; evolution, value and threats. *International Journal of Scientific and Research Publications*, *9*, 384-398. http://dx.doi.org/10.29322/IJSRP.9.05.2019.p8946

Haché, S., Solymos, P., Fontaine, T., Bayne, E., Cumming, S., Schmiegelow, F., & Stralberg, D. (2014). *Analyses to support critical habitat identification for Canada Warbler, Olive-sided Flycatcher, and Common Nighthawk: Final Report 1 and 2.* Zenodo. https://doi.org/10.5281/zenodo.2433885

Hämäläinen, P. (2019). *Lakota America*. Yale University Press

Hamao, S., Higuchi, M., Jinbo, U., Maeto, K., & Furuki, K. (2016). Interaction among birds, mosses, and insects in bird nests. *Japanese Journal of Ornithology, 65*(1), 37-42.DOI: 10.3838/jjo.65.37

Henebry, G. (1993). Detecting change in grasslands using measures of spatial dependence with landsat TM data. *Remote Sensing of Environment, 46*(2), 223–234. https://doi.org/10.1016/0034-4257(93)90097-H

Herakovich, H., Barber, N. A., & Jones, H. P. (2021). Assessing the impacts of prescribed fire and bison disturbance on birds using bioacoustic recorders. *The American Midland Naturalist*, *186*(2), 245-262. https://doi.org/10.1674/0003-0031-186.2.245

Heuer, K. (2019). *Plains bison reintroduction in Banff National Park pilot project 2017-2022: 2018 progress report.* Parks Canada. http://www.publications.gc.ca/site/eng/9.891745/publication.html

Hummel, S., Meyer, L., Hackländer, K., & Weber, D. (2017). Activity of potential predators of European hare (Lepus europaeus) leverets and ground-nesting birds in wildflower strips. *European Journal of Wildlife Research*, *63*, 1-13. https://doi.org/10.1007/s10344-017-1158-6

Jackson, R. D., Paine, L. K., & Woodis, J. E. (2010). Persistence of native C4 grasses under high-intensity, short-duration summer bison grazing in the eastern tallgrass prairie. *Restoration Ecology*, *18*(1), 65-73. https://doi.org/10.1111/j.1526-100X.2008.00439.x

Jaroszewicz, B., Borysowicz, J., & Cholewińska, O. (2021). Forest floor plant diversity drives the use of mature spruce forests by European bison. *Ecology and Evolution, 11*(1), 636-647. https://doi.org/10.1002/ece3.7094

Johnson, T. N., Kennedy, P. L., DelCurto, T., & Taylor, R. V. (2011). Bird community responses to cattle stocking rates in a Pacific Northwest bunchgrass prairie. *Agriculture, Ecosystems & Environment, 144*(1), 338–346. https://doi.org/10.1016/j.agee.2011.10.003

Jung, T., Stotyn, S., & Czetwertynski, S. (2015). Dietary Overlap and Potential Competition in a Dynamic Ungulate Community in Northwestern Canada. *The Journal of Wildlife Management, 79*(8), 1277-1285. http://www.jstor.org/stable/24764386

Karp, A. T., Behrensmeyer, A. K., & Freeman, K. H. (2018). Grassland fire ecology has roots in the late Miocene. *Proceedings of the National Academy of Sciences - PNAS, 115*(48), 12130–12135. https://doi.org/10.1073/pnas.1809758115

Kauffman, J. B., Cummings, D. L., Kauffman, C., Beschta, R. L., Brooks, J., MacNeill, K., & Ripple, W. J. (2023). Bison influences on composition and diversity of riparian plant communities in Yellowstone National Park. *Ecosphere, 14*(2). https://doi.org/10.1002/ecs2.4406

Kayes, L. J., Anderson, P. D., & Puettmann, K. J. (2010). Vegetation succession among and within structural layers following wildfire in managed forests. *Journal of Vegetation Science, 21*(2), 233–247. http://www.jstor.org/stable/40925483

Keery, L. (2019). *Evaluating the potential impacts of reintroduced plains bison (Bison bison bison) contained in a soft-release pasture in Banff National Park* [Master's Thesis, Royal Roads University]. VIURRSpace (Royal Roads University Archive)

Klingbeil, B., & Willig, M. (2015). Bird biodiversity assessments in temperate forest: the value of point count versus acoustic monitoring protocols. *PeerJ, 3*, e973–e973. https://doi.org/10.7717/peerj.973

