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American Bison Ecology and Bison-Cattle Interactions in an Isolated Montane Environment

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AMERICAN BISON ECOLOGY AND BISON-CATTLE INTERACTIONS IN AN

ISOLATED MONTANE ENVIRONMENT

by

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ABSTRACT

American Bison Ecology and Bison-Cattle Interactions in an Isolated Montane

Environment

by

Dustin H. Ranglack, Doctor of Philosophy

Utah State University, 2014

Major Professor: Johan T. du Toit
Department: Wildland Resources

I investigated bison-cattle competition in the Henry Mountains of southern Utah,

basic bison ecology and how it could be used to measure habitat quality, and to provide a

potential new management framework. Data were collected between 2011-2013 through

the use of GPS and VHF telemetry, direct observation, and sample collection. Grazing

exclosures and measures of habitat use and overlap were used to test for potential

competition. I tested the hypotheses that if bison and cattle compete for forage resources,

1) bison visitation at each exclosure site should be a significant predictor of grass

biomass depletion, and 2) bison and cattle will be the two primary grass consumers.

Using habitat use and overlap, I tested the following *a priori* hypotheses: 1) rankings of

bison habitat preferences are similar to overall rankings by which local ranchers claim

those habitats to be important for their cattle; 2) any correlation in rankings of bison

habitat preference and rancher-reported cattle habitat needs is greatest in the winter

season, when forage quality and quantity are both at their lowest, and 3) bison habitat preferences in summer and rancher-reported cattle habitat needs in winter are correlated, given the particular concern over summertime grazing by bison on allotments designated for cattle winter use.

Bison are examined as bioindicators of habitat quality by testing whether 1) manipulated habitats offer higher quality forage, 2) bison respond to differences in habitat quality, and 3) burned and mechanically treated habitats offer similar forage qualities. Bison were not found to be strong competitors with cattle in any case. Instead, lagomorphs emerged as the strongest competitive threat to cattle for forage resources. Further, burned areas were found to be of higher quality than mechanically treated areas. Still, given that any negative impacts from this public bison population are felt by only a small number of stakeholders, I proposed a new management framework that would allow for the increase in the bison population, while compensating those stakeholders. These investigations and management recommendations have implications for bison restoration and management at ecologically meaningful scales throughout the bison's historic range.

(160 pages)

PUBLIC ABSTRACT

American Bison Ecology and Bison-Cattle Interactions in an Isolated Montane

Environment

Dustin H. Ranglack

As bison are considered to be ecologically extinct, and negative interactions

between bison and cattle are perceived to limit bison restoration and cattle production, I

designed a series of studies to test for potential competition between bison (*Bison bison*)

and cattle (*Bos taurus*) for forage on the Henry Mountains in southern Utah. These

studies provide insight into key information gaps previously identified by the Utah

Division of Wildlife Resources (UDWR), Bureau of Land Management, and the local

grazing association. The results indicate that bison and cattle are not strong competitors

for forage on the Henry Mountains. Jackrabbits (*Lepus californicus*) emerged as the

strongest competitive threat to cattle, consuming more than twice the amount of forage

consumed by bison. Further, bison habitat preferences did not match with cattle habitat

needs as reported by a survey of the local ranching community. This suggests that

negative impacts on cattle due to bison have been overstated. Still, any potential negative

impacts of bison will be felt by a small group of local individuals. This prompted me to

design a new management scheme, which has the potential to increase the number of

bison on the Henry Mountains while also compensating local ranchers for reducing the

number of cattle they graze in the area. This system should be mutually beneficial for the

local ranching community and the UDWR, and easily implemented by taking advantage

of the currently exiting conservation license program.

ACKNOWLEDGMENTS

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for either of us. I truly appreciate all the sacrifices you have made to make this happen.

Words cannot express my love and appreciation.

Dustin H. Ranglack

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CHAPTER 1

INTRODUCTION

With commercial ranching and subsistence pastoralism practiced on 40% of the earth's land surface, resolving human-wildlife conflicts on rangelands is a major challenge confronting global biodiversity conservation (Wrobel & Redford 2010). Rangelands constitute much of the matrix of land within which protected areas are embedded and this matrix is especially important for sustaining viable populations of large grazing ungulate species (Redford et al. 2011). World-wide, commercial ranchers and subsistence pastoralists typically hold negative attitudes towards native, large herbivores that are perceived to be competitors with livestock (du Toit 2011). This attitude has contributed to the near eradication of many wildlife species, exemplified in North American by the plains bison (*Bison bison*). Once numbering in the millions, the North American plains bison species declined to <25 wild animals by the late 1800s (Hedrick 2009), primarily due to commercial hunting. Bison numbers have since rebounded due to conservation efforts, but only 20,000 of the presently estimated 500,000 bison in North America now occur in conservation herds (Freese et al. 2007).

Despite the conservation success of numerous bison conservation herds and the large number of commercial bison herds, the question of whether bison have been ecologically recovered as a species is still without an answer (Freese et al. 2007). Most conservation bison herds are small, isolated, and intensively managed populations in fenced areas without natural predators (Gates & Ellison 2010). Importantly, the total number of bison in conservation herds has remained relatively constant despite the increasing number of bison in conservation herds (Freese et al. 2007). Given the lack of

public lands both large enough for bison restoration and cattle free, it is imperative to learn how bison and cattle can coexist. One of the few places where genetically pure, free-ranging bison comingle with cattle on open rangeland is in the Henry Mountains (HM) of southern Utah.

Most studies of bison and cattle have focused on the ecological comparability of the two grazers (Allred et al. 2011; Kohl et al. 2013), which is important considering that cattle have replaced bison across the majority of the historic bison range. However, for the restoration of bison at an ecologically meaningful scale, bison and cattle must graze concurrently on shared rangelands. This has led to many concerns from the livestock producer community, primarily disease transmission, property damage (especially to crops and fences), and competition for grazing resources (although these types of conflict are not uncommon with other large herbivores; Gates et al. 2010). With adequate surveillance and management, disease concerns can be mitigated (Nishi et al. 2002) and the movements of cattle across the landscape can be controlled through spatial management of water and mineral licks (Porath et al. 2002; Bailey 2004), reducing the need for fencing. Competition, however, is difficult to manage, and so it is important to understand the competitive potential of bison and cattle on shared rangelands.

Competition results in a decline in ecological fitness among individuals of both species, but actual measures of fitness are beyond the scope of many studies of long-lived species, thus overlap in diet and/or space use between species are often used as indicators of potential competitive interactions (Prins 2000). Early work in the HM discovered that bison and cattle have 91% dietary similarity (van Vuren & Bray 1983). This large diet

overlap, combined with their conspicuous presence on the landscape caused by their herding behavior, dust wallowing, trampling, and large cattle-like dung pats, has led to a perception that bison are significant competitors with cattle for grazing resources. Smaller and more cryptic herbivores including lagomorphs such as black-tailed jackrabbits (*Lepus californicus*), are less obvious as potential competitors with cattle, but might be important consumers of high-quality forage (Rebollo et al. 2013). Cyclically high population densities of such species, combined with their high mass-specific metabolic demands, can result in larger impacts on forage resources than might be expected from their low detectability and small individual body size (Currie & Goodwin 1966; Rebollo et al. 2013).

In addition, dietary overlap alone might not be a good indicator of competition if habitat use by bison and cattle is differentiated in time and space. A study in one part of the HM identified a 29% overlap in space use, with bison ranging farther – in both distance and elevation - from water than cattle (van Vuren 2001). Patterns are similar in the Great Plains, where cattle have been found to stay close to water and prefer wooded areas, whereas bison movements are less influenced by distance to water and display no preference for wooded areas (Allred et al. 2011; Kohl et al. 2013). While overlap in space use throughout the year is important in understanding the overall dynamics of a mixed-species grazing system, competition is most likely to occur during the season in which grazing resources are most limiting (Odadi et al. 2011). On the HM rangeland winter is the most limiting season, when annual grasses have died and perennial grasses have reallocated nutrients to their roots.

Established in the early 1940s with bison from Yellowstone National Park (Popov & Low 1950; Nelson 1965), the HM bison herd now numbers ~325 adults (post-hunt). This population, like many other NA game species, is controlled primarily by sport hunting under the North American model of wildlife conservation (Geist et al. 2001), which is based on the legal doctrine that wildlife resources are held in the public trust and managed by government agencies. This Public Trust Doctrine, which is rooted in Roman law and was first invoked by the U.S. Supreme Court in the mid-19th century, is now represented in laws that differ among states (in the USA) and provinces (in Canada) but which all preclude personal or communal profit from wildlife (Organ & Mahoney 2007). Implementation of management and enforcement of laws by state and provincial wildlife agencies is funded to a greater or lesser extent by the sale of hunting and fishing licenses. So while the model's purpose is to protect wildlife from over-exploitation, it is paradoxically dependent upon the financial support of those that it seeks to regulate. As a consequence, populations of wildlife species are typically managed to maximize hunting opportunities, subject to resistance from other local land users.

This traditional, command-and-control, top-down management approach is credited for having brought several iconic wildlife species back from the brink of extinction, however it also reflects the species-focused "Maximum Sustained Yield" paradigm of wildlife management, which is now being challenged by the "resilience paradigm" of the 21st century (Chapin et al. 2009; Allen et al. 2011). Resilience thinking conceptualizes multiple linkages between social and ecological systems that enhance the resilience of the coupled system against shocks and disturbances, which are naturally

inherent in global change (Walker & Salt 2006). Reconciling conservation, agriculture, and other competing land uses within a resilience framework involves changing the culture of the relevant management agencies - rather than replacing them – and calls for an integrated approach at the landscape scale (Sayer et al. 2013).

The current management objective of 325 adult bison, post-hunt, was agreed upon by the Utah Division of Wildlife Resources (UDWR), Bureau of Land Management (BLM), and the HM Grazing Association, as more and more AUMs (animal unit months; 1 AUM = forage required to support 1 cow + 1 calf for one month) have been designated for bison use though acquisitions from willing sellers. This provided sufficient forage for the targeted bison population objective, along with additional AUMs to act as a conservation buffer against changing environmental conditions (UDWR 2007).   It is important to consider the impacts that small population sizes have on genetic diversity. For bison, the minimum genetically viable population size has been estimated to be 1000 individuals (Gross & Wang 2005). However, attempting to manage for a population of that size on the HM would be unwise as it may result in damage to the resource base (Allen et al. 2011) and would only serve to increase the conflict between local ranchers and the UDWR. A meta-population management technique could be used to increase the effective population size without negatively impacting the resource base, as individuals from other genetically pure bison herds could be exchanged to maintain/increase genetic diversity (Boyd et al. 2010). However, even with a meta-population management scheme, increasing the population size would be beneficial in reducing negative impacts on genetic diversity.

Not only are larger population sizes preferred for conservation efforts, they also provide increased opportunity for bison hunting. The HM represent the only free-ranging, disease-free, genetically pure, and huntable bison herd in the world. As such, the opportunity to hunt wild bison in this unique environment has both intrinsic and extrinsic value. At the Western Hunt Expo in Salt Lake City, UT in 2014, Sportsman for Fish and Wildlife (SFW) sold two HM bison tags for $19,000 and $18,500. The tags were auctioned under the UDWR conservation permit program with the funds going primarily to the UDWR for use in projects that benefit bison (with input from SFW). In 2013, 5,618 Utah residents and 2,517 non-residents applied to hunt bison on the HM. A total of 86 resident, and 9 non-resident permits were issued through a lottery system. With permit fees of $413 for residents and $1,518 for non-residents, nearly $50,000 of revenue was generated by the UDWR.

Under the current model of wildlife conservation, wildlife species belong to the public for the enjoyment of all. Any negative impacts, however, may only be felt by a small number of individuals. In the HM, a small number of grazing permittees from the local ranching community bear any potential negative impacts from bison. While disease and genetic issues are not of concern in the HM, competition between bison and livestock is perceived as a real threat to the local cattle industry and is leveraged as a political tool by the ranching community to exert influence on state and federal wildlife management agencies. A search for mentions of the HM bison in a major daily newspaper in Utah (*Deseret News*), together with the Utah Legislature archives, revealed an increase in this conflict over time; there were no mentions prior to 1991, eight mentions between 1991

and 1995, and 13 mentions in the 2000s, all of which occurred from 2007-2012. This latter period coincided with drought in the HM. The main concerns expressed by the grazing permittees in that area were doubt over the accuracy of official annual bison counts and a perception that grazing by bison in summer was reducing the standing crop of grass on grazing allotments that were designated for cattle in winter. To complicate the issue, the HM bison herd is a public resource managed by a state agency (UDWR) but the HM rangeland is a checkerboard of primarily federal and state land primarily managed by a federal agency (the BLM), which is responsible for regulating cattle grazing. The BLM permits ~25,600 AUMs of cattle grazing on the HM rangeland during the winter and ~2,600 during the summer. This is the equivalent of ~4,200 cattle present at any given time in the winter and ~800 cattle present at any given time in the summer, mixed in with 350-400 bison year round. Given this large disparity in abundance (bison <10% of winter cattle abundance), in order for bison to negatively impact cattle, their impacts on forage availability and spatial overlap with cattle must be substantial, though not necessarily simultaneous.

This study attempts to address the issues outlined above and fill key knowledge gaps that have been identified by the UDWR. My first objective, which will be discussed in chapter 2, was to quantify the relative impacts of bison, cattle, and lagomorphs on the shared forage resources in the HM public rangeland, with specific attention to the summertime use by bison of grazing areas designated as winter range for cattle. I predicted, (1) that if bison do significantly reduce forage availability for cattle, then bison visitation will be a significant predictor of grass depletion at sampling sites. I also

predicted, (2) that if bison are the main competitor with cattle for grazing resources, then bison and cattle will be the two predominant grass consumers in the system. I examined those predictions experimentally through the use of paired grazed and ungrazed (exclosure) plots, replicated across 20 sites in an area of ~160 km^2. Plots were grazed by cattle in winter and accessible to bison year-round. The results were then compared against a quantification of the local ranchers' perceptions of the competitive impact of bison on cattle grazing.

In Chapter 3, I attempted to identify in which habitats and seasons competition between bison and cattle on the HM is most likely to occur. I used of GPS telemetry on bison and a survey of local rancher perceptions of cattle habitat needs. Under the assumptions that bison and cattle are competing for forage resources on the HM (as claimed), and that local ranchers are accurate in their assessment of the HM rangeland resources, I made the following *a priori* predictions: (1) rankings of bison habitat preferences are similar to overall rankings by which local ranchers claim those habitats to be important for their cattle; (2) any correlation in rankings of bison habitat preference and rancher-reported cattle habitat needs is greatest in the winter season, when forage quality and quantity are both at their lowest. Additionally, given the particular concern over summertime grazing by bison on allotments designated for winter use by cattle, I predict that (3) there is a correlation between bison habitat preferences in summer and rancher-reported cattle habitat needs in winter. If those predictions were upheld, combined with the known overlap in diet, my findings would support the contention that bison and cattle are potential competitors on an open rangeland.

I use an ideal free distribution theory framework (Fretwell & Lucas 1970; Fretwell 1972) in Chapter 4 to indicate the relative quality of four different habitat types (open, closed, burned, and chained) in two different phases of the seasonal cycle with the use of several physiological and behavioral measures. Fecal nitrogen (N), body condition (BC), and endoparasite load were monitored to track seasonal variation in the nutritional status of the HM bison. Higher fecal N and BC scores, along with lower endoparasite loads, should indicate a higher nutritional plane (Caron et al. 2003). As habitat manipulations are intended to improve habitat quality, I predicted that (1) previously burnt and mechanically manipulated habitats offer higher quality forage for bison than undisturbed habitats, as indicated by site-specific fecal N. I further predicted that (2) group size, group composition, and feeding-moving ratio (F:M) vary along a resource quality gradient, such that high quality habitats (as indicated by fecal N) have larger bison group sizes, more mixed-sex groups, and a higher percentage of foraging time devoted to feeding. I was also interested in whether mechanical destruction of trees and burning resulted in habitats of similar quality to bison, expecting that burned areas would be of higher quality due to the rapid release of nutrients during combustion (Allred et al. 2011). Thus, I predicted that (3) group size, group composition, fecal N, and F:M differ accordingly between the two habitat types. I tested all three predictions using data collected through direct observation of bison and fecal sampling from May 2011 to August 2013.