Knapp, A., Blair, J., Briggs, J., Collins, S., Hartnett, D., Johnson, L., & Towne, E. (1999). The Keystone Role of Bison in North American Tallgrass Prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *BioScience*, *49*(1), 39-50. doi:10.1525/bisi.1999.49.1.39

Knopf, F. L., Sedgwick, J. A., & Cannon, R. W. (1988). Guild Structure of a Riparian Avifauna Relative to Seasonal Cattle Grazing. *The Journal of Wildlife Management*, *52*(2), 280–290. https://doi.org/10.2307/3801235

Knopf, F. L. 1996. Prairie legacies: birds. In: F. B. Samson and F. L. Knopf (eds.). *Prairie conservation: Preserving North America's most endangered ecosystem.* (pp. 135–148). Island Press.

Kowalczyk, R., Kamiński, T., & Borowik, T. (2021). Do large herbivores maintain open habitats in temperate forests? *Forest Ecology and Management*, *494*, 119310.

Lusk, J. (2009). *The effects of grazing on songbird nesting success in Grasslands National Park of Canada* [Master's Thesis, University of Manitoba]. University of Manitoba MSpace Library

MacArthur, R., & MacArthur, J. (1961). On Bird Species Diversity. *Ecology*, *42*(3), 594-598. doi:10.2307/1932254

Maehr, D., Noss, R., Larkin, J., & Sunquist, M. (2001). Large Mammal Restoration: Ecological And Sociological Challenges In The 21St Century. Island Press.

Mahony, N. A., Dale, B. C., & Miller, D. A. (2022). Grassland bird population declines at three Breeding Bird Survey spatial scales in contrast to a large native prairie. *Ecosphere*, *13*(12), e4309. https://doi.org/10.32854/agrop.v15i10.2239

McMillan, B. R., Pfeiffer, K. A., & Kaufman, D. W. (2011). Vegetation Responses to an Animal-generated Disturbance (Bison Wallows) in Tallgrass Prairie. *American Midland Naturalist*, *165*(1), 60–73. https://doi-org.uml.idm.oclc.org/10.1674/0003-0031-165.1.60

Menz, M. H., Dixon, K. W., & Hobbs., R. J. (2013). Hurdles and Opportunities for Landscape-Scale Restoration. *Science (American Association for the Advancement of Science)*, *339*(6119), 526–527. https://doi.org/10.1126/science.1228334

Miller, E. A., & Halpern, C. B. (1998). Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. *Journal of Vegetation Science*, *9*(2), 265-282.

Moran, M. D. (2014). Bison grazing increases arthropod abundance and diversity in a tallgrass prairie. *Environmental Entomology*, *43*(5), 1174-1184.

Morgantini, L. (1988). Behavioural adaptive strategies of wapiti (Cervus elaphus) in the Canadian Rocky Mountains [Doctoral dissertation, University of Alberta]. Education & Research Archive.

Morgantini, L., & Hudson, R. (1989). Nutritional Significance of Wapiti (Cervus elaphus) Migrations to Alpine Ranges in Western Alberta, Canada. *Arctic and Alpine Research*, *21*(3), 288-295. doi:10.2307/1551568

Mosher, B. A., Saab, V. A., Lerch, M. D., Ellis, M. M., & Rotella, J. J. (2019). Forest birds exhibit variable changes in occurrence during a mountain pine beetle epidemic. Ecosphere, 10(12), e02935. https://doi.org/10.1002/ecs2.2935

National Park Service. (2021, February 12). *History of Bison Management in Yellowstone.* National Park Service Website. https://www.nps.gov/articles/bison-history-yellowstone.htm

National Park Service. (2017, November 2). *Bison Bellows: America's New National Mammal.* National Park Service Website. https://www.nps.gov/articles/bison-bellows-5-12-16.htm#:~:text=Afterpercent20fourpercent20yearspercent20ofpercent20outreach,makingpercent20thepercent20bisonpercent20ourpercent20national

Nickell, Z., Varriano, S., Plemmons, E., & Moran, M. D. ( 2018). Ecosystem engineering by bison (Bison bison) wallowing increases arthropod community heterogeneity in space and time. *Ecosphere, 9*(9) e02436. https://doi.org/10.1002/ecs2.2436

Parks Canada. (2013) *PLAN FOR REINTRODUCTION OF PLAINS BISON IN BANFF NATIONAL PARK.* http://www.parkscanadahistory.com/publications/banff/plains-bison-reintro-e-2013.pdf

Patterson, M., & Best, L. (1996). Bird Abundance and Nesting Success in Iowa CRP Fields: The Importance of Vegetation Structure and Composition. *The American Midland Naturalist*, *135*(1), 153-167. doi:10.2307/2426881

Pengelly, W. L. (1963). *Thunder on the Yellowstone.*

Pérez-Granados, C., Bota, G., Giralt, D., Barrero, A., Gómez-Catasús, J., Bustillo-De La Rosa, D. and Traba, J. (2019), Vocal activity rate index: a useful method to infer terrestrial bird abundance with acoustic monitoring. *Ibis, 161*: 901-907. https://doi.org/10.1111/ibi.12728

Perez-Ordonez, D. J., Titulaer, M., Correll, M. D., Strasser, E. H., Baeza-Tarin, F., Martin, R. L., & Harveson, L. A. (2022). The role of temperature and microclimate in the survival of wintering grassland birds. *Avian Conservation and Ecology*, *17*(1), 1. https://doi.org/10.5751/ACE-02010-170101

Plumb, G., & Dodd, J. (1993). Foraging Ecology of Bison and Cattle on a Mixed Prairie: Implications for Natural Area Management. *Ecological Applications*, *3*(4), 631-643. doi:10.2307/1942096

Porzig, E. L., Seavy, N. E., Eadie, J. M., Gardali, T., Humple, D. L., & Geupel, G. R. (2018). There goes the neighborhood: White-crowned Sparrow nest site selection and reproductive success as local density declines. *The Condor: Ornithological Applications*, *120*(1), 234-244. https://doi.org/10.1650/CONDOR-17-149.1

Powell, A. (2006). Effects Of Prescribed Burns And Bison (BOS BISON) Grazing On Breeding Bird Abundances In Tallgrass Prairie. *The Auk, 123*(1), 183–197. https://doi.org/10.1642/0004-8038(2006)123[0183:EOPBAB]2.0.CO;2

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Ranglack, D. H., Durham, S., & du Toit, J. T. (2015). Competition on the range: science vs. perception in a bison-cattle conflict in the western USA. *Journal of Applied Ecology, 52*(2), 467–474. http://www.jstor.org/stable/43869589

Richardson, A. N. (2012). Changes in grassland songbird abundances through time in response to burning and grazing in the northern mixed-grass prairie [Master's Thesis, University of Manitoba]. University of Manitoba MSpace Library

Richardson, A. N., Koper, N., & White, K. A. (2014). Interactions between ecological disturbances: burning and grazing and their effects on songbird communities in northern mixed-grass prairies. *Bird Conservation and Ecology, 9*(2), 5. http://dx.doi.org/10.5751/ACE-00692-090205

Robel, R., Briggs, J.N., Dayton, A., & Hulbert, L.C. (1970). Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management, 23*, 295-297.

Rosas, C. A., Engle, D. M., & Shaw, J. H. (2005). Potential ecological impact of diet selectivity and bison herd composition. *Great Plains Research, 15*(1), 3–13. http://www.jstor.org/stable/23779835

Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., ... & Marra, P. P. (2019). Decline of the North American avifauna. *Science, 366*(6461), 120-124. https://doi.org/10.1126/science.aaw1313

Roth, R. (1976). Spatial Heterogeneity and Bird Species Diversity. *Ecology*, *57*(4), 773-782. doi:10.2307/1936190

Rothstein, S., Verner, J., & Steven, E. (1984). Radio-Tracking Confirms a Unique Diurnal Pattern of Spatial Occurrence in the Parasitic Brown-Headed Cowbird. *Ecology*, *65*(1), 77-88. doi:10.2307/1939460

Rivers, J., Jensen, W., Kosciuch, K., & Rothstein, S. (2010). Community-level Patterns of Host Use by the Brown-headed Cowbird (Molothrus ater), a Generalist Brood Parasite. *The Auk*, *127*(2), 263-273. doi:10.1525/auk.2009.09053

Sallabanks, R., Haufler, J. B., & Mehl, C. A. (2006). Influence of Forest Vegetation Structure on Bird Community Composition in West-Central Idaho. *Wildlife Society Bulletin*, *34*(4), 1079–1093. http://www.jstor.org/stable/4134319