In Chapter 5, I present and discuss one possible option for successful bison restoration and management in Utah and throughout North America. Allowing a fair

system for the local ranching community to benefit directly from the bison that share the public rangeland with their cattle, while also securing bison conservation, might be a solution. I investigate the feasibility of incrementally raising the escapement threshold for the HM bison population, commensurately reducing the stocking rate of cattle, using benefits from bison hunting to compensate the affected ranchers, and providing a fund of bison benefits for community development. My objective is to explore options for integrating bison conservation into the local ranching community to enhance the resilience of this unique social-ecological system.

My results contribute to current knowledge of bison ecology and bison-cattle interactions. For bison to be restored at ecologically meaningful scales in North America, bison and cattle will likely be required to share rangelands. If bison impacts on cattle are found to be overstated, my study provides hope that, with appropriate ecological monitoring and adaptive management, restoration efforts can be accomplished without negatively effecting (and perhaps enhancing) local economies.

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CHAPTER 2

COMPETITION ON THE RANGE: SCIENCE *VERSUS* PERCEPTION IN A BISON-

CATTLE CONFLICT IN THE WESTERN USA[1]

Summary

1. Competition between livestock and wild ungulates is commonly perceived to occur on shared rangelands but is seldom quantified. In the Henry Mountains (HM) of Utah, a free-ranging population of bison (*Bison bison*) has raised concerns among ranchers holding grazing permits on these public lands. Bison are the most conspicuous potential competitors with cattle, but lagomorphs (mainly jackrabbits, *Lepus californicus*) are abundant in this area where the coyote (*Canis latrans*) population is suppressed by state and federal agencies, as well as by private bounty hunters. The local ranching community is applying political pressure on state and federal agencies to resolve "the bison problem", but the relative grazing impacts of bison, cattle, and lagomorphs have not previously been quantified.

2. We constructed 40 grazing exclosures (each 5.95 m^2) in the conflict area, of which 20 excluded bison + cattle ("partial") and 20 excluded bison + cattle + lagomorphs ("full"). All exclosures, each with a paired open reference plot, were monitored for one year and above-ground primary production was measured by harvest. GPS telemetry (bison) and scheduled grazing (cattle) allowed visitation to be quantified for each ungulate species based on the number of 'animal days' in

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the area. Rancher perceptions of wildlife-cattle interactions were recorded in a questionnaire survey.

3. Ranchers perceived bison as a medium to medium-high competitor with cattle whereas lagomorphs were consistently perceived as low-level competitors.

4. Grazed reference plots yielded an average ($\pm$ SE) of 22.7 g m^{-2} ($\pm$ 5.16) of grass, compared to 36.5 g m^{-2} ($\pm$ 7.33) in the partial exclosures and 43.7 g m^{-2} ($\pm$ 7.61) in the full exclosures. Exclusion of bison + cattle thus resulted in a 13.8 g m^{-2} increase in grass biomass relative to the reference plots ($p = 0.005$), with the additional exclusion of lagomorphs resulting in a further 7.18 g m^{-2} increase ($p = 0.048$).

5. Overall, lagomorphs accounted for 34.1%, bison 13.7% and cattle 52.3% of the total grass biomass removed by all herbivores on the shared range.

6. Synthesis and applications: We conclude that cattle face a greater competitive challenge from lagomorphs than from bison on the HM range and coyote population control should be reconsidered. This case-study illustrates the need for science-based management of social-ecological systems in which even long-term resource users might under-estimate the complexities of trophic interactions.

Introduction

Natural resource management is increasingly being conducted within a social-ecological framework with the views and knowledge of local peoples being integrated into management schemes, with varying degrees of effectiveness (Bohensky & Maru 2011). These integrated management schemes are often politically charged and therefore

require a firm scientific basis to ensure that local knowledge is scientifically sound (Davis & Ruddle 2010). The practice of integrating local knowledge into management has primarily focused on artisanal fisheries and subsistence pastoral systems in the developing world (Berkes, Colding & Folke 2000). In contrast, comparatively little attention has been paid to testing local knowledge on wildlife–livestock interactions in commercial animal production systems (Brook & McLachlan 2009). As a case in point, little has been done to test the perceptions and constantly evolving knowledge base of ranchers on rangelands in the western USA (Knapp & Fernandez-Gimenez 2009). Much of the local knowledge that ranchers have developed is undoubtedly accurate and useful, but science is ultimately required for revealing processes underlying observed patterns in rangeland ecosystems (Fernandez-Gimenez 2000). Here, we describe an experimental test of the causal factors contributing to wildlife-livestock competition in the western USA, using it as a case-study to illustrate the need for scientific verification of emotive and politically sensitive disputes between land users and land managers.

World-wide, commercial ranchers and subsistence pastorialists typically have negative views of large herbivores that are perceived to be competitors with livestock (du Toit 2011). This attitude has contributed to the near eradication of many wildlife species, with bison (*Bison bison*) being a specific example in North America. Once numbering in the millions, the entire North American plains bison species declined to <100 wild animals (Hedrick 2009). Bison numbers have rebounded due to conservation efforts, but only 20,000 of the presently estimated 500,000 bison in North America now occur in conservation herds (Freese *et al*. 2007). Of those herds, many are intensively managed on

fragmented landscapes and are introgressed with cattle genes. In addition to concerns of disease transmission, perceived competition with livestock is one of the main factors prohibiting large-scale bison restoration at the continental scale. One of the few places where free-ranging bison comingle with cattle on open rangeland is in the Henry Mountains (HM) of southern Utah.

Established in the early 1940s with bison from Yellowstone National Park (Popov & Low 1950; Nelson 1965), the HM bison herd now numbers ~325 adults (post-hunt) and is controlled primarily by sport hunting. The presence of bison on public allotments leased for cattle grazing has become a source of contention between local cattle ranchers and the state and federal management agencies (UDWR 2007). A search for mentions of the HM bison in a major daily newspaper in Utah (*Deseret News*), together with the Utah Legislature archives, revealed an increase in the conflict over time with no mentions prior to 1991, eight mentions between 1991 and 1995, and 13 mentions in the 2000s of which all occurred during 2007-2012. This latter period coincided with drought in the HM. The main concerns expressed by the grazing permittees in that area were doubt over the accuracy of official annual bison counts and a perception that grazing by bison in summer was reducing the standing crop of grass on grazing allotments that were designated for cattle in winter. To complicate the issue, the HM bison herd is a public resource managed by a state agency (the Utah Division of Wildlife Resources, or UDWR) but the HM rangeland is a checkerboard of primarily federal and state land with a federal agency (the Bureau of Land Management, or BLM) being responsible for regulating cattle grazing. BLM grazing permits are quantified in AUMs (animal unit months; 1 AUM = 1 cow + 1

calf for one month) and there are ~25,600 AUMs permitted on the HM rangeland during

the winter and ~2,600 during the summer. This is the equivalent of ~4,200 cattle present

at any given time in the winter and ~800 cattle present at any given time in the summer,

mixed in with 350-400 bison year round. The cattle are privately owned by individual

ranchers and corporations with various economic goals and environmental values.

Early work discovered that bison and cattle have 91% dietary similarity in the

HM, indicating a high potential for competition (van Vuren & Bray 1983). This diet

overlap, combined with their conspicuous presence on the landscape caused by their

herding behavior, dust wallowing, trampling and large cattle-like dung pats, has led to a

perception that bison are important competitors with cattle for grazing resources. Smaller

and more cryptic herbivores including lagomorphs such as black-tailed jackrabbits (*Lepus*

californicus) are less obvious as potential competitors with cattle but might be important

consumers of high-quality forage (Rebollo *et al*. 2013). Cyclically high population

densities of such species, combined with their high mass-specific metabolic demands, can

result in larger impacts on forage resources than might be expected from their low

detectability and small individual body size (Currie & Goodwin 1966, Rebollo *et al*.

2013).

Our objective was to quantify the relative impacts of bison, cattle, and

lagomorphs on the shared forage resources in the HM public rangeland, where a specific

concern to ranchers is the summertime use by bison of grazing areas designated as winter

range for cattle. We predicted (1) that if bison do significantly reduce forage availability

for cattle, then bison visitation will be a significant predictor of grass depletion at

sampling sites. We also predicted (2) that if bison are the main competitor with cattle for grazing resources, then bison and cattle will be the two predominant grass consumers in the system. We examined those predictions experimentally through the use of paired grazed and ungrazed (exclosure) plots replicated across 20 sites in an area of ~160 km^2 that was grazed by cattle in winter and accessible to bison year-round. The results were then compared against a quantification of the local ranchers' perceptions.

Methods

Study area

The Henry Mountains (HM) study area (Fig. 2-1) in south-central Utah [38°5' N, 100°50'W] includes arid, semi-arid, and subalpine habitats for bison, which migrate seasonally between northern (summer) and southern (winter) parts of the range and utilize almost all vegetation types and elevations in-between. Apart from bison, cattle are the only other large grazers in the region. Mule deer (*Odocoileus hemionus*) are present on the HM, but their preference for forbs would suggest negligible levels of competition with the grazers (van Vuren & Bray 1983). Black-tailed jackrabbits and desert cottontail rabbits (*Sylvilagus audubonii*) are common in the low- and mid-elevations. The only large predators are mountain lions (*Puma concolor*) and coyotes, but their population densities are limited by long-standing predator control efforts implemented by both government and private entities. For a description of the study area see Nelson (1965) and van Vuren and Bray (1986).

This study focused on the Steele Butte North grazing allotment (~15,800 ha), which encompasses the areas known as Stephen's Mesa, Applebrush Flat, and Pete Steele Bench. These relatively low elevation areas (1545-2334 m) are located on the west side of Mount Ellen and have become a focus of concern to the UDWR, BLM, and local ranchers. Traditionally used as winter range for cattle, bison have been using these areas during the summer months for the last 15 years or so, leading to concerns of overgrazing. The semi-arid landscape is vegetated primarily with desert grassland, shrubland, and mixed grassland–shrubland communities, with some piñon–juniper woodlands intermixed. The topography is relatively flat, with intermittent areas of rolling hills and some steep ravines dividing the three areas.

Data collection

A five-question postal survey (Table 2-1) was mailed to 21 cattle producers holding grazing permits in the area used by the HM bison population. Producers were asked to rate (high, medium, or low) their perceptions of various possible bison-cattle interactions, habitat types, and potential wildlife competitors for the forage resources used by their cattle. Ratings were scored (low = 1; high = 3) and averaged within each response category.

In late October 2011, 20 exclosure sites were systematically selected on the Steele Butte North cattle grazing allotment (Fig. 2-1) from a list of randomly generated GPS locations (using ArcGIS) in the allotment. We followed a specific set of rules for site selection. Each site was 50-200 m from the nearest road and >100 m from its nearest neighboring site. As part of a larger study on bison habitat selection in the area, 44 GPS

telemetry collars had been deployed on bison in the HM area in January 2011, transmitting location data at 6-hour intervals (00:00, 06:00, 12:00, 18:00). Location data from these collars were used to ensure that selected exclosure sites were in areas frequented by bison. All 20 sites were located in grassland, grass-shrub mix, or shrubland habitat types.

Selected sites were relatively flat so that all exclosures and their adjacent grazed reference plot were identical in layout. Sites had to be relatively rock-free to allow for the construction of grazing exclosures.

At each selected site, two exclosures (each 5.95 m^2, i.e. 8' x 8') and one equally-sized reference plot were constructed 10 m apart (Fig. 2-2). Both exclosures were constructed with T-posts and 10-line cattle panels with mesh sizes that exclude large herbivores but allow free access to lagomorphs and smaller animals (horizontal mesh spacing of 20.3 cm; vertical mesh spacing of 10.2 cm or 15.2 cm). At each site, one of these exclosures was skirted with finer mesh (2.54 cm diameter) poultry wire such that it extended 60 cm vertically up the side of the exclosure and 60 cm horizontally from the edge, with rocks to weigh it down. The skirting was constructed to minimize the need to remove surrounding vegetation and therefore preserve the microsite hydrologic conditions. This 'full' exclosure was intended to exclude lagomorphs in addition to all large herbivores, while the other 'partial' exclosure was to exclude only large herbivores. The overall design was thus an experimental array of 20 study sites comprising a total of 40 exclosures (20 full; 20 partial) and 20 reference plots.

Each site was visited in October 2011 (set-up) and October 2012. During the October 2012 visit, the standing crop of vegetation in the grazed reference plot and both exclosures (partial and full) was clipped and separated into four vegetation types (grass, forb, shrub, and cactus). The clipped vegetation was transported to the laboratory in paper bags where it was air dried at 22°C for at least 2 months and then weighed.

Statistical analysis

As a metric of bison visitation, a relative density index (*RDI*) was calculated by constructing a circular area around each site of 0.5 km^2 using ArcGIS. *RDI* was calculated for Site i as: *RDI* = *Si/A*; where *Si* = frequency of bison GPS locations in the circle around Site i; *A* = frequency of bison GPS locations expected 'on average' in any random area of 0.5 km^2 within the habitat (grassland, grass-shrub mix, and shrubland) in which Site i occurs. Thus, if $RDI_i > 1$, then more bison were at Site i than would be expected for the habitat in which Site i occurs. *RDI* was calculated for each site based on the date that each exclosure was established and bison visitation at each site during the study period. Because *RDI* varies asymmetrically about 1, log *RDI* was used in the statistical analysis. Given the large proportion of the population that was telemetered, the impacts of non-telemetered bison were considered to be minimal.

To examine the effect of varying usage among sites by bison on grass, forb, cactus or shrub biomass, the difference in biomass between the inside of the partial exclosure and its paired reference plot (both clipped in October 2012) for each vegetation class was linearly regressed on *RDI*. One-way, randomized block design ANOVA with sites as random blocks was used to compare full and partial exclosure types, with the

response variable being the difference in clipped biomass between the exclosure plot and reference plot for each exclosure type. Given this response variable, the mean difference between full and partial exclosure types estimates the lagomorph impact on biomass, and the mean for the partial exclosure type estimates the large herbivore impact. Significance tests were one-tailed, consistent with our predictions. All models were fitted using the GLIMMIX procedure in the SAS System for Windows Release 9.3 and SAS/STAT Version 12.3.

To further examine the relative impacts of bison and cattle, 'animal days' were calculated for both species in the grazing allotment that constituted the study area during the study period. A total count of the HM bison population was conducted in August 2011 and 2012 in a helicopter survey by the UDWR. A sightability adjustment was applied to the data, resulting in a total population estimate for each year. The study period was broken into two segments (Oct. 2011- April 2012 and May – Oct. 2012) based on the timing of calving and recruitment, and the number of bison days during each segment was calculated uniquely based on bison population estimates for that year. For each segment, p_t is the proportion of all GPS collars in the bison population that were in the study area on day t and N is the total bison population size for that year, such that the first segment used the population estimate from August 2011, and the second segment used the population estimate from August 2012. Bison days (*BD*) were calculated as the sum of p_tN over the number of days d in the segment as follows (Eq. 1):

$$BD = \sum_{t=1}^{d} p_tN$$

Cattle days (*CD*) were calculated as the actual cattle use in the study area summed over the number of days they were present during the study, as reported by the grazing permittees for the area.

For the purposes of this analysis, bison and cattle days were assumed to be equal with regards to the daily intake of forage by each species. Our analysis included only adults (both bison and cattle), as calves are considered to be part of the mother cow until 1 year of age. Though bison, especially bulls, can be much larger than cattle, the BLM uses a 1:1 ratio when allocating animal unit months (AUMs) to each species. A search of bison production information on state agriculture extension websites revealed bison AUM equivalence ranges from 0.8 to 1.8 depending on age, sex, reproductive status, and the source of the information. This analysis assumed cow:calf ratio to be constant across bison and cattle, but in fact there are far fewer calves per cow in the bison population, thus compensating to some extent for the larger bison bulls in the population.

Results

Of the 21 cattle producers surveyed, 12 responded to the postal survey (response rate = 57.1%. Those 12 cattle producers hold 3556 of the 5019 cattle grazing permits on the allotments within the Henry Mountains (HM) bison range, thus representing most (70.9%) of the cattle production in the area. Ranchers indicated that competition for forage, especially in the summer and fall seasons when bison are grazing on cattle winter range, is their primary concern. Overall, bison were perceived by the respondents as a medium to medium-high competitor against cattle, with summer and fall ranked highest and winter lowest. Lagomorphs were consistently perceived as a low-level competitor

with cattle, with the winter value only slightly higher than the other three seasons (Table 2-2). All respondents reported their perception that the coyote population should be controlled.

A total of 61.3 kg (dry mass) of vegetation was clipped. The reference plots had a mean ($\pm$ SE) of 22.7 ($\pm$ 5.16) g m^{-2} of grass, compared to 36.5 ($\pm$ 7.33) g m^{-2} in the partial exclosures and 43.7 ($\pm$ 7.61) g m^{-2} in the full exclosures (Fig. 2-3). The regression model found that *RDI* did not significantly ($p = 0.17$) explain the variation across sites with respect to differences in grass biomass between the partial exclosures and reference plots (Fig. 2-4). These results fail to support our *a priori* prediction (1) that site-specific bison visitation (*RDI*) should drive the variation in grass depletion across sites.

The exclusion of only large herbivores (partial exclosure) resulted in a 13.9 g m^{-2} increase in grass biomass relative to the reference plots ($t_{19} = 2.93$, one-tailed, $\mu_{partial} > \mu_{reference}, p = 0.004$), with the additional exclusion of lagomorphs (full exclosure) resulting in a further increase of 7.18 g m^{-2} of grass biomass (Table 2-3) relative to the partial exclosures ($t_{19} = 1.75$, one-tailed, $\mu_{full} > \mu_{partial}, p = 0.048$). Grass biomass in reference plots and both exclosure types covaried across sites due to variation in site-specific productivity (Fig. 5), yet variation in grass biomass in reference plots explained more of the variation in partial ($R^2 = 0.67$) than in full ($R^2 = 0.53$) exclosures (Fig. 2-6). No statistical differences were detected for forb, cactus, or shrub biomass.

The UDWR helicopter surveys in August of 2011 and 2012, after adjusting for sightability, produced an estimate (*N*) of 385 adult bison in 2011 and 432 adult bison in 2012. There were 176 days in which at least 1 bison GPS location was within the Steele

Butte North grazing allotment during the entire study period. Of those 176 days, 45 fell

during the 2011 population year and 131 in the 2012 population year. For the 2011

segment of the study, 310 GPS locations out of 10,979 were located within the study area

($p = 0.028$). The 2012 segment had 5,755 GPS locations out of 15,564 located within the

study area ($p = 0.37$). Bison days (using Eq. 1) were calculated as $BD = 21,415$. Cattle

days amounted to $CD = 81,949$, as verified by the grazing permittees and the local BLM

office. Total bison and cattle days in the study area over the entire study period were thus

$BD + CD = 103,364$. Bison, therefore, represented 20.7 % of the combined grazing effect

of both species based on the number of animal days on the allotment during the year over

which the study was run. Breaking down the 'large herbivore grazing effect' into the

respective impacts of bison and cattle using the percentage of animal days represented by

each species, bison accounted for 2.88 g m^{-2} of grass removed whereas cattle accounted

for 11.0 g m^{-2}. On a percentage basis, this equates to cattle accounting for 52.3%,

lagomorphs 34.1%, and bison 13.7% of the total grass depletion attributable to the main

vertebrate herbivores in this system over one year. This result does not support our *a*

priori prediction (2) that bison are the main wildlife competitor in the system.

Discussion

Contrary to our *a priori* predictions, at current population densities the bison

impact on the grazing resource is minor in comparison to lagomorph and cattle impacts.

These findings demonstrate that the local ranchers' perceptions were either based on a

misunderstanding of the ecological interactions in this system or were reported with bias

to suit their political stance in the HM bison controversy. Either way, our study illustrates

how management decisions based on perceptions are unlikely to lead to the desired outcome, highlighting the need for science when integrating local ecological knowledge into management strategies (Davis & Ruddle 2010). In the HM, given that lagomorphs consume more than twice the forage used by bison, there is a greater potential to reduce competition with cattle by reducing lagomorph abundances than by attempting to manage bison habitat use (through hazing, fencing, etc.) or population size (with hunting and live removals).

Lagomorph populations in the USA's desert-southwest are cyclical (Rosen 2000; Stoddart, Griffiths, & Knowlton 2001; Bartel & Knowlton 2005), and in the HM where predators are controlled, are likely driven by bottom-up processes. Local state and federal biologists (David Cook, Wade Paskett, pers. comm) estimate that the lagomorph population in the HM during the time of this study was in the low-middle of the cycle. Our results are, therefore, likely to be an underestimate of long-term averages, in terms of lagomorph impacts on grazing resources. Lagomorph impacts will likely be larger than we reported during high population years, and slightly smaller during low population years. Anecdotal evidence from other grazing exclosures in central Utah also indicate that lagomorphs are having a larger than expected impact (David Dahlgren, pers. comm.), indicating that our finding is not unique to the HM but is likely a widespread phenomenon deserving further study.

Predator control, primarily focused on coyotes, has become standard practice on western rangelands, especially in Utah where $1.35 million is spent annually on coyote population control alone. The HM area is designated as a trophy mule deer unit, which

drives strong support from hunters for coyotes to be killed on sight in this area. The

UDWR contracts with federal management agencies and private individuals to remove

coyotes, and a $50 bounty is paid to the general public for each coyote killed (upon

verification). In the HM area, state and federal agencies reported a combined total of 156

coyotes (*Canis latrans*) killed in official control operations from July 2010 through

January 2014. Actual numbers were likely higher, as some coyotes killed by private

individuals are not reported. Because lagomorphs represent one of the primary prey

species for coyotes throughout the seasonal cycle (Rosen 2000; Bartel & Knowlton

2005), sustained suppression of the coyote population should increase jackrabbit densities

(Henke & Bryant 1999). Should predator removals be reduced or eliminated, lagomorph

densities will likely decrease and the oscillations in the lagomorph population cycle

would likely be dampened as top-down forces take effect (Rosen 2000), leading to more

stable range conditions. On western USA rangelands, the trophic cascade associated with

undisturbed coyote populations has the potential to compensate for depredation on

livestock (Wagner 1988).

Coyotes are killed primarily due to the political pressure imposed on government

agencies to improve conditions for mule deer and livestock. Bison numbers are

maintained below the level that could be sustained by the rangeland due to the same

political pressures, at the possible expense of genetic diversity and long-term population

viability (Hedrick 2009). Our research findings could be used in an adaptive management

framework to improve the profitability of the HM rangeland. By reducing or eliminating

expensive coyote population control efforts, the jackrabbit density should decline and the

standing crop of available forage should increase, thereby improving the winter range for cattle without the need to further manage the bison population. This seems especially prudent given the relative ineffectiveness of predator control in increasing vital rates of ungulate populations in many situations (Ballard *et al*. 2001; Hurley *et al.* 2011). Nevertheless, we do recognize that the political landscape adds complexity to social-ecological systems such as the HM rangeland, where government agencies have to strive to reduce conflict among multiple, often competing, interests. As such, direct control measures on lagomorph populations may be more acceptable and should accomplish the same result, just at greater cost.

Our data show that at the present population density, bison cause very modest forage availability for cattle. Furthermore, they are not the predominant wildlife competitor with cattle for grazing resources. These results align with a concurrent study on grazing impacts on plant community composition in the HM, which also found that bison grazing caused no significant impacts on plant species composition due to bison grazing (Ware, Terletzky & Adler 2014). In contrast, grazing effects of small herbivores are commonly underestimated but must be accounted for as a potential driver of grassland structure and diversity (Rebollo *et al.* 2013). Because bison range widely across the landscape whereas cattle are central place foragers, usually focusing their grazing around water sources, bison and cattle exhibit spatial segregation on shared rangelands (van Vuren 2001; Allred *et al.* 2011). The purported negative impacts of bison on cattle can thus be overstated, at least in the HM.

Continued monitoring of our permanent exclosure sites, partnered with direct measurement of lagomorph abundance, is needed to determine the long-term effects of lagomorphs on the HM rangeland. This should include further study of the impact of coyote population control on lagomorph population densities. Our present study serves to illustrate why caution should be used when integrating local ecological knowledge into natural resource management (Krupnik & Jolly 2002; Gilchrist, Mallory & Merkel 2005; Ruddle & Davis 2009). The knowledge-base of local communities might not match current conditions or might become biased by political pressures to misrepresent the complexities of the system. Scientific verification of local ecological knowledge is thus crucial (Raymond *et al.* 2010), without discounting the importance of local stakeholders as active participants in management planning. For bison to be restored at ecologically meaningful scales in North America, bison and cattle will likely be required to share rangelands. Our study provides hope that, with appropriate ecological monitoring and adaptive adjustments to the densities of all the main grazers in the system, this can be accomplished without negatively effecting (and perhaps enhancing) local economies.

Data accessibility

If accepted, the data will be made available at ResearchGate.

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Table 2-1. A short survey was developed in coordination with the local Bureau of Land

Management office (Hanksville, Utah) to gauge the relative importance and influence of

various factors affecting bison-cattle interactions on the Henry Mountains. The local

ranching community was asked to rate the following interactions, habitat types, and

potential wildlife competitors as high, medium, or low for each season (Spring, Summer,

Fall, and Winter). In addition, they were asked to indicate if they felt the coyote

population should be controlled and to rank the benefit that wild and domestic species

might receive from that. Results were scored such that high=3 and low =1.

1. **How do bison interact with cattle?**

   Competition for forage   Competition for water

   Aggression or disturbance   Other (Please explain)

2. **How valuable are these habitat types for cattle?**

   Barren Ground   Grassland   Grass-Shrub Mix

   Shrubland   Piñon-juniper woodland   Riparian

   Chained piñon-juniper woodland   Oakbrush   Aspen woodland

   Coniferous woodland   Alpine Meadow

3. **How much might these wildlife species compete with cattle?**

   Mule deer   Bison   Jackrabbit   Other (Please explain)

4. **Should the coyote population be controlled in the HM?**

   Yes   No

5. **Which species benefit from coyote control in the HM area?**

   Mule deer   Livestock   Other (Please explain)

Table 2-2. Rancher respondents' mean ratings with standard errors (SE) of perceived competition from bison and lagomorphs towards cattle on the HM rangeland, on a scale of 1-3, where 1 is "low" and 3 is "high". Of the 21 cattle producers surveyed, 12 responded to the postal survey (57.1%). Those 12 producers account for 70.9% of the grazing permits in the HM area.

Season	Bison Mean	SE	Lagomorph Mean	SE
Spring	2.18	0.30	1.09	0.09
Summer	2.36	0.28	1.09	0.09
Fall	2.36	0.28	1.09	0.09
Winter	1.82	0.30	1.18	0.09
Annual	2.18	0.25	1.11	0.11

Table 2-3. Mean increase in grass biomass (dry mass) relative to reference plots as a result of herbivore exclusion on the HM rangeland. Full exclosure represents the small-herbivore effect (lagomorphs) + the large-herbivore effect (bison and cattle), while partial represents the large-herbivore effect only. The difference between partial and full is the small-herbivore effect only. P-value is the result of a one-tailed paired t-test, along with 95% confidence limits.