Schmidt, A., Fartmann, T., Kiehl, K., Kirmer, A., & Tischew, S. (2022). Effects of perennial wildflower strips and landscape structure on birds in intensively farmed agricultural landscapes. *Basic and Applied Ecology*, *58*, 15-25. https://doi.org/10.1016/j.baae.2021.10.005

Shonfield, J., & Bayne, E. M. (2017). Autonomous recording units in avian ecological research: current use and future applications. *Avian Conservation & Ecology*, *12*(1). https://doi.org/10.5751/ACE-00974-120114

Senft, R., Coughenour, M., Bailey, D., Rittenhouse, L., Sala, O., & Swift, D. (1987). Large Herbivore Foraging and Ecological Hierarchies. *BioScience*, *37*(11), 789-799. doi:10.2307/1310545

Shaw, J. (1995). How Many Bison Originally Populated Western Rangelands? *Rangelands*, *17*(5), 148–150. https://doi.org/10.2527/1992.70113498x

Short, R. E., James, L. F., Panter, K. E., Staigmiller, R. B., Bellows, R. A., Malcolm, J., & Ford, S. P. (1992). Effects of feeding ponderosa pine needles during pregnancy: comparative studies with bison, cattle, goats, and sheep. *Journal of animal science*, *70*(11), 3498-3504.

Shryock, D. F., Esque, T. C., & Chen, F. C. (2015). Topography and climate are more important drivers of long-term, post-fire vegetation assembly than time-since-fire in the Sonoran Desert, US. *Journal of Vegetation Science*, *26*(6), 1134–1147. http://www.jstor.org/stable/43912937

Silber, K. M., Mohankumar, N. M., Hefley, T. J., & Boyle, W. A. (2023). Emigration and survival correlate with different precipitation metrics throughout a grassland songbird's annual cycle. *The Journal of Wildlife Management*, *87*(3), e22371. https://doi.org/10.1002/jwmg.22371

Simonson, Allen, H. D., & Coomes, D. A. (2014). Overstorey and topographic effects on understories: Evidence for linkage from cork oak (*Quercus suber*) forests in southern Spain. *Forest Ecology and Management*, *328*, 35–44. https://doi.org/10.1016/j.foreco.2014.05.009

Singer, F. J., Swift, D. M., Coughenour, M. B., & Varley, J. D. (1998). Thunder on the Yellowstone Revisited: An Assessment of Management of Native Ungulates by Natural Regulation, 1968-1993. *Wildlife Society Bulletin (1973-2006)*, *26*(3), 375–390. http://www.jstor.org/stable/3783750

Singer, F. J., & J. A. Mack. (1999). Predicting the effects of wildfire and carnivore predation on ungulates in T.W. Clark, A.P. Curlee, S.C. Minta, and P.M. Kareiva, (Eds.), Carnivores in Ecosystems: The Yellowstone Experience. (pp. 189–237 ). Yale University Press https://doi.org/10.1659/0276-4741(2000)020[0381:CIETYE]2.0.CO;2

Skre, O., & Oechel, W. C. (1981). Moss Functioning in Different Taiga Ecosystems in Interior Alaska. I. Seasonal, Phenotypic, and Drought Effects on Photosynthesis and Response Patterns. *Oecologia*, *48*(1), 50–59. http://www.jstor.org/stable/4216267

Sliwinski, M. S. (2011). *Changes in grassland songbird abundance and diversity in response to grazing by bison and cattle in the northern mixed-grass prairie*. [Master's Thesis, University of Manitoba]. Umanitoba MSpace.

Sliwinski, M., & Koper, N. (2015). Managing Mixed-grass Prairies for Songbirds Using Variable Cattle Stocking Rates. *Rangeland Ecology and Management*, *68*, 470-475. https://doi.org/10.1016/j.rama.2015.07.010

Smit, I. P. J, & Coetsee, C. (2019). Interactions Between Fire and Herbivory: Current Understanding and Management. In Gordon, J. I., & Prins H. H. T. (1st Edition), *The Ecology of Browsing and Grazing II* (pp. 301-319). Springer. https://doi.org/10.1007/978-3-030-25865-8

Stockdale, C.A., Macdonald, S.E., & Higgs, E. (2019). Forest closure and encroachment at the grassland interface: a century-scale analysis using oblique repeat photography. *Ecosphere, 10*(6). https://doi.org/10.1002/ecs2.2774