Increase in grass biomass (g m^{-2})	SE	P-Value	Lower CL	Upper CL
Partial	13.9	4.79	0.005	3.86	23.9
Full	21.1	4.11	0.048	12.5	29.7
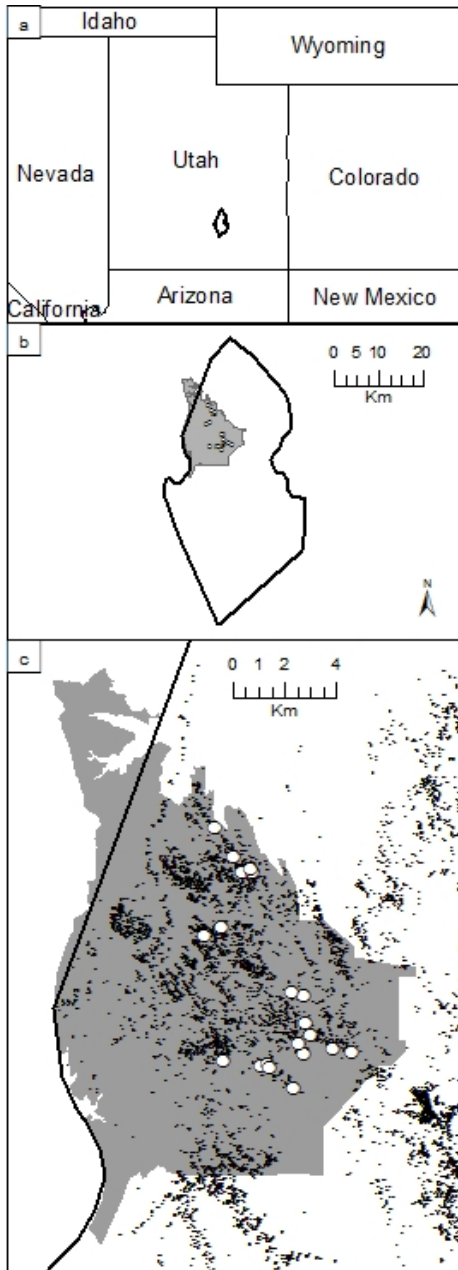
Fig. 2-1. Location of the Henry Mountain (HM) rangeland in the state of Utah (a); the Steele Butte North grazing allotment (grey), upon which the study was conducted, in relation to the HM, with the exclosure sites represented by white circles (b); the grazing allotment (grey), exclosure sites (white circles), and the bison GPS locations (black dots) collected during the exclosure study period (c).
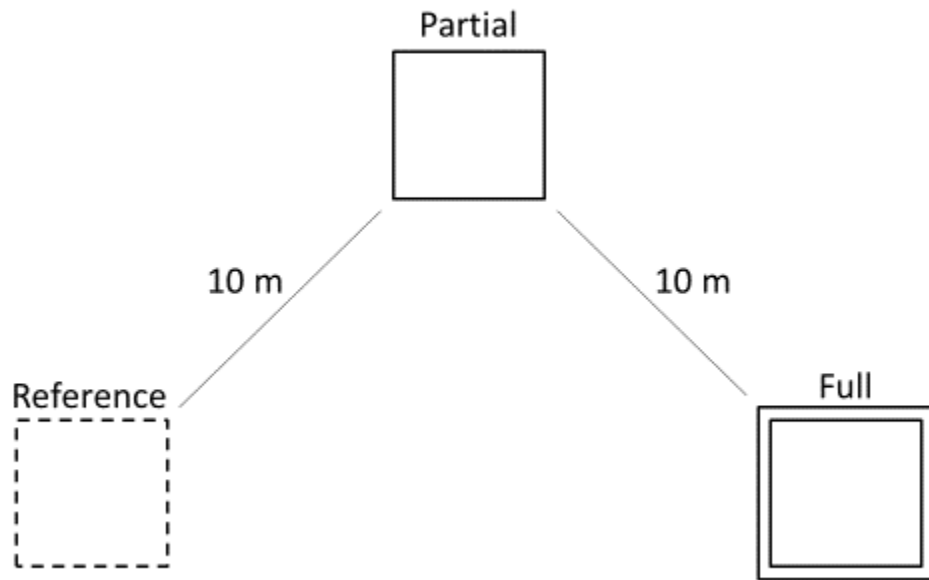
Fig. 2-2. The layout of each exclosure site is detailed with dashed squares representing open plots and solid squares representing excluded areas. All treatments, grazed reference plots or excluded areas, are 5.95 m^2 (i.e. 8' x 8'). The partial exclosure is designated by a single solid line and the full exclosure by a double solid line. All sites were erected in Oct. 2011. The standing crop in both exclosures and the reference plot at each site were clipped in Oct. 2012.
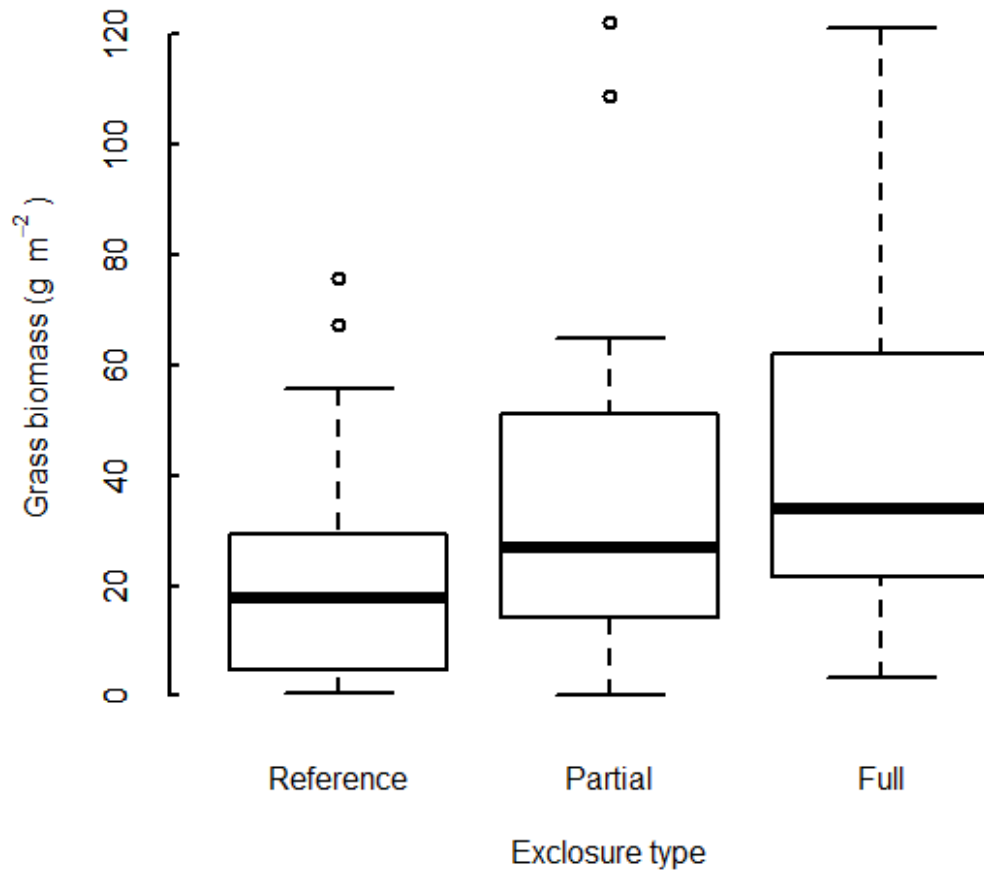
Fig. 2-3. Boxplots of grass biomass clipped to measure standing crop after one year for each of the treatment types ($n = 20$ per type): grazed reference plot; partial exclosure (cattle + bison out); and full exclosure (cattle + bison + lagomorphs out). Significant differences were found among all three plots ($p < 0.05$). The difference between the reference and partial is the large herbivore effect (bison and cattle), and the difference between partial and full is the small herbivore effect (lagomorphs). Total grazing impact is represented by the difference between reference and full. Box plot shows quartiles, median, and 1.5x interquartile range. Circles show outliers beyond 1.5x interquartile range.
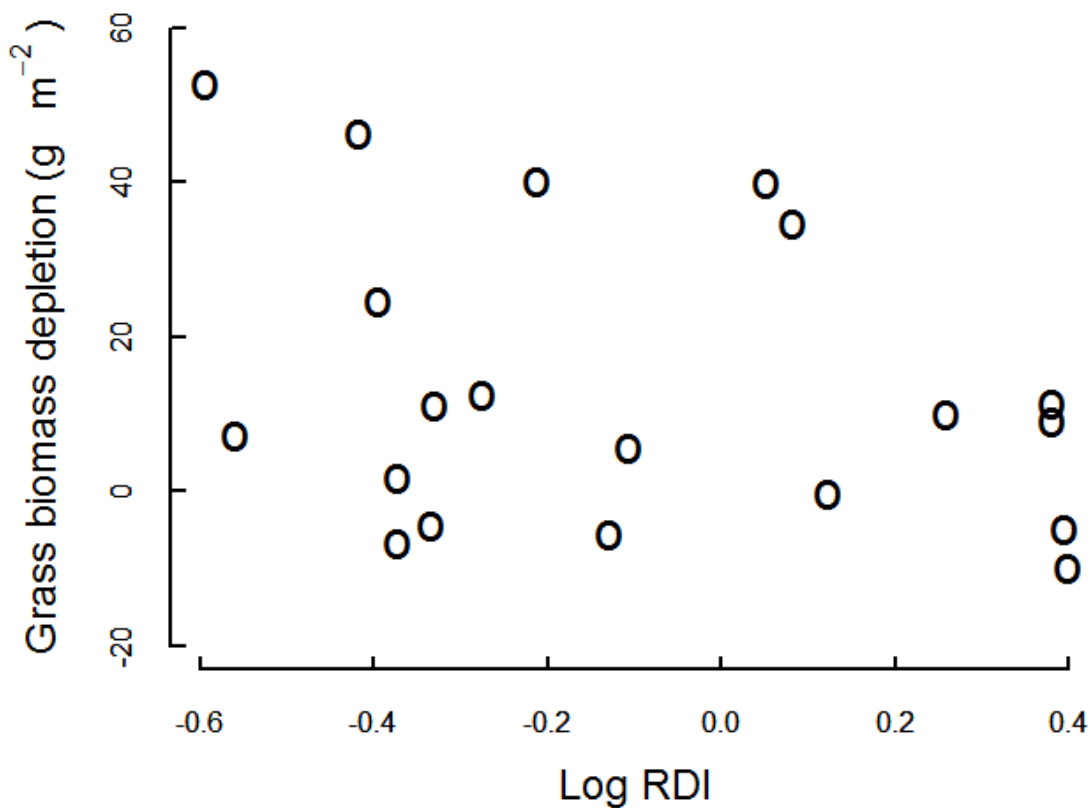
Fig. 2-4. Variation in site-specific grass depletion (difference in grass dry mass between reference plot and the partial exclosure at each site) is not explained by variation in bison visitation (log *RDI*) across sites ($p = 0.17$), contrary to the positive relationship expected by Prediction 1. Data points represent the difference in grass biomass (partial – reference) for each site.
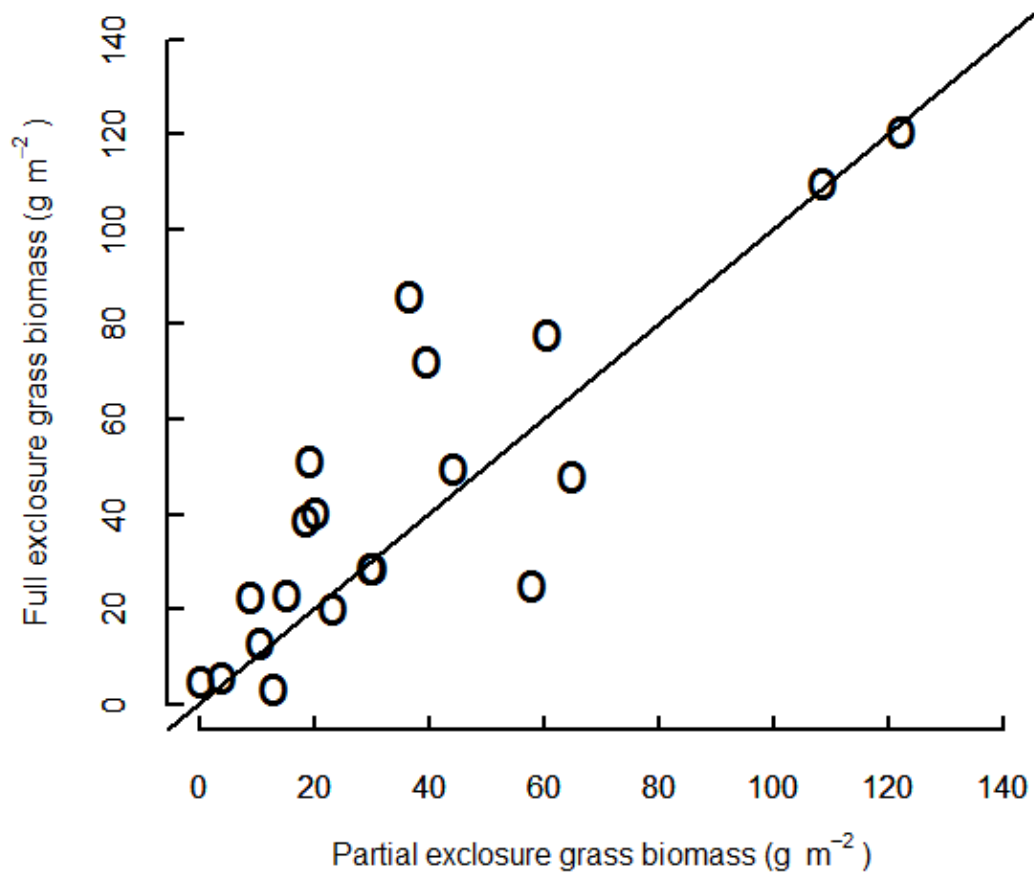
Fig. 2-5. Comparison of grass biomass (g m^{-2}) clipped in the partial and full exclosures for each of the 20 grazing exclosure sites plotted with a 1:1 reference line. Residuals above the line indicate the size of the lagomorph effect on grazing resources across exclosure sites.
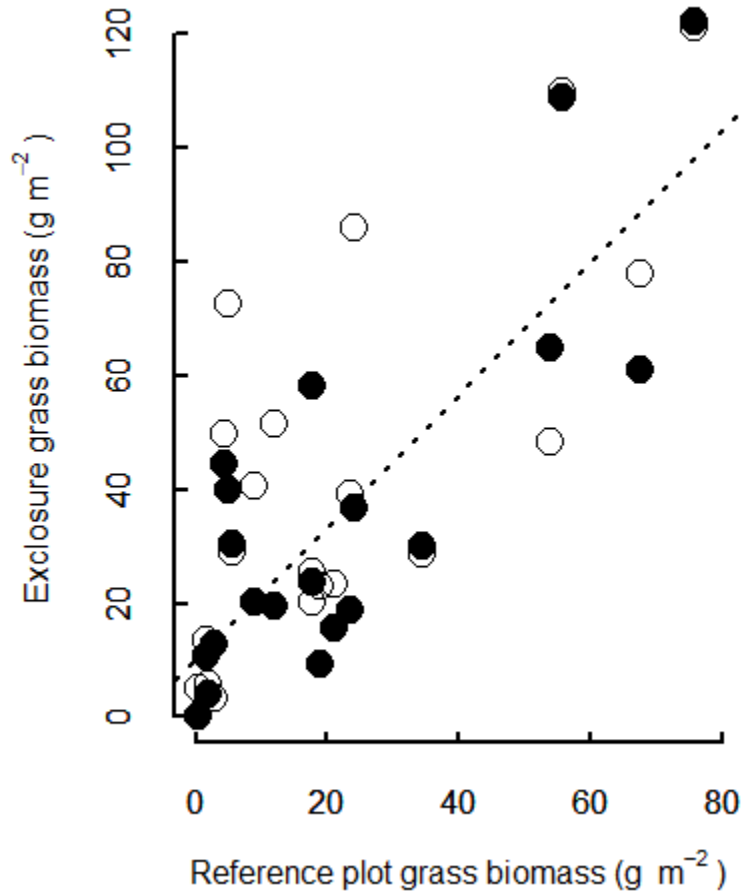
Fig. 2-6. Grass biomass (dry mass) clipped after one year in reference plots, plotted against partial exclosures (closed circles) and full exclosures (open circles). Values covaried across sites because of variation in site-specific productivity. Nevertheless, variation in grass biomass in reference plots explained more of the variation in partial exclosures (dashed line; $R^2 = 0.67$) than in full exclosures (not plotted; $R^2 = 0.53$). Lagomorphs had access to reference plots and partial exclosures, but not to full exclosures, resulting in more similarity between reference plots and partial exclosures than between reference plots and full exclosures.

CHAPTER 3

TESTING OF CONTENTION IN PUBLIC GRAZING: DO BISON PREFER THE

SAME HABITATS PERCEIVED BY RANCHERS AS IMPORTANT FOR CATTLE?[2]

Abstract

One of the few places where bison (*Bison bison*) and cattle (*Bos taurus*) comingle

on shared rangelands is in the Henry Mountains (HM) of southern Utah. This joint use

has created conflict between local livestock producers and state and federal management

agencies due to concerns over competition. Summertime grazing by bison in allotments

designated for cattle winter use is of particular concern. It is known that bison and cattle

in the HM have a high degree of dietary overlap, but spatial overlap has previously only

been quantified for a small portion of the HM. Here, we use GPS telemetry on bison and

a survey of local ranchers' perceptions of cattle habitat needs to identify in which habitats

and seasons competition between bison and cattle is most likely to occur on the HM

rangeland. Sexual segregation was also measured to determine if bison bulls exert

localized impacts by congregating in certain habitats separate from cow/calf groups.

Annual bison habitat preference showed only marginal correlation with rancher

perceptions of cattle habitat needs ($r_s = 0.57$, $p = 0.066$). No statistically significant

correlation was detected in any season except for fall ($r_s = 0.611$, $p = 0.045$).

Additionally, no significant correlation was found between bison summer habitat use and

rancher-reported winter cattle habitat needs ($r_s = 0.541$, $p = 0.085$). The HM bison also

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[2] Coauthored by D. H. Ranglack and J. T. du Toit.

exhibit very low levels of sexual segregation for both the breeding ($SC = 0.048$) and non-breeding seasons ($SC = 0.112$). This leads us to believe that, at current population densities, competition between bison and cattle is limited on the HM. Our findings should hopefully ease tensions between the local ranching community and the state and federal government agencies regarding free-ranging bison and cattle in this unique case-study for wildlife conservation in the USA.

INTRODUCTION

A key principle for reconciling agriculture, conservation, and other competing land uses is that there has to be a "common concern entry-point," meaning that differences in values, beliefs, and objectives among stakeholders have to be at least reduced before moving forward with collaborative adaptive management (Sayer et al. 2013). That involves building trust, which requires local knowledge to be solicited, verified (Davis and Ruddle 2010) and incorporated into the management of natural resources within a social-ecological system (Bohensky and Maru 2011). Integration of local knowledge into management is well advanced in the developing world, especially with subsistence pastoral systems and artisanal fisheries (Berkes et al. 2000). Yet comparatively little has been done to test local knowledge on wildlife–livestock interactions in commercial animal production systems (Brook and McLachlan 2009), especially concerning the ever-evolving knowledge base and perceptions of western American ranchers (Knapp and Fernandez-Gimenez 2009). Much of the ecological knowledge expressed by ranchers is undoubtedly accurate, but science is necessary for revealing processes underlying observed patterns in rangeland ecosystems (Fernandez-

Gimenez 2000). Considering the influence that ranchers have over rangelands, which constitute much of the matrix within which protected areas are embedded, reconciling ranching and conservation is important especially for sustaining viable populations of large grazing ungulate species (Wrobel and Redford 2010, Redford et al. 2011). Here we focus on the American bison (*Bison bison*) as a case in point.

Once numbering in the millions, the entire North American plains bison population declined to <100 wild animals by the late 1800s (Hedrick 2009). Bison numbers have rebounded to ~500,000 thanks to conservation efforts, but only ~20,000 of those now occur in conservation herds (Freese et al. 2007). Of those, most are intensively managed on fragmented landscapes and are introgressed with cattle genes. In addition to concerns of disease transmission, perceived competition with livestock is one of the main factors prohibiting large-scale bison restoration at the continental scale (Freese et al. 2007). One of the only places where free-ranging plains bison comingle with cattle on open rangeland is in the Henry Mountains (HM) of southern Utah.

Established in the early 1940s with bison from Yellowstone National Park (Popov and Low 1950, Nelson 1965), the HM bison herd now numbers ~325 adults (post-hunt) and is controlled primarily by sport hunting. The presence of bison on public allotments leased for cattle grazing has become a source of contention between local cattle ranchers and the state and federal management agencies (UDWR 2007). A search for mentions of the HM bison in a major Utah daily newspaper (*Deseret News*) and the Utah Legislature archives revealed an increase in the conflict, with no mentions prior to 1991, eight mentions between 1991 and 1995, and 13 mentions in the 2000s, all of which occurred

between 2007 and 2012. This latter period coincided with below-average rainfall in the HM when the grazing permittees in the area began expressing doubt over the accuracy of annual bison counts. Additionally, there was concern that bison were reducing the standing crop of grass in summer on allotments that were designated for cattle in winter.

To complicate the issue, the HM bison herd is a public resource managed by a state agency (Utah Division of Wildlife Resources), but the HM rangeland is mainly a checkerboard of federal and state land with a federal agency (Bureau of Land Management) being responsible for regulating cattle grazing. The cattle permitted to graze the HM area, of which approximately 4,200 are present during the winter and 800 during the summer, are privately owned by individual ranchers and corporations with various economic goals and environmental values.

Most studies of bison and cattle together have focused on the ecological comparability of the two grazers (Allred et al. 2011, Kohl et al. 2013), which is important considering that cattle have replaced bison across the majority of the historic bison range. However, for the restoration of bison at an ecologically meaningful scale, bison and cattle must graze on shared rangelands. This leads to many concerns from the livestock producer community, primarily disease transmission, property damage (especially to crops and fences), and competition for grazing resources, though these types of conflict are not uncommon with other large herbivores (Gates et al. 2010). With adequate surveillance and management, disease concerns can be controlled (Nishi et al. 2002), and the movements of cattle across the landscape can be controlled through spatial management of water and mineral licks (Porath et al. 2002, Bailey 2004), reducing the

need for fencing. Competition, however, is difficult to manage, and so it is important to understand the competitive potential of bison and cattle on shared rangelands.