Stoney Nakoda Nations. (2022). *Enhancing the Reintroduction of Plains Bison in Banff National Park Through Cultural Monitoring and Traditional Knowledge*. https://a.storyblok.com/f/112697/x/d0b9253d5a/stoney_bison_report_final_rev2.pdf

Stuart-Smith, A. K., Hayes, J. P., & Schieck, J. (2006). The influence of wildfire, logging and residual tree density on bird communities in the northern Rocky Mountains. *Forest ecology and management*, 231(1-3), 1-17. https://doi.org/10.1016/j.foreco.2006.02.053

Sutton, A. O., Strickland, D., Freeman, N. E., Newman, A. E., & Norris, D. R. (2019). Autumn freeze-thaw events carry over to depress late-winter reproductive performance in Canada jays. *Royal Society Open Science*, *6*(4), 181754. https://doi.org/10.1098/rsos.181754

Tarleton, P. & Lamb, E. G. (2020). Modification of Plant Communities by Bison in Riding Mountain National Park. *Écoscience (Sainte-Foy), 28*(1), 67–80. https://doi.org/10.1080/11956860.2020.1850622

Taschereau, M. D. (2020). “Last of the buffalo”: bison extermination, early conservation, and visual records of settler colonization in the North American west. *Settler Colonial Studies, 10*(1), 126–147. https://doi.org/10.1080/2201473X.2019.1677134

Tastad, A. (2013). *The relative effects of grazing by bison and cattle on plant community heterogeneity in northern mixed prairie* [Master’s Thesis, University of Manitoba]. University of Manitoba MSpace Library.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. and Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, *31*, 79-92. https://doi.org/10.1046/j.0305-0270.2003.00994.x

Towne, E. G., Hartnett, D. C., & Robert C. Cochran. (2005). Vegetation Trends in Tallgrass Prairie from Bison and Cattle Grazing. *Ecological Applications, 15*(5), 1550–1559. http://www.jstor.org/stable/4543462

Truett, J., Phillips, M., Kunkel, K., & Miller, R. (2001). Managing Bison to Restore Biodiversity. *Great Plains Research, 11*(1), 123-144.

Turetsky, M. R., Mack, M. C., Hollingsworth, T. N., & Harden, J. W. (2010). The role of mosses in ecosystem succession and function in Alaska’s boreal forest. Canadian Journal of Forest Research, 40(7), 1237-1264. https://doi.org/10.1139/X10-072

Veen, G. F. (Ciska), Blair, J. M., Smith, M. D., & Collins, S. L. (2008). Influence of Grazing and Fire Frequency on Small-Scale Plant Community Structure and Resource Variability in Native Tallgrass Prairie. *Oikos, 117*(6), 859–866. http://www.jstor.org/stable/40235472

Vinton, M., Hartnett, D., Finck, E., & Briggs, J. (1993). Interactive Effects of Fire, Bison (Bison bison) Grazing and Plant Community Composition in Tallgrass Prairie. *The American Midland Naturalist, 129*(1), 10-18. doi:10.2307/2426430

Wallace, L., and Crosthwaite, K. (2005). The effect of fire spatial scale on Bison grazing intensity. *Landscape Ecology,* 20, 337–349. https://doi-org.uml.idm.oclc.org/10.1007/s10980-005-5648-7

Wallace, L. L., Turner, M. G., Romme, W. H., O'Neill, R. V., & Wu, Y. (1995). Scale of heterogeneity of forage production and winter foraging by elk and bison. *Landscape Ecology*, *10*, 75–83. https://doi-org.uml.idm.oclc.org/10.1007/BF00153825

Whitehorne, I., Harrison, M., Mahony, N. A., Robinson, P., Newbury, A., & Green, D. J. (2011). Effects of cattle grazing on birds in interior Douglas-fir (Pseudotsuga menziesii) forests of British Columbia. *Journal of Ecosystems and Management*, *12*(3). https://doi.org/10.22230/jem.2011v12n3a82

Whitehorne, I., Alaine, C., Véronique, C., Newbury, A., Middleton, H., & Krebs, E. (2013). *Bird Conservation Strategy for Bird Conservation Region 10 Pacific and Yukon Region: Northern Rockies*. Environment Canada. https://www.canada.ca/en/environment-climate-change/services/migratory-bird-conservation/regions-strategies/description-region-10/pacific-yukon.html#_Toc355602851