Competition results in a decline in fitness among individuals of both species, but actual measures of fitness are beyond the scope of many studies of long-lived species. Overlap in diet and/or space use between species are often used as indicators of the degree of competitive interaction (Prins 2000). Early work in the HM discovered that bison and cattle have 91% dietary similarity (van Vuren and Bray 1983) indicating a high potential for competition and leading to a local perception that bison are strong competitors with cattle for grazing resources. Dietary overlap alone might not, however, be an indicator of competition if habitat use by bison and cattle is differentiated in time and space. Early work in one part of the HM identified only a 29% overlap in space use, with bison ranging farther – in both distance and elevation - from water than cattle (van Vuren 2001). In the Great Plains too, cattle stay close to water and prefer wooded areas, whereas bison movements are less influenced by distance to water and they display no preference for wooded areas (Allred et al. 2011). As sexual segregation is common in bison elsewhere, we also measured sexual segregation to determine if bison bulls have distinct patterns of habitat use. This was to check on the possibility that bison bulls, although small in number, could degrade certain habitats if they 'camped' there in bachelor groups while mixed cow-calf groups roamed more widely.

While overlap in space use throughout the year is important in understanding the overall dynamics of a mixed-species grazing system, competition is most likely to occur during the season in which grazing resources are most limiting (Odadi et al. 2011). On

the HM rangeland, winter is the most limiting season, when annual grasses have died and perennial grasses have reallocated nutrients to their roots. Our objective was to identify in which habitats and seasons competition between bison and cattle on the HM is most likely to occur. Our approach featured the use of GPS telemetry on bison and a survey of local rancher perceptions of cattle habitat needs. Given the relatively small number of bison present on the HM compared to cattle ($<10\%$ of the permitted cattle numbers in winter), for bison to negatively impact forage availability for cattle they must show strong preference for those habitat types that are important for cattle.

If bison and cattle are competing for forage resources on the HM as claimed, and local ranchers are accurate in their assessment of the HM rangeland resources, the following predictions should hold: (1) rankings of bison habitat preferences will be similar to overall rankings by which local ranchers claim those habitats to be important for their cattle; and (2) any correlation in rankings of bison habitat preference and rancher-reported cattle habitat needs will be greatest in winter, when forage quality and quantity are both at their lowest and the cattle population is at its highest. Additionally, given the particular concern over summertime grazing by bison on allotments designated for winter use in cattle, we predict (3) a correlation between bison habitat preferences in summer and rancher-reported cattle habitat needs in winter. If those predictions were upheld, combined with the known overlap in diet, our findings would support the contention that bison and cattle are potential competitors on the open rangeland.

METHODS

Study area

The Henry Mountains (HM) study area (Fig. 3-1) in south-central Utah [38°5' N, 100°50'W] includes arid, semi-arid, and alpine habitats for bison during their seasonal migrations from low to high altitudes. Apart from bison, cattle are the only other large grazers in the region. Mule deer (*Odocoileus hemionus*) are present on the HM, but their preference for forbs would suggest negligible levels of competition with the grazers (van Vuren and Bray 1983). A small herd (~20 animals) of elk (*Cervus canadensis*) is also present, though the Utah Division of Wildlife Resources actively manages against elk using sport hunting in an attempt to eradicate the herd to prevent competition with the highly-prized mule deer. Black-tailed jackrabbits (*Lepus californicus*) and desert cottontail (*Sylvilagus audubonii*) are common in the low- and mid-elevations. Mountain lions (*Puma concolor*) and coyotes (*Canis latrans*) utilize the study area, but their populations are controlled by government and private entities. A detailed description of the study area can be found in Nelson (1965) and van Vuren and Bray (1986).

Data collection

It proved infeasible to attach telemetry collars to a representative sample of cattle across the HM rangeland and so the local ranchers were surveyed to quantify their perceptions of habitat needs for their cattle. A five-question postal survey was mailed to 21 cattle producers holding grazing permits in the area used by the HM bison population (Table 3-1). Producers were asked to rate (high, medium, or low) their perceptions of various possible bison-cattle interactions, habitat types, and potential wildlife competitors

for the forage resources used by their cattle. Scores (low = 1; high = 3) were averaged within each response category.

Satellite-download GPS telemetry collars were deployed on bison in the HM area in January 2011, transmitting location data at 6-hour intervals (00:00, 06:00, 12:00, 18:00). Collars that stopped transmitting due to damage, death of the individual, or premature drop-off were replaced in January 2012, June 2012, and January 2013. A total of 47 individual bison, 28 females and 19 males, wore a GPS collar for some duration during the study period of January 2011 – December 2013.

Any data collected within 10 days of an individual's capture were removed from the data set to reduce disturbance effects. Any locations that were collected outside of the designated collection schedule or with a dilution of precision (DOP) greater than 8 (D'eon and Delparte 2005) were also removed to ensure the accuracy of the collected data. The data were then grouped by sex and season. Spring was designated as March – May, summer as June – August, fall as September – November, and winter as December – February. The female locations for each season, plus annual use, were used to create minimum convex polygons (MCP) using ArcGIS. These were used to delineate the area within which classified habitats (landcover types) were assumed to be available to the HM bison population in each season, resulting in 5 separate MCPs. Random GPS points were then generated using Geospatial Modeling Environment at a 1:1 ratio to the actual number of bison locations for each season to allow for the direct comparison of used (GPS collar data) to available (random GPS points) habitat types and landscape variables.

Landcover classifications, digital elevation models, and the locations of roads and water sources were obtained from the Utah Automated Geographic Reference Center, the Bureau of Land Management, and the Utah Division of Wildlife Resources, all at the 30 x 30 m scale. All landcover data were verified and corrected where needed through ground-truthing and the use of recent (2011) National Agriculture Imagery Program (NAIP) aerial photography. South West GAP data (USGS 2004) were used to construct a landcover dataset, with landcover descriptions collapsed into 12 types: alpine meadow, aspen woodland, barren, "burn," "chaining," coniferous woodland, grassland, grass-shrub mix, shrubland, oakbrush, piñon-juniper woodland, and riparian. In the "burn" landcover type most trees were absent and the herbaceous vegetation comparatively dense, following prescribed or accidental fires in recent years. The 'chaining' areas had been intentionally created in past decades, by breaking down piñon-juniper woodland using parallel bulldozers connected with chains, as a management intervention to improve grazing conditions for cattle. Euclidean distance (km) to roads and water sources was calculated for each pixel, and aspect and slope were calculated from the digital elevation model in ArcGIS. Aspect was then reclassified for analysis as a categorical variable with eight levels (N, NE, E, SE, S, SW, W, and NW).

The cattle on the HM rangeland are cows with calves and so we were sex-specific in our analysis of bison habitat use. For sexual segregation analysis, direct observation of bison on the HM was conducted between May 2011 and August 2013. Seasons were defined as breeding (July-August) and non-breeding (September–June). Observations were primarily collected during the summer months (May–August), with monthly trips

throughout the remainder of the seasonal cycle as possible. Direct observation of bison proved difficult in the winter months as the bison tended to use a large roadless area with extremely rough topography that made access prohibitively difficult. When a bison group was located, group size and composition (numbers of bulls, cows, and calves) was recorded, as well as the habitat type in which they were found. For statistical analysis, only those observations that resulted in every individual in the group being classified as adult male, adult female, or calf were used (yearlings were classified as adults).

Statistical analysis

Habitat types were ranked in order of most to least preferred by bison using a resource selection function (RSF) framework (Manly et al. 2002) with aspect, elevation, slope, distance to road, distance to water, and landcover type as covariates to control for differences between sites. Burnt and chained landcover types were combined for this analysis to allow for direct comparison to the rancher survey data, which did not ask for a ranking of burnt areas. A generalized linear mixed model (GLMM; binomial distribution, logit link) with a random effect for individual (and season when using annual data; Hebblewhite et al. 2008, Bolker et al. 2009), accounting for repeated measures and allowing for an unbalanced number of locations among individuals and seasons (Bennington and Thayne 1994). The GLMM was applied using the lme4 package version 1.0-5 for R version 3.0.2. For categorical variables, piñon-juniper woodland was selected as the reference category for vegetation because it represented one of the most common landcover classes and was expected from field observations to be of low preference to bison during each season. North-facing slopes were designated as the reference category

for aspect. Variables were screened for collinearity using scatterplots and variation

inflation factors but no colinearity issues were identified, thus all variables were included

in the model. A total of 5 different models were created; one for each season and the

annual model for females only. The resulting RSF coefficient estimates were used to rank

landcover types from most to least preferred. Those rankings were compared to the

perceived cattle habitat rankings derived from the rancher questionnaire survey using

Spearman's rank correlation coefficient to test for associations annually (Prediction 1), by

season (Prediction 2), and summer bison – winter cattle (Prediction 3).

Conradt's (1998) segregation coefficient (*SC*) for habitat was used to test for the

relative strength of sexual segregation in the bison population for the breeding (July-

August) and the non-breeding seasons (September–June) using the group composition

data. Additionally, a subset of 1000 GPS locations per sex per season was used to

construct a chi-squared contingency table with a family of simultaneous Bonferroni 95%

confidence intervals to test for habitat selection in each sex and season following Neu et

al. (1974). A chi-squared contingency table was also used to test for intersexual

differences in habitat use profiles for each season.

RESULTS

Of the 21 cattle producers surveyed, 12 responded to the postal survey (response

rate = 57.1%). Those 12 cattle producers hold 71% of grazing permits for the allotments

within the HM bison range, thus representing most of the cattle production in the area. Of

the 12 respondents, one did not supply data regarding habitat rankings, thus reducing the

response rate and % of cattle represented in the data to 54.4% and 69.7% respectively for

that part of the survey (Table 3-1). Mean scores of perceived habitat importance for cattle varied from 1.09 for the least important (coniferous woodland) to 2.73 for the most important (grassland) habitat type, with slight variation in each season. Ranchers also scored fall as the season where competition for forage is of the largest concern, with an average score of 2.42, with summer and spring having an average score of 2.08, and winter being of the least concern with an average score of 1.92.

A total of 84,623 bison GPS locations were collected, with 27,713 from male bison and 56,910 from female bison across an area of nearly 125,000 ha. All 56,910 female bison GPS locations were used for the RSF analyses (and thus 56,910 random points were also generated). The resulting ranks of annual female bison RSF values were compared to the annual average ranks from the rancher survey of each habitat type's perceived importance to cattle (cows and their calves) using Spearman's correlation. This revealed a marginally significant correlation (Fig. 3-2; $r_s = 0.57$, $p = 0.066$). Further comparisons using the same method within each season found no significant correlation for spring, summer, and winter, but a significant correlation for fall (Fig. 3-3; $r_s = 0.611$, $p = 0.045$). No significant correlation was found between rank profiles of bison habitat preferences in summer and rancher-reported cattle habitat needs in winter (Fig. 3-4; $r_s = 0.541$, $p = 0.085$).

From the chi-squared contingency table, the bison sexes were found to have significant seasonal differences in their habitat use profiles in the fall and winter, but not in the spring and summer (Table 3-2). Conradt's (1998) segregation coefficient (*SC*), however, revealed strikingly low levels of sexual segregation in this population overall,

though, as expected, there was a slight increase in segregation from the breeding (SC = 0.048) to the non-breeding season (SC = 0.112). Winter showed the largest intersexual difference in bison habitat selection profiles, followed by fall, summer, and spring respectively (Table 3-2). The chi-squared contingency table and Bonferroni confidence intervals identified 'grassland', 'recently burned' and 'chaining' as important habitats for both sexes throughout the year, with 'grassland' and 'recently burned' being important in winter especially (Table 3-2).

DISCUSSION

We found that annual rank profiles of bison habitat preferences, as determined through RSF analysis, and rancher-reported cattle habitat scores were marginally correlated (Prediction 1) although the highest correlation between bison and rancher scores was not during winter (the leanest season), but during the fall (contrary to Prediction 2). It is important to consider that Spearman's rank correlation does not take into account where in the rankings the correlation is taking place, thus close matches at the bottom of the rankings can strongly influence the overall coefficient, despite having little meaning ecologically. During the fall season, only one of the top five habitat types (shrubland) was an exact match, but the top habitat for bison was ranked fourth in importance for cattle by the ranchers and the lower ranked habitats were better correlated (Fig. 3-3). This is also evident in the annual ranking, as the top three only share one habitat type in common (grassland) whereas the bottom three have all the habitat types in common, but in reverse order (Fig. 3-2). There is some evidence for annual (p = 0.066) and fall (p = 0.045) correlations, but much of this likely has little meaning ecologically,

despite marginal statistical significance, as the exact order of the less preferred habitats is likely less important than the order of the most preferred habitats. Additionally, no correlation was found between summertime grazing by bison and rancher reported winter habitat needs for cattle ($p = 0.085$; contrary to Prediction 3), which was a concern among the ranchers. These results do not support the contention that bison and cattle (as reported by rancher knowledge) are competing at the habitat scale on the HM range, even with temporal separation in habitat use. Rather, our results are consistent with an experimental grazing exclosure study (Ranglack et al, in review) and a concurrent study on plant community composition on the HM (Ware et al. 2014), which both showed very weak bison-cattle competition at the patch scale. A study on bison–cattle space use in the HM from 1977-78 revealed similar patterns: despite high dietary overlap, bison and cattle spatial distributions showed relatively little overlap (29%) as bison used steeper slopes and higher elevations than cattle, which remained close to water sources (van Vuren 2001). An absence of overlap in observed habitat use could, if both species have freedom of movement, be the result of competitive displacement (Sale 1974). However, cattle cannot be spatially displaced by bison on the HM rangeland because the cattle are herded within spatial delineations prescribed by grazing permits. The reverse could nevertheless apply if bison actively avoid areas occupied by cattle, which deserves further study. Additionally, these findings illustrate that the perceptions of local ranchers were either based on a misunderstanding of the ecological system or were reported with bias to suit their political stance. Either way, our study highlights how management actions based on local stakeholders' perceptions could lead to unsatisfactory outcomes, further

emphasizing the need for scientific verification before incorporating local ecological knowledge into management strategies (Davis and Ruddle 2010).

We expected to see sexual segregation because of the sexual size dimorphism in bison (Ruckstuhl and Neuhaus 2000). If found, this might have indicated intersexual competition and therefore intraspecific competition in the bison population but from the low *SC* levels this is unlikely and so interspecific competition between bison and cattle is also unlikely (Connell 1983, Weisberg et al. 2002). The low *SC* values indicate that bison bulls are unlikely to be having distinct impacts, separate from cow-calf groups, on forage availability for cattle. Despite significantly different habitat profiles in the fall and winter, the number of bison bulls that were segregated from cow-calf groups was low. On the National Bison Range in Montana, spatial segregation between the bison sexes was also low (*SC* = 0.068; Mooring et al. 2005), indicating that the low *SC* values we found for the HM bison (*SC* = 0.048-0.112) were not unusual. We also expected sexual segregation to be most pronounced during the most limiting season, as competition will be highest when resources are most limiting (Odadi et al. 2011), and indeed sexual segregation was most pronounced during the winter, though still low. This was also reflected in the chi-squared contingency table for the overall habitat preference profiles, where winter showed the largest differences between the sexes. Thus, while we expect the potential for competition between bison and cattle to be strongest during the winter, there is currently no evidence for it.

While these findings are somewhat surprising given the contention over bison-cattle competition on the HM rangeland, they are not entirely unexpected on ecological

grounds. Bison in the HM are large, generalist feeders and mostly in good body condition, indicating generally that food quality is not a limiting factor. When resources are not limiting, competition is unlikely (Sale 1974, Putnam 1996). Despite this apparent lack of competition, however, bison might still reduce forage availability for cattle. Bison grazing is permanent and free-ranging across the HM rangeland, whereas cattle grazing is temporally and spatially constrained by the specific details of the grazing permit. Additionally, rancher knowledge of cattle habitat needs could be imperfect and, although it was impossible in our study, GPS data from cattle might have revealed different patterns.