Wiens, J. (1973). Pattern and Process in Grassland Bird Communities. *Ecological Monographs, 43*(2), 237-270. doi:10.2307/1942196

Williams, M., Paige, G., Thurow, T., Hild, A., & Gerow, K. (2011). Songbird Relationships to Shrub-Steppe Ecological Site Characteristics. *Rangeland Ecology & Management, 64*(2), 109-118. https://doi.org/10.2111/REM-D-10-00076.1

Van Yuren, D. (1984). Summer diets of bison and cattle in southern Utah. *Rangeland Ecology & Management/Journal of Range Management Archives, 37*(3), 260-261.

Venier, L. A., Holmes, S. B., Holborn, G. W., Mcilwrick, K. A., & Brown, G. (2012). Evaluation of an automated recording device for monitoring forest birds. *Wildlife Society Bulletin*, *36*(1), 30-39. https://doi.org/10.1002/wsb.88

Vickery, J., Carter, N., & Fuller, R. J. (2002). The potential value of managed cereal field margins as foraging habitats for farmland birds in the UK. *Agriculture, Ecosystems & Environment*, *89*(1-2), 41-52. https://doi.org/10.1016/S0167-8809(01)00317-6

# Chapter 4: Summary & Management Implications

## Summary

It is hard to overstate the scope of the Banff bison reintroduction in terms of both its ambition and its actual physical scale. In my study I attempted to capture but one of many impacts the bison herd may potentially bring in the coming years. The question I asked was twofold: what draws the bison to different parts of the landscape and how are some of the creatures living in those different parts of the landscape affected by how intensely the bison use those same areas?

In chapter 2 I investigated the first of those questions by performing a resource selection function based on the GPS collar data following thirteen members of the herd's movements throughout the reintroduction zone. I found evidence for the Banff herd's preference for spending time in areas that had been experienced at least ten burns since 1909, and that were in grassier or shrubbier ecosystems close to sources of water and on flat slopes.

In chapter 3 I found that vegetation structure changed with ecosystem type rather than bison usage, with understory height and the density of vegetation below 1 meter increasing in grassland/shrubland ecosystems and the density of vegetation above 1 meter decreasing in grassland/shrubland ecosystems. Regarding the percentages of ground cover, the coverage of forbs increased with increasing bison usage, the coverage of mosses increased with increasing bison usage in forests but showed the opposite response in grasslands, and that bare ground, shrubs and trees showed no response to any of the variables I investigated. When I examined the bird community, the total abundance of the birds in the reintroduction area  decreased with increasing bison usage  However, once vegetation was factored into the models there were no longer any significant associations between my factors and bird abundance and species richness. I also examined four focal species within the bird community, with Wilson's Warblers and White-crowned Sparrows showing declines in abundance since 2018 and in warmer years, Brown-headed Cowbirds declining in warmer years, and Townsend's Warblers showing declines with increasing bison usage. Finally, I made predictions for how the bison herd would affect two common bird species and three at-risk bird species in Banff National Park. I predicted that the common species, American Robins and Canada Jays, would not be significantly affected by bison in the long run. For the at-risk species, I predicted that Evening Grosbeaks would decline in population while Common Nighthawks and Olive-sided Flycatchers would increase in population due to the changes bison make to the critical habitat for all three species.

## Management Implications

The Plains Bison truly encapsulates the title of *ecosystem engineer*. Forests are opened and grasslands expand through their actions as they roam the mountain landscape (Babin et al., 2011; Knapp et al., 1999). They, along with fire, are the great disturbances that create a patchwork of heterogeneity across the land which displace some species whilst creating room for new ones (Henebrey, 1993; Truett et al., 2001). It is a relationship that was well understood by humans who have maintained this land since time immemorial, and one that would be wise to maintain in the years to come for the Banff herd (Anderson & Barbour, 2003).

Banff National Park has decided to continue the plains bison reintroduction past the pilot stage (Banff National Park, 2022). This is encouraging news, as it means we will be able to bear witness to the long-term effects of a reintroduction on this scale. My results highlight just some of the complex relationships that will play out in the coming years.