In terms of habitat preference by bison, several interesting patterns emerge (Table 3-2). Similar to bison in the Great Plains (Allred et al. 2011), HM bison consistently prefer disturbed (burned and chained) habitat types across both sexes and all seasons, with female summer use of burned areas being the only instance of significantly low preference. This can be explained by the location of the burned areas in relation to summer breeding grounds, which are spatially separate. Barren ground and piñon-juniper woodland are significantly low preference areas for both sexes and all seasons. This highlights the potential value of habitat improvement projects such as chainings and prescribed fire in converting low preference piñon-juniper woodland into high preference grazing patches.

Seasonal variation in bison habitat preference is also of interest. Bison exhibited a seasonal switch in preference by at least one sex in seven of the 12 habitat types, with preference generally being high during the summer and low during at least one other

season (generally spring). The habitat types preferred in summer were likely cooler in that season, but did not offer sufficient foraging opportunities to justify their use during the more limiting fall and winter seasons. We would expect the range of habitats used by bison to change through the seasonal cycle, with productive seasons allowing for the use of more habitat types (Fritz et al. 1996). Indeed, during the winter we found bison to focus on burned areas, chainings, and grasslands, with low or neutral preference for every other habitat type. Summer and fall had the broadest range of preferred habitat types, with nine and six habitats respectively preferred by at least one sex. Spring and winter each had two or three preferred habitat types depending on the sex (Table 3-2).

In conclusion, we found little evidence that bison prefer the habitats viewed by ranchers as important for their cattle on an annual basis (contrary to Prediction 1). We did find evidence from bison (some sexual segregation, more focused habitat selection) that winter is the most limiting season on the HM rangeland, as expected, but no evidence that bison and cattle compete at the habitat scale during that season (contrary to Prediction 2). Our study demonstates why caution should be used when natural resource management seeks to integrate local ecological knowledge (Krupnik and Jolly 2002, Gilchrist et al. 2005, Ruddle and Davis 2009). The knowledge-base of local communities might be biased by political or social pressures to misrepresent the complexities of the system or might not match current ecological conditions. Local ecological knowledge should therefore be scientifically verified (Raymond et al. 2010), while still emphasizing the importance of local stakeholders as active involvement in management planning. Our findings should hopefully ease tensions between the local ranching community and the

state and federal government agencies regarding the potential impact of bison on cattle grazing. An opportunity now exists for collaborative adaptive management to enhance and conserve the habitats used by both species on the shared rangeland.

On a broader scale, our results show that despite similarities in body size and diet, differences between bison habitat preferences (our RSF analysis) and cattle habitat needs (rancher reported) should allow for the coexistence of both species on the same rangeland. Concerns of disease transmission and property damage by bison need special consideration (Freese et al. 2007), but the concern of interspecific competition has been over-stated. The HM rangeland serves as an example of a wild area where a free-ranging bison population can be maintained at low density by controlled hunting and coexist with cattle within a public grazing framework. Replicating this system across other public lands could allow for bison populations to be restored at ecologically meaningful scales, which to this point has only occurred in a few select places such as the Greater Yellowstone Ecosystem (Sanderson et al. 2008). As bison are considered to be the keystone species in North American grazing ecosystems (Knapp et al. 1999), expanding the practice of mixed bison-cattle grazing should also expand the cascading effects of bison grazing at the landscape scale, potentially enhancing biodiversity conservation on rangelands.

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Table 3-1. A questionnaire survey was developed in coordination with the local Bureau of Land Management office (Hanksville, Utah) to gauge local ranchers' perceptions of the relative importance and influence of wildlife-cattle interactions on the Henry Mountains public rangeland. Ranchers with grazing permits were asked to rank the relevant interactions, habitat types, and potential wildlife competitors as high, medium, or low for each season. In addition, they were asked to indicate if they felt the coyote population should be controlled and to rank the benefit that various species, both wild and domestic, receive from coyote removal. Results were scored on a 3-point scale (high = 3, low = 1).

1. How do bison interact with cattle?			
Competition for forage	Competition for water	Aggression or disturbance	Other (Please explain)
2. How valuable are these habitat types for cattle?			
Barren Ground	Grassland	Grass-shrub mix	Shrubland
Piñon-juniper woodland	Riparian	Chaining	Oakbrush
Aspen woodland	Coniferous woodland	Alpine Meadow	
3. How much might these wildlife species compete with cattle?			
Mule deer	Bison	Jackrabbit	Other (Please explain)
4. Should the coyote population be controlled in the HM?			
Yes		No	
5. What species benefit from coyote control in the HM area?			
Mule deer	Livestock	Other (Please explain)	

Table 3-2. Habitat preferences of GPS-collared female (♀) and male (♂) bison in each season as determined by the method of Neu et al. (1974), by which observed use is below (-), within (0), or above (+) the 95% Bonferroni confidence interval around the expected proportional use of each habitat. Mean rancher reported habitat importance for cattle (± SE) is also indicated, where high = 3 and low = 1, for all habitat types except 'burned'.

Habitat	Spring			Summer			Fall			Winter		
	♀	♂	Rancher	♀	♂	Rancher	♀	♂	Rancher	♀	♂	Rancher
Alpine meadow	-	-	1.55 (0.21)	+	+	1.64 (0.24)	0	0	1.55 (0.21)	-	-	1.45 (0.21)
Aspen woodland	-	0	1.27 (0.47)	+	+	1.45 (0.21)	-	0	1.55 (0.25)	-	-	1.36 (0.67)
Barren ground	-	-	1.36 (0.24)	-	-	1.27 (0.19)	-	-	1.36 (0.20)	-	-	1.27 (0.19)
Chaining	+	+	1.73 (0.27)	+	+	1.91 (0.28)	+	+	1.82 (0.26)	0	+	1.73 (0.27)
Coniferous woodland	-	-	1.09 (0.09)	+	+	1.09 (0.09)	-	+	1.09 (0.09)	-	-	1.09 (0.09)
Grass-shrub mix	0	-	2.36 (0.24)	+	+	2.00 (0.27)	+	+	2.00 (0.23)	-	-	2.45 (0.21)
Grassland	+	-	2.73 (0.19)	+	+	2.64 (0.20)	+	+	2.73 (0.14)	+	+	2.55 (0.25)
Oakbrush	-	-	1.45 (0.21)	+	0	1.82 (0.26)	-	-	1.73 (0.27)	0	-	1.09 (0.09)
Piñon-juniper woodland	-	-	1.18 (0.12)	-	-	1.09 (0.09)	-	-	1.09 (0.09)	-	-	1.09 (0.09)
Burned	+	+	NA	-	0	NA	+	+	NA	+	+	NA
Riparian	0	-	1.55 (0.25)	+	0	1.82 (0.26)	-	0	1.64 (0.28)	0	0	1.64 (0.28)
Shrubland	-	-	1.64 (0.28)	+	+	1.82 (0.26)	+	+	1.91 (0.31)	0	0	1.91 (0.31)
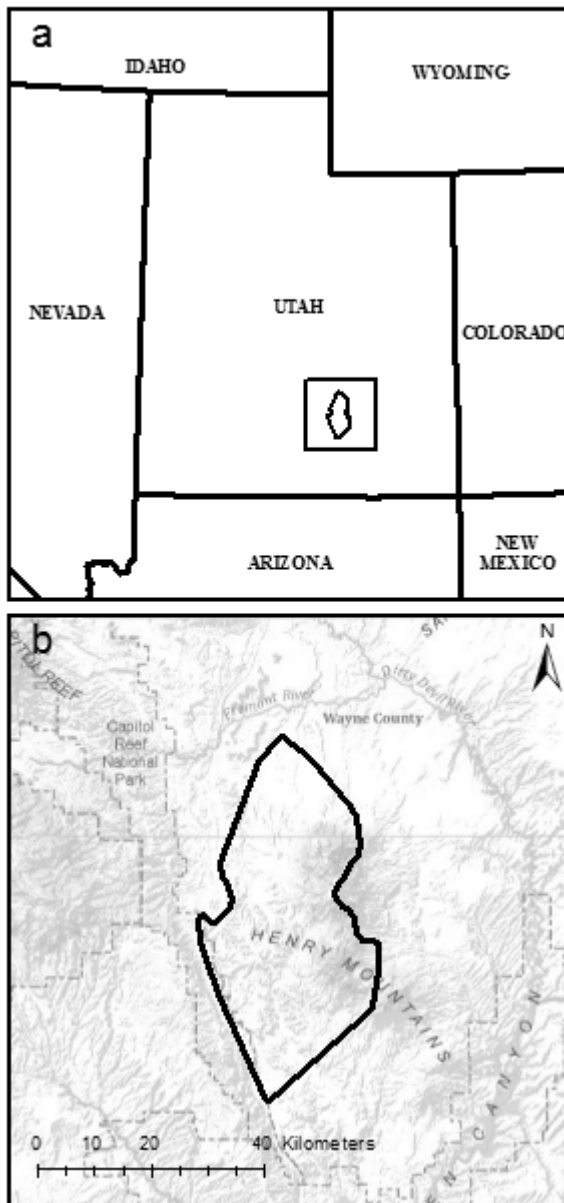
Fig. 3-1. The location of the Henry Mountain (HM) rangeland in the state of Utah (a); the Henry Mountains area of southern Utah (b) with the area used by the bison herd designated by the black line.
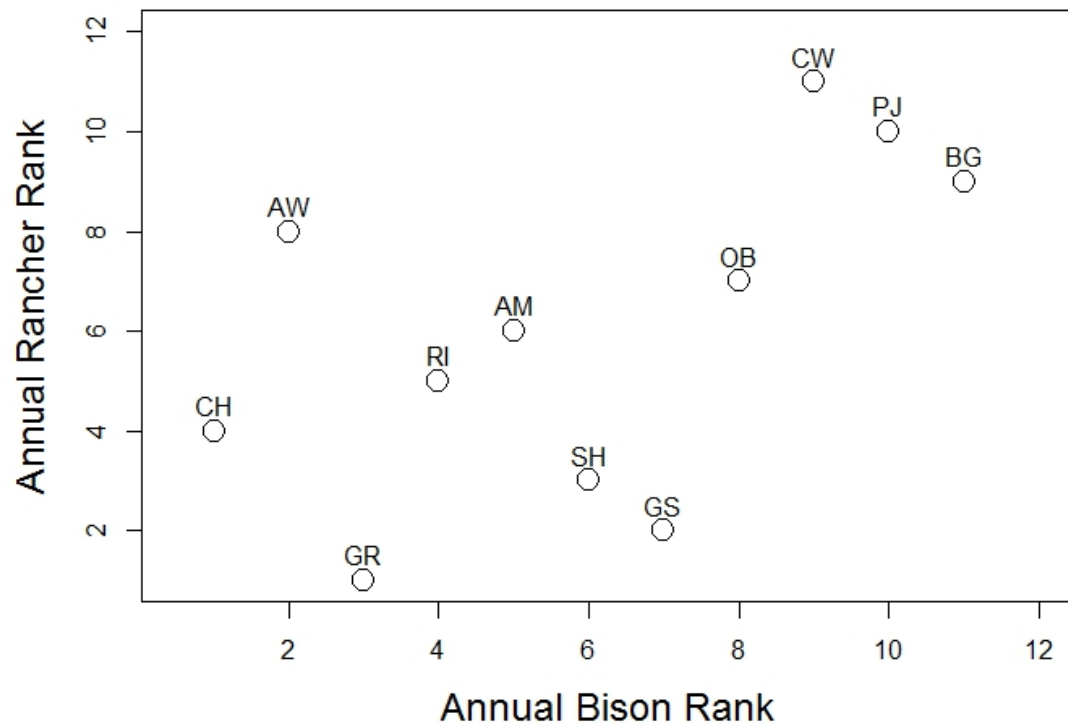
Fig. 3-2. Overall (annual) comparison of rancher-declared habitat ranks for cattle against actual GPS-based habitat RSF ranks for bison ($r_s = 0.57$, $p = 0.066$). AM = alpine meadow, AW = aspen woodland, BG = barren ground, CH = chaining, CW = coniferous woodland, GR = grassland, GS = grass-shrub mix, OB = oak brush, PJ = piñon-juniper woodland, RI = riparian, and SH = shrubland.
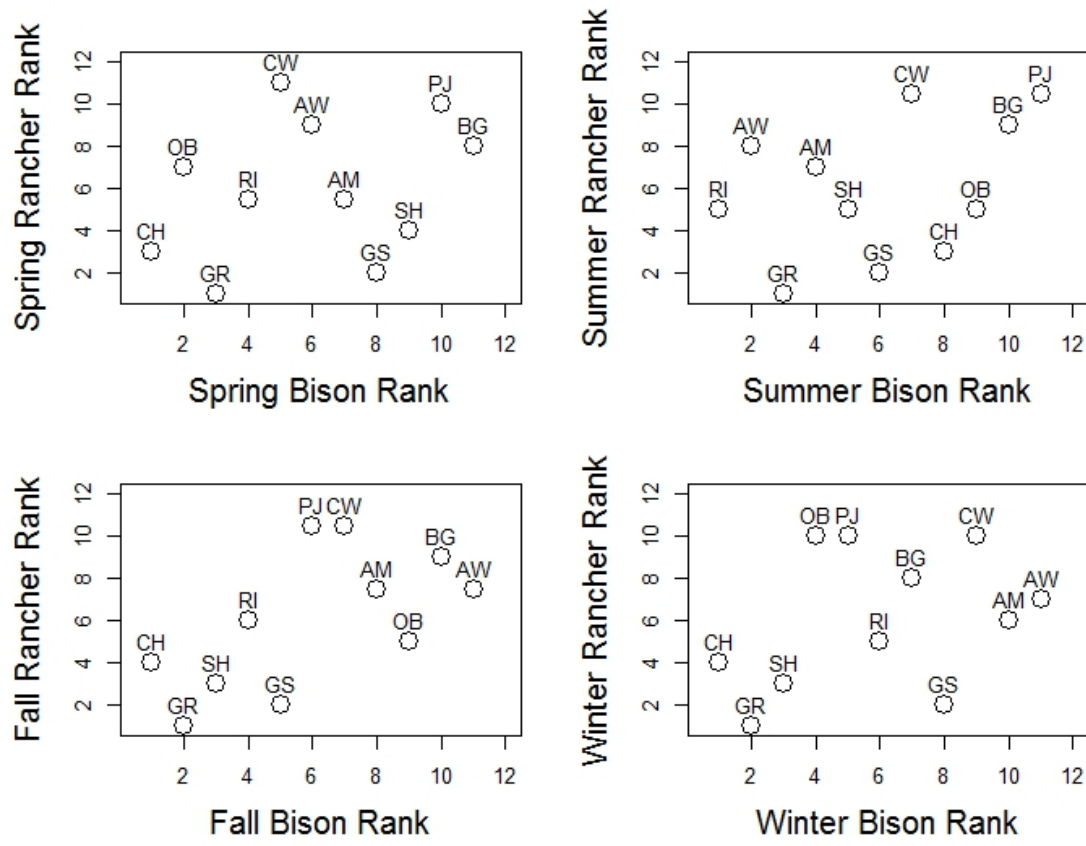
Fig. 3-3. Seasonal comparisons of rancher-declared habitat ranks for cattle against actual GPS-based habitat RSF ranks for bison. Spring $r_s = 0.305$, summer $r_s = 0.377$, fall $r_s = 0.611$ ($p < 0.05$), and winter $r_s = 0.349$. Habitat codes are the same as in Fig. 2.
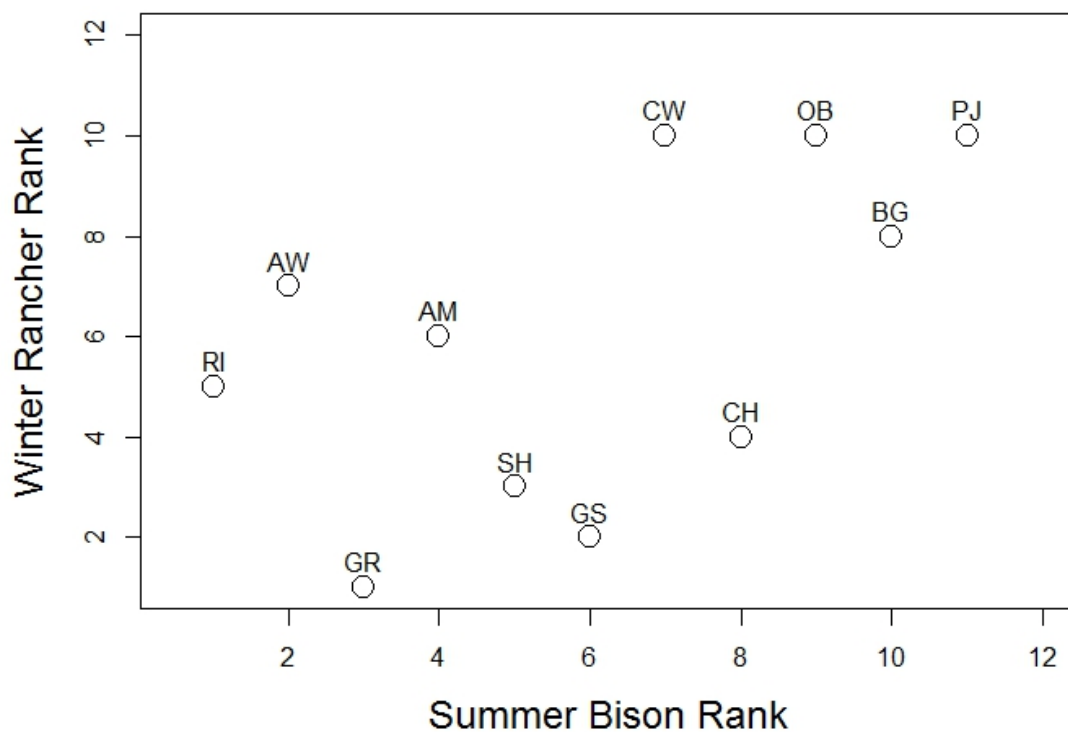
Fig. 3-4. Comparisons of rancher-declared winter habitat rank for cattle against actual GPS-based habitat RSF ranks for bison summer use ($r_s = 0.54$, $p = 0.085$), to reflect the concern over summertime grazing by bison in allotments designated for cattle winter use. Habitat codes are the same as in Fig. 2.