The Banff bison are unique from other reintroductions done in the prairies in their reluctance to travel quite as far from water sources present in their home range as, though they exhibit the same reluctance to scale steep slopes as other herds unless sufficiently high-quality forage is present at the top of them. That desire for good forage may be what also motivates their preference for burned areas over unburned ones, as burns often contain nutritious, palatable plants as vegetation regrows (Verrall & Pickering, 2019; Raynor et al., 2015; Proffitt et al., 2015). The preference the herd expressed for grassland and shrubland ecosystems is unsurprising, as these ecosystems often contain more desirable forage when compared to forests, though bison are known to forage within forests if better sources of food are unavailable (Sanderson et al., 2008, Hecker et al., 2021, Keene et al., 2021). Predation risk may have played a factor in how the bison selected for different sites on the land as well. Most of the collared bison were female which could have led to a bias in selecting for more open habitats like grasslands and shrublands because of a lower perceived risk of predation due to their tendency to travel in large groups (Post et al., 2001). While the preference for wide open, grassy, and shrubby areas makes intrinsic sense for a species like the plains bison, the Banff herd still makes use of the forests within the reintroduction zone. Continuing to build an understanding of what forces drive resource selection by the bison will be important in being able to decide how to best apply management practices like prescribed burning to encourage biodiversity within the reintroduction zone.

One of the largest potential impacts of the bison on the landscape could be the prevention of forests re-establishing themselves after a fire, leading to a greater proportion of grasslands on the landscape in the coming decades. The current bison herd has not had the numbers nor the time to make substantial changes to the landscape yet, but we can start to see some small effects at this early point in the reintroduction. For instance, while there were no noted effects on vegetation structure, bison have been associated with an increase in forb coverage. This is potentially due to bison opening room for forbs to other species to expand into patches that they are disturbing through disturbances like grazing. The overall lack of significant impacts from the bison herd on the vegetation community is an explanation for the few responses that were noted in birds. However, again there were some small, early impacts that may provide some insight into how things are starting to change.

Most bird species showed either a decline or no response at all to increasing bison presence or in the years since the reintroduction took place. It is too early to say how much, if at all, the bison have influenced species richness, though in time the impacts of bison on the bird community in general may become more apparent. We may see established species declining in number as their habitat is disturbed and new ones are entering the ecosystem as space opens for them. Yet, given the declines grassland songbirds have experienced due to habitat loss elsewhere, the conservation value of improving habitat for grassland songbirds may be worth any potential losses to established closed-canopy forest species (Sauer & Link, 2011).

Maintaining and potentially expanding the prescribed burning program will be important in both creating good grazing habitat for the Banff herd and for allowing the land to resume its natural cycles of disturbance. Additionally, the expansion of the reintroduction zone itself would be an admirable goal, allowing for a greater population of bison to be sustained on the landscape and minimizing the risk of over usage. An expansion into provincial lands to the east would also be a landmark achievement of inter-agency cooperation along with Indigenous groups and local stakeholders; one that could set the standard for similar reintroductions in North America.

It will be important to avoid the degradation of vegetative communities in the future, as it is a problem faced by other wild plains bison herds in North America like in Yellowstone National Park (Kauffman et al., 2023). The US National Park Service currently maintains a bison cull each year to attempt to mitigate this issue in Yellowstone National Park (National Park Service, 2021). Parks Canada would be wise to think towards a future where the bison herd sees this level of successful reproduction and how that might be managed. Hunting by humans was historically one of the biggest sources of mortality for bison, with buffalo jumps taking hundreds of animals and providing the necessities of life for entire communities for a year (National Park Service, 2021). Beginning a hunting program with Indigenous peoples within the reintroduction zone would be a major step towards reconciling National Park management principles and Indigenous knowledge and sovereignty. A yearly bison harvest will allow for an important cultural reconnection while maintaining management goals of preventing landscape degradation.

Continued collaboration with organizations like the Yellowstone to Yukon Conservation Initiative and the signatories to the Buffalo Treaty will be an important goal in the long-term. Banff is but one of many locations within which bison once roamed and can serve both as an example to strive for and to learn from as other reintroductions on similar scales take place. In time we may very well see a reconnection of bison in many senses. To the landscapes that they have been absent from for so long. To the peoples to whom they hold immense cultural importance. And of the herds themselves, one day flowing freely between this 'patchwork' of reintroduction zones, much as they once did.