CHAPTER 4

BISON AS BIO-INDICATORS OF THE EFFECTS OF HABITAT MANIPULATION

IN A SEMI-ARID RANGELAND[3]

Abstract

Habitat manipulations through the use of fire or mechanical treatments are often used to combat woody plant encroachment and increase foraging opportunities for wildlife and livestock. This creates spatial heterogeneity in habitat quality that large herbivores should respond to in ways predicted by ideal free distribution theory. We monitored free-ranging bison to test whether, (1) manipulated habitats offer higher quality forage than habitats in undisturbed rangeland, (2) bison respond through changes in herd composition or activity to differences in habitat quality, and (3) burned and mechanically treated habitats offer similar forage qualities. We found that habitat types burned ~10 years ago continue to produce higher quality forage as evidenced by bison fecal N concentration (14.4 g kg^{-1} dry mass) than open (10.5 g kg^{-1}), closed (10.6 g kg^{-1}), or mechanically manipulated habitats (11.7 g kg^{-1}). Bison herd composition and activity did not vary across habitat types within seasons, despite some between-season variation in overall group composition with sexual segregation being most evident before mid-summer. For semi-arid rangelands encroached with woody vegetation (e.g. piñon-juniper in the western USA) our evidence from free-ranging bison indicates that burning results in higher quality forage than occurs in both mechanically manipulated and undisturbed habitats. Bison roam widely from water, sample available vegetation continuously, and

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[3] Coauthored by D. H. Ranglack and J. T. du Toit

are long-lived gregarious animals that learn to exploit the spatiotemporal heterogeneity in their large home ranges. Bison also have very similar diets to cattle and so, where bison and cattle are allowed to comingle, we suggest that free-ranging bison are effective bioindicators of rangeland quality for cattle.

1. Introduction

On a global scale, encroachment of woody plants into grasslands and savannas has increased dramatically over the last century (van Auken, 2009), and is represented by particularly worrisome declines in range quality for livestock in North American grasslands, shrublands, and savannas (Ratajczak et al., 2012). In response to this, various habitat manipulation methods, including fire and chemical and mechanical treatments, have been employed to restore these encroached communities to their previous states or at least to more desirable alternatives (Ansley and Castellano, 2006; Ansley et al., 2006; Aro 1971). The goal of such treatments is usually to increase foraging opportunities for domestic livestock and wildlife (Powell and Box, 1966) and success is typically measured in terms of increased abundance of herbaceous vegetation. Such increases will not, however, indicate success unless they are associated with foraging responses from local livestock and wildlife populations. Here we investigate the use of wild, free-ranging grazing herbivores as bioindicators of habitat quality on rangelands. Bison (*Bison bison*) in particular have been shown to respond to, and create, habitat heterogeneity and are considered a keystone species of grazing communities (Knapp et al., 1999). We expect that a free-ranging bison population should respond to spatial variation in rangeland conditions created by habitat manipulations. Also, because bison are biologically similar

to cattle, we expect their response to variations in habitat quality should serve as an indicator of the success of habitat manipulation efforts to improve rangeland conditions for cattle.

Spatiotemporal heterogeneity in overall habitat quality influences many aspects of the behavior of animals in groups, such as group size, group composition, and activity within groups including when, where, and for how long group members forage (Lima and Zollner, 1996; Wallis De Vries, 1996). Optimal foraging theory predicts that higher quality resource patches lead to larger group sizes (Hirth, 1977; Schoener, 1971) and higher proportions of time spent feeding versus vigilance (Lima, 1995; Lima and Dill, 1990). In sexually dimorphic species, we would also expect a change in group composition with changes in resource quality. The smaller juveniles and adult females are more efficient feeders on short high-quality swards whereas the larger males are able to use lower quality forage due to longer retention time in the gut (Demment and van Soest, 1985; Ruckstuhl and Nehaus, 2000, 2002). These expectations have been demonstrated in a variety of wild and domestic populations of animals from mice to moose (Kie, 1999). Also, ideal free distribution (IFD) theory predicts that the equilibrium distribution of organisms among habitats of different quality, such as results after some patches of rangeland have or have not been subjected to habitat manipulation, will indicate the relative resource qualities of those habitats (Fretwell, 1972; Fretwell and Lucas, 1970).

The relationship between bison and fire is well documented for plains ecosystems (Fuhlendorf et al., 2008), with bison exhibiting a strong preference for recently burned

areas, attracted by the high quality forage that emerges due to nutrient release (Allred et al., 2011). Before European settlement, fire would have been common on the Great Plains, but on the Colorado Plateau, such as in the Henry Mountains (HM) of southern Utah, where the vegetation is sparse and topography rugged, the fire return interval would have been longer and more sporadic. Nevertheless, fire would have prevented shrub and conifer encroachment into open habitat types and maintained piñon-juniper (*Pinus edulis – Juniperus osteosperma*) woodlands in a more savanna–like state (West, 1984) except in steep and rocky areas. With anthropogenic changes in the fire regime and intensified grazing by cattle, dense stands of piñon–juniper emerged across the landscape, virtually eliminating the understory plant communities (Miller and Rose, 1995). In an effort to restore these areas and provide more forage for livestock and wildlife species, controlled burning and mechanical treatments are commonly used but with comparatively little follow-up to determine the subsequent use of treated areas by herbivores (Kennedy and Fontaine, 2009). In the HM, mechanical treatments have been used to open up foraging areas for wild and domestic ungulates, and several large wildfires have also occurred within the last 15 years. We set out to understand how bison use these disturbed areas compared to undisturbed habitats to gain insight into the value of habitat management, as well as to determine if and how bison foraging behavior varies across undisturbed, burnt, and mechanically transformed habitats.

We invoked IFD theory to indicate the relative qualities of four different habitat types (open, closed, burn, and chaining) in two different phases of the seasonal cycle through the use of several physiological and behavioral measures. Fecal nitrogen (N),

body condition (BC), and endoparasite load were monitored to track seasonal variation in the nutritional status of the HM bison. Higher fecal N and BC scores, along with lower endoparasite loads, should indicate a higher nutritional plane (Caron et al., 2003). As habitat manipulations are intended to improve habitat quality, we predicted (1) that previously burnt and mechanically manipulated habitats offer higher quality forage for bison than undisturbed habitats, as indicated by site-specific fecal N. We further predicted (2) that group size, group composition, and feeding:moving (F:M) ratio vary along a resource quality gradient, such that high quality habitats (as indicated by fecal N) have larger bison group sizes, more mixed-sex groups, and a higher percentage of foraging time devoted to feeding. We were also interested in whether mechanical destruction of trees and burning resulted in habitats of similar quality to bison, expecting that burned areas would be of higher quality due to the rapid release of nutrients during combustion (Allred et al., 2011). We thus predicted (3) that group size, group composition, fecal N, and F:M ratio differ accordingly between the two habitat types. We tested all three predictions using data collected through direct observation of bison and fecal sampling from May 2011 to August 2013.

2. Methods

2.1 Study Area

The Henry Mountains (HM) study area in south-central Utah included arid, semi-arid, and alpine habitats for bison during their seasonal migrations from low to high altitudes. Established in the early 1940s with bison from Yellowstone National Park (Nelson, 1965; Popov and Low, 1950), the HM bison herd now numbers ~325 adults

(post-hunt) and is controlled primarily by sport hunting. Apart from bison, cattle are the only other large grazers in the region. The HM are host to a healthy herd of mule deer (*Odocoileus hemionus*), but their preference for forbs would suggest negligible levels of competition with the grazers (van Vuren and Bray, 1983). A small (~20) herd of elk (*Cervus canadensis*) is also present on the HM, though the Utah Division of Wildlife Resources actively manages against elk in an attempt to eradicate the herd. Black-tailed jackrabbits (*Lepus californicus*) and desert cottontail (*Sylvilagus audubonii*) are common in the low and mid elevations. Mountain lions (*Puma concolor*) and coyotes (*Canis latrans*) utilize the study area, but are highly controlled by government and private entities, keeping population sizes relatively low. A detailed description of the study area can be found in Nelson (1965) and van Vuren and Bray (1986).

Habitat manipulations in the HM are primarily conducted to improve foraging conditions for wildlife and cattle. Two large fires burned ~146 km^2 in 2003, which were subsequently reseeded from the air with a seed mix designed for that area by the Bureau of Land Management. Much of this area has regenerated into oakbrush (*Quercus gambelii*) and aspen (*Populus tremuloides*) stands but large portions have been converted from piñon-juniper woodland to grasslands. 'Chaining' has been used as a mechanical treatment in the HM since the 1960s, with ~2.43 km^2 of piñon-juniper woodland having been broken down using parallel bulldozers connected with chains. It is standard practice for desirable plant species to be seeded into an area as it is being chained to enhance rangeland quality.

2.2 Data Collection

VHF and GPS telemetry was used to locate bison without visibility bias between open versus closed habitat types, with effort taken to balance observations among all habitat types to the extent possible. Observations were primarily collected during the summer months (May – August), with opportunistic observations throughout the remainder of the seasonal cycle depending on accessibility. Direct observation of bison proved difficult in the winter months as the bison tended to use a large roadless area with extremely rough topography that made access prohibitively difficult. When a bison group was located, group size and composition (numbers of bulls, cows, and calves) were recorded. For statistical analysis, only those observations that resulted in every individual in the group being classified as male, female, or calf were used.

Adult female body condition (BC) was scored between 1 and 5, with 1 being poor condition and 5 being excellent, following the visual condition scoring scale used by Prins (1996) for African buffalo (*Syncerus caffer*). BC was then averaged to derive one score for the herd at that time and place. The habitat the bison were occupying was classified into one of 12 habitat types (alpine meadow, aspen woodland, barren ground, recently burned, chaining, coniferous woodland, grass-shrub mix, grassland, oakbrush, piñon-juniper woodland, riparian, shrubland). If the focal group was not disturbed by the observers, the behavioral scans were conducted at 5-10 minute intervals depending on group size, where behavior was classified into 12 different categories (grazing, browsing, drinking, lying, lying ruminating, walking, socializing, horning, wallowing, standing alert, standing resting, and standing ruminating). Scans were conducted for up to five

hours, dependent upon the focal group remaining visible. This population of bison is

extremely wary of human presence as a result of yearly bison hunts, thus many of the

observations did not result in the collection of all the data mentioned above. Group size

was always determined.

From May 2012 to April 2013, fecal samples were collected from fresh dung pats

after each focal bison group had departed from the area in which it had been classified.

Approximately five fecal samples were collected from each group, depending on the size

of the group, along a transect perpendicular to the movement of the bison group to avoid

sampling the same individual twice. Each fecal sample was homogenized and divided

into sub-samples for analysis of total nitrogen content (g N kg^{-1} dry feces) and

endoparasite load using a modified McMaster technique (Zajac and Conboy, 2006). The

fecal N sub-samples were frozen within three hours of collection, whereas the

endoparasite load sub-sample was refrigerated until analysis could be completed in the

field, generally within five hours of collection, to prevent the degradation of helminth

eggs. Fecal N (assayed by the Utah State University Analytical Laboratory) was used as

an index of dietary quality as it represents dietary crude protein for grazing ungulates

(Leslie and Starkey, 1987). As endoparasite load was only used as an adjunct to tracking

bison condition, total egg counts were performed without noting endoparasite species.

2.3 Statistical analysis

Due to the relative scarcity of some habitat types and the difficulty in obtaining

observations during the winter season, habitat classes were collapsed into four categories:

open (alpine meadow, grass-shrub mix, grassland, riparian, shrubland), closed (aspen

woodland, coniferous woodland, oakbrush, coniferous woodland), recently burned (~10 years prior to this study), and chaining. Season was classified as early (January – June) and late (July – December). This timing reflects an observed change in bison habitat use and behavior that occurs during the mid-summer in preparation for the rutting season (July – August). For analysis, activity classes were collapsed into six categories: feeding (including drinking); resting (lying or standing); ruminating (lying or standing); moving (walking); socializing (including horning and wallowing); alert (standing).

Herd composition and behavioral data were expressed in percentages of animals in the herd. Feeding:moving (F:M) was expressed as the percent of scanned individuals engaged in feeding divided by the total number of scanned individuals engaged in feeding and moving. This represents the proportion of ingestion activity achieved during foraging (feeding and moving). Analysis of variance (ANOVA) used data at the herd level (unless otherwise noted) to test the effects of habitat and season on group size, F:M ratio, and fecal N (individual sample level) and the effects of season on BC and endoparasite load (individual sample level). Because individual bison do not behave independently, a binomial approach to analysis (as recommended by Warton and Hui, 2011) would be inappropriate. Rather, an arcsine square roote transformation was used on F:M data and a square root transformation was used on parasite load data to satisfy normality and homogeneity of variance assumptions. Multiresponse permutation procedure (MRPP) was used to test the effects of habitat and season on herd composition and activity. In analyses incorporating both predictor variables, the interaction term was not included as no data were available for the late season x burn combination, as bison

were not directly observed using this habitat type during this season, though GPS data showed that such use did occur. This analysis therefore assumes that the effect of season is the same in each habitat and that the differences among habitats are the same in each season. Tukey's test was used for *post hoc* investigations of differences among habitat type. Additionally, MRPP was used to test the effects of group size on activity independent of habitat and season, with group size being categorized into small (<20), medium (20-100), and large (>100). All statistical analyses were performed in R version 3.0.2. (2013), with "vegan" version 2.0-10 (2013) being used for MRPP.

3. Results

A total of 198 bison groups were observed during the study period (Table 4-1). Of those, complete herd composition was obtained for 110 groups. Approximately 170 hours of behavioral observations were obtained from 125 groups. BC was determined for 63 groups. Fecal N was determined for 126 samples, collected from 40 groups. Parasite load was determined for 150 samples from 39 groups.

Both habitat and season were significant ($p < 0.001$) predictors of fecal N. Across all habitats during the early season (before mid-summer) the fecal N concentration (mean $\pm$ SE) was higher (12.8 g kg^{-1} $\pm$ 0.50) than in the late season (10.2 g kg^{-1} $\pm$ 0.23). Across both seasons, Tukey's test showed no significant differences among chaining, open and closed habitats, but significant differences between burn and either chaining ($p = 0.019$), open ($p < 0.001$), or closed ($p < 0.001$) habitats (Table 4-2, Fig. 4-1).

Season was a significant predictor of BC ($p = 0.012$), with higher mean ($\pm$ SE) in the late season (BC = 3.00 ± 0.06) than the early season (BC = 2.66 ± 0.13; Fig. 4-2a).

The cows only gained body condition after mid-summer when the nutritional loads of late gestation and lactation were reduced.

Endoparasite (helminth) eggs were detected in 93 of 150 fecal samples, leading to a prevalence rate of 62%. Season was found to be significant predictor of fecal parasite load ($p < 0.01$) with early season counts (84.9 eggs g^{-1} ± 11.3) being double late season counts (41.8 eggs g^{-1} ± 5.11; Fig. 4-2b).