## Literature Cited

Anderson, M. K., & Barbour, M. G. (2003). Simulated indigenous management: A new model for ecological restoration in National Parks. *Ecological Restoration*, *21*, 269–277. https://doi-org.uml.idm.oclc.org/10.3368/er.21.4.269

Babin, J., Fortin, D., Wilmshurst, J.F. & Fortin, M. (2011). Energy gains predict the distribution of plains bison across populations and ecosystems. Ecology, 92, 240-252. https://doi.org/10.1890/10-0252.1

Banff National Park. (2022) *Report on the Plains Bison Reintroduction Pilot, 2017 - 2022.* https://parks.canada.ca/pn-np/ab/banff/info/gestion-management/bison/rapport-reintroduction-report

Hecker, L. J., Coogan, S. C., Nielsen, S. E., & Edwards, M. A. (2021). Latitudinal and seasonal plasticity in American bison Bison bison diets. *Mammal Review*, *51*(2), 193-206. https://doi.org/10.1111/mam.12229

Henebry, G. (1993). Detecting change in grasslands using measures of spatial dependence with landsat TM data. *Remote Sensing of Environment*, *46*(2), 223–234. https://doi.org/10.1016/0034-4257(93)90097-H

Kauffman, J. B., Cummings, D. L., Kauffman, C., Beschta, R. L., Brooks, J., MacNeill, K., & Ripple, W. J. (2023). Bison influences on composition and diversity of riparian plant communities in Yellowstone National Park. *Ecosphere, 14*(2). https://doi.org/10.1002/ecs2.4406

Keene, K. A., Gulsby, W. D., Colter, A. G., Miller, D. A., Johannsen, K. L., Miller, K. V., & Martin, J. A. (2021). Short-term effects of loblolly pine thinning intensity on coverage of preferred white-tailed deer forage plants. *Canadian Journal of Forest Research, 51*(4), 604-610.

Knapp, A., Blair, J., Briggs, J., Collins, S., Hartnett, D., Johnson, L., & Towne, E. (1999). The Keystone Role of Bison in North American Tallgrass Prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *BioScience, 49*(1), 39-50. doi:10.1525/bisi.1999.49.1.39

National Park Service. (2021, February 12). *History of Bison Management in Yellowstone.* National Park Service Website. https://www.nps.gov/articles/bison-history-yellowstone.htm

Post, D. M., Armbrust, T. S., Horne, E. A., & Goheen, J. R. (2001). Sexual segregation results in differences in content and quality of bison (Bos bison) diets. *Journal of Mammalogy, 82*(2), 407-413.

Proffitt, DeVoe, J., Barker, K., Durham, R., Hayes, T., Hebblewhite, M., Jourdonnais, C., Ramsey, P., & Shamhart, J. (2019). A century of changing fire management alters ungulate forage in a wildfire-dominated landscape. *Forestry (London), 92*(5), 523–537. https://doi.org/10.1093/forestry/cpz017

Raynor, E., Joern, A., & Briggs, J. (2015). Bison foraging responds to fire frequency in nutritionally heterogeneous grassland. *Ecology, 96*(6), 1586-159. https://doi.org/10.1890/14-2027.1

Sanderson, E.W., Redforda, K. H., Weber, B., Aune, K., Baldes, D., Berger J., Carter, D., Curtin, C., Derr, J., Dobrott, S., Fearn, E., Fleener, C., Forrest, S., Gerlach, C., Gates, C.C., Gross, J.E., Gogan, P., Grassel, S., Hilty, J. A., Jensen, M., Kunkel, K., Lammers, D., List, R., Minkowski, K., Olson, T., Pague, C., Robertson, P. B., Stephenson, B. (2008). The ecological future of the north American Bison: Conceiving long-term, large-scale conservation of wildlife. *Conservation Biology, 22*, 252–266. doi: 10.1111/j.1523-1739.2008.00899.x

Sauer, J. R., & Link, W. A. (2011). Analysis of the North American breeding bird survey using hierarchical models. *The Auk*, *128*(1), 87-98. https://doi.org/10.1525/auk.2010.09220

Truett, J., Phillips, M., Kunkel, K., & Miller, R. (2001). Managing Bison to Restore Biodiversity. *Great Plains Research*, *11*(1), 123-144.

Verrall, B., & Pickering, C. M. (2019). Recovery of subalpine grasslands 15 years after landscape level fires. Australian Journal of Botany, 67(5), 425-436. https://doi.org/10.1071/BT19020