Habitat type was not a significant predictor of group size and was therefore dropped from the model. Season was found to be a significant predictor of group size ($p < 0.005$), with larger groups occurring in the late season (Fig. 3). Mean group size (± SE) was 31.9 individuals (± 4.12) and 49.6 individuals (± 3.37) for early and late season respectively.

Habitat type was not a significant predictor of herd composition so it was dropped from the model. Season did prove to be a significant predictor of group composition ($p = 0.041$), indicating that herd structure changes as the year progresses. This change is a shift from a more sexually segregated group structure in the early season to mixed groups during and after the rut, which occurs in late summer.

No significantly detectable between-season differences existed in the percentage of foraging time devoted to feeding. However, weak evidence ($p = 0.097$) was found for differences between habitat types, with closed habitat types showing a lower percentage of foraging time devoted to feeding compared to chained, open, and burned (Table 4-1), supporting field observations that bison travel through (and rest in) closed habitats to feed in open habitats.

Main peaks in feeding activity were during the early morning, early afternoon, and evening, separated by a bout of resting and ruminating. Movement and rumination were fairly evenly distributed throughout the day (Fig. 4-4). No significantly detectable differences existed in bison activity patterns between seasons, indicating that bison in the HM exhibit the same overall activity profile throughout the year. However, group size proved to be a significant predictor of overall activity pattern ($p = 0.006$). The main separation appeared to be between large and medium group sizes, with large groups participating in more 'busy' activities (moving, feeding, alert), while medium groups showed more 'lazy' activities (resting, ruminating). Small groups were much more variable in their activity patterns, perhaps because of the increased influence of each individual on overall group behavior when in smaller groups.

4. Discussion

Despite maintaining good body condition, the HM bison were found to subsist on a lower quality diet, as indicated by fecal N, than bison on the Konza prairie in Kansas (Post et al., 2001), Yellowstone National Park (Hernandez and Laundre, 2005), and the National Bison Range, Montana (Mooring et al., 2005). Mean group size for the early season was higher than reported for Yellowstone and Wind Cave National Parks. Late season (breeding) mean group size was lower than reported for Yellowstone National Park (McHugh, 1958) and the National Bison Range, but higher than reported for Catalina Island, California (Lott, 1974). European bison (*Bison bonasus*), found in the Bialowieza and Borecka forests in Poland, are found in much smaller group sizes than HM bison (Krasinska and Krasinski, 2007; Krasinski and Krasinska, 1992). This is not

unexpected as forest dwelling ungulates are typically found in smaller groups than those in more open areas (Estes, 1974; Jarman, 1974) and wood bison in North America also exhibit smaller group sizes (Fuller, 1960). European bison also tend to be more sexually segregated than HM bison (Krasinska and Krasinski, 1995; Krasinski and Krasinska, 1992).

African buffalo (*Syncerus caffer*) in both the Serengeti and Manyara ecosystems of East Africa utilize higher quality forage, as indicated by fecal N, than HM bison (Sinclair, 1977; Prins and Beekman, 1989). In the Kruger ecosystem of South Africa, dry (lean) season fecal N for buffalo was roughly equivalent to early season fecal N in the HM bison (Macandza et al*.,* 2013). Even during the early season, when HM fecal N levels were at their highest, they were only slightly higher than the fecal N levels during the leanest seasons in Africa. African buffalo are also found in much larger herd sizes than currently occurs with bison in North America (Prins, 1996). African buffalo body condition and parasite load varied similarly to the HM bison, with females losing condition and gaining parasites through the lean season (Caron et al., 2003).

Following our assumption that habitats and seasons with higher levels of fecal N are of higher quality in terms of grazing resources, we classify burned habitats as highest in quality, with mechanically manipulated (chained) being similar to open habitats, in partial support of Prediction 1. While it may not be surprising that chained and open habitat types were statistically indistinguishable with regards to fecal N, it is surprising that they were both statistically indistinguishable from closed, as closed habitats in the HM support little grass cover. However, bison in the HM achieved the lowest foraging

efficiency in the closed habitat types, as shown by the F:M data (Table 4-1). Fecal

material collected in the closed habitat thus largely reflected food ingested in one of the

other habitat types, whereas fecal material collected in the burned, chained, and open

habitat types were more likely to represent a "true" signal of local forage quality. Our

results reflect that chaining transforms closed habitats into open, which may increase

habitat quality, but burning does the same while further improving grazing conditions.

Whereas bison group dynamics and activity in general (F:M being a possible exception)

did not respond to within-season differences in habitat quality at the spatial scale of our

study (contrary to Prediction 2), they did respond to seasonal variations in overall

environmental conditions. The early season showed higher fecal N from the spring

vegetation green-up (Fig. 4-1), but lower body condition and higher parasite load (Fig. 4-

2), with smaller and more sexually segregated groups compared with the larger and more

mixed groups in the late season (Fig. 4-3). The mixed message from the physiological

indicators in the early season likely reflect the lag in responses of improving body

condition and declining parasite load after the winter nutritional 'crunch' period. Various

life cycle process (gestation, lactation, etc.) are also influencing these patterns.

Mechanical treatments are often used as fire surrogates (Kennedy and Fontaine,

2009) but our results for bison show that burned areas offer significantly higher quality

forage (based on fecal N) than the other habitat types (supporting Prediction 3) despite

only a weak signal of improved foraging efficiency and no detectable effect on

aggregation (contrary to Prediction 3). Our ability to detect a bison response was likely

limited by sample size for the burned areas, as most bison burn use occurred during the

winter months when access was problematic. Moe and Wegge (1997) found higher

nitrogen levels in grasslands that were cut and burned or burned alone compared to those

that were just cut, and a corresponding increases of axis deer (*Axis axis*) use in the burned

grasslands, but their findings were from recently burned areas. In Serengeti National

Park, burning caused only a four-month nutrient pulse that was reflected in plant

regrowth and herbivore abundance (Eby et al*.,* 2014). In contrast the burned areas on the

HM rangeland were ~10 years old and so the higher quality forage we observed is

unlikely a direct result of a post-fire nutrient pulse. There are several other possible

mechanisms operating independently or in combination. First, the burned area was

reseeded with various wheatgrass species (*Agropyron spp.* and *Thinopyrum spp.*) and

alfalfa (*Medicago sativa*), which would have germinated without competition from

established plants and with the benefit of the post-fire pulse in soil nutrients. If this

herbaceous community has persisted then it is to be expected that it will be of

comparatively high quality to large herbivores. Second, if grazers were attracted to the

post-burn flush of herbaceous growth then grazing lawns could have developed

(Archibald, 2008) and been maintained to the present by bison grazing, defecating and

urinating on these sites. Lastly, the areas where the burns occurred might have been of

comparatively high soil nutrient status pre-burn, and so the post-burn vegetation is of

higher forage quality than chained areas for reasons unrelated to the burn. Whereas the

first two possibilities are feasible, using GIS data layers on elevation, slope, aspect,

historic imagery of the pre-burn vegetation, and GPS locations of the fecal samples, we

were able to dismiss the third. The fecal sampling sites in the burn habitat would have

been in the same landcover types as those in the chaining if neither habitat manipulation had occurred. In the absence of detailed sampling and analyses it is impossible to determine causality, but we argue that bison can serve as bioindicators of where grazing conditions are better, which is ultimately what rangeland managers need to know.

Bison in the HM meet the main assumptions of IFD theory (Fretwell, 1972) in that: they are energy maximizers (van Vuren, 2001); are long-lived animals in a population that has been present on the HM for many generations, allowing all foraging patches to be discovered and known (Nelson, 1965; Popov and Low, 1950); are sexually size-dimorphic and thus have different dietary tolerances, but little sexual segregation is observed in the HM (Ranglack and du Toit, in prep), indicating that intraspecific competition is minimal. We thus feel confident that the HM bison population is free to sample its environment fully and utilize the best resource patches when they are available, thus serving as a reliable bioindicator of rangeland condition through the seasonal cycle. Compared with cattle, bison are able to forage more widely by making longer trips from water (van Vuren, 2001) and so they can sample the heterogeneity of a rangeland to a greater extent. Also, cattle on public lands are moved around grazing allotments on a seasonal basis by ranchers and so their foraging performance is strongly influenced by management. Where feasible for rangelands in North America, we thus recommend maintaining bison with cattle to provide a robust bioindicator of spatial and temporal variation in rangeland quality. This is in addition to the multiple other benefits that would accrue to social-ecological systems if bison populations were restored across more of their former range in North America (Freese et al., 2007).

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Table 4-1. Sample sizes for each of the bison variables measured by both habitat and season. Efforts were taken to distribute sampling across habitat types and seasons, though this was not always possible. For the fecal variables, the number of groups represented in the sample size is indicated in parentheses.

Bison variable	Season		Habitat				Total
	Early	Late	Burn	Chaining	Open	Closed	
Group size	62	136	10	56	96	36	198
Group composition	30	80	2	39	56	13	110
Activity	33	92	5	39	64	17	125
Fecal N	45(18)	81(22)	11(4)	32(16)	58(14)	25(6)	126(40)
Fecal parasite load	53(17)	97(22)	10(3)	53(16)	62(14)	25(6)	150(39)
Body condition	13	50	2	22	31	8	63

Table 4-2. Mean values (with SE) per variable for HM bison in relation to season and habitat type, as determined from direct observation and fecal analyses. Unless otherwise indicated (*), values are only presented if there was statistically significant ($p < 0.05$) variation across seasons and/or habitat types. Feeding:Moving is represented by the percentage of foraging behavior (feeding + moving) devoted to feeding. The results of the *post-hoc* Tukey's test for differences between habitat types are indicated with superscripts, where different letters indicate significant differences.

Bison variable	Season		Habitat			
	Early	Late	Burn	Chaining	Open	Closed
Body condition score	2.66 (0.13)	3.00 (0.06)				
Parasite load (eggs g^{-1})	84.9 (11.3)	41.8 (5.11)				
Fecal N (g kg^{-1})	12.8 (0.5)	10.2 (0.23)	14.4 $(0.81)^b$	11.7 $(0.49)^a$	10.5 $(0.37)^a$	10.6 $(0.44)^a$
Group size	31.9 (4.12)	49.6 (3.37)				
Feeding:Moving*			91.6 $(4.07)^b$	75.5 $(3.75)^{ab}$	78.8 $(2.80)^{ab}$	67.4 $(6.79)^a$

*$p < 0.1$.
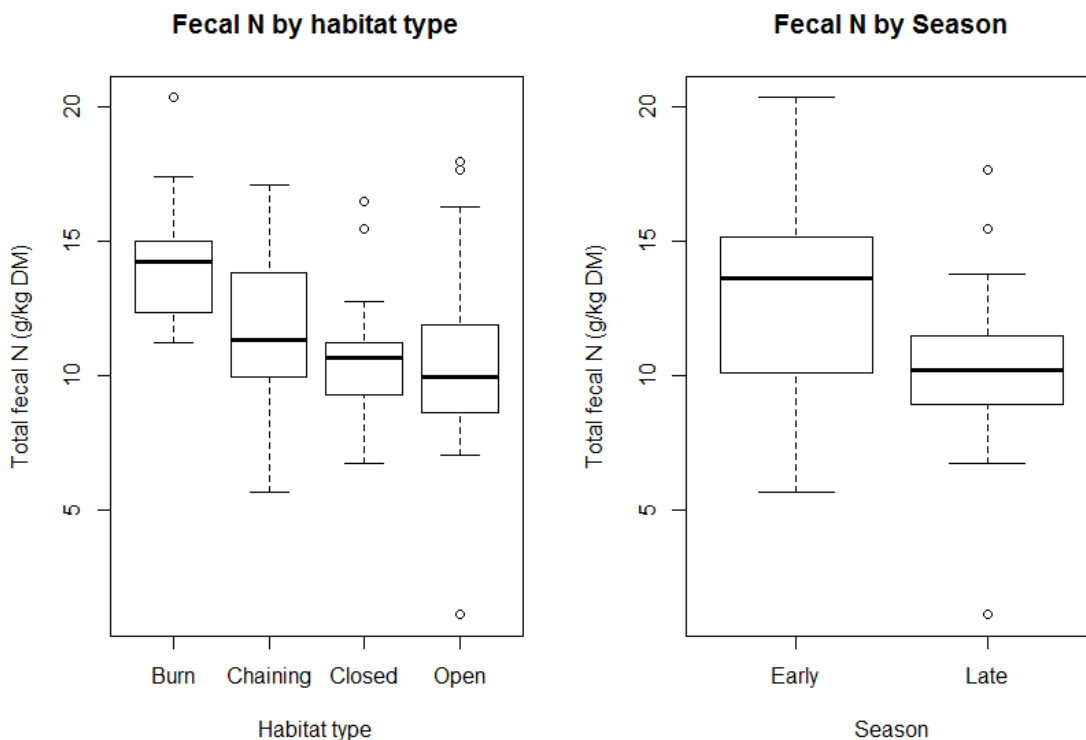
Figure 4-1. Bison total fecal N (g kg^{-1} dry matter) for four habitat types (burn, chaining, closed, and open) and 2 seasons (early: January – June, and late: July – December) in the Henry Mountains of S. Utah, as determined from 126 fecal samples collected from 39 different groups of bison from May 2012 – April 2013. Burned habitat is significantly different from the other three habitat types, which are statistically indistinguishable. Early season is significantly different from late season. Box plot shows quartiles, median, and 1.5x interquartile range. Circles show outliers beyond 1.5x interquartile range.
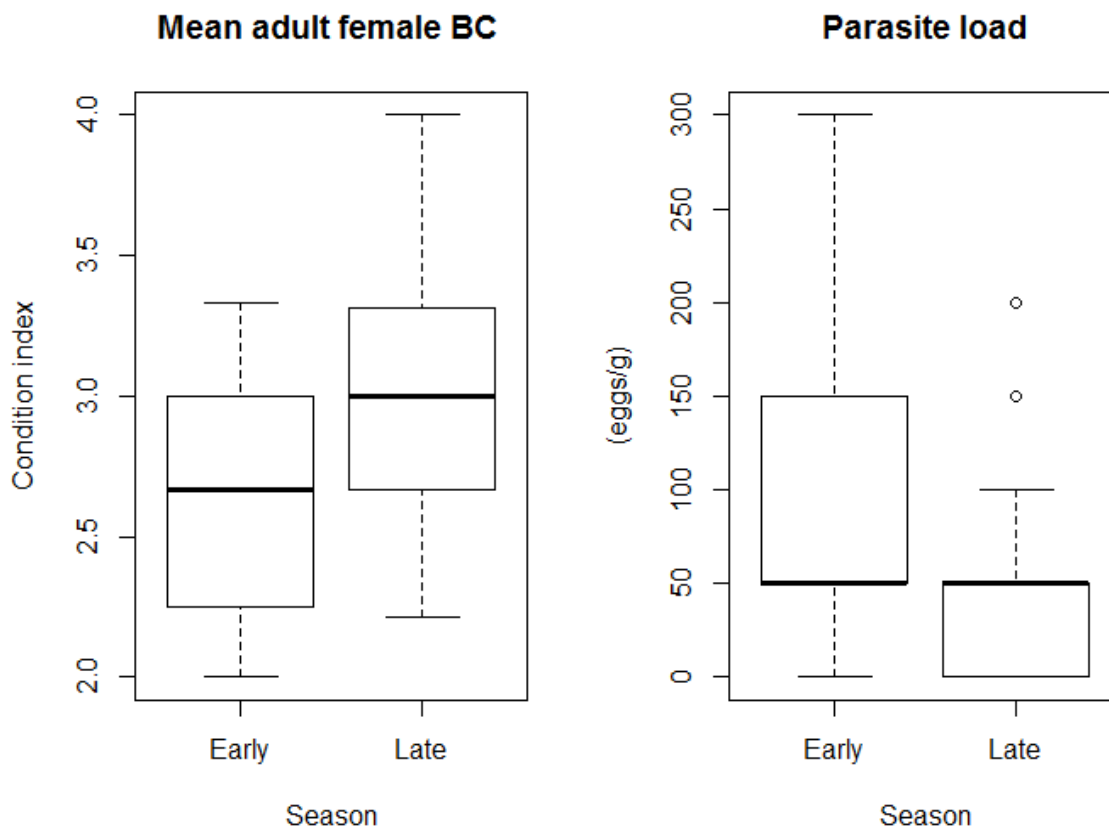
Figure 4-2. Adult female bison body condition in the Henry Mountains of S. Utah by season, early (January – June) and late (July – December), as determined through condition scans following Prins (1996), for 63 different groups of bison from May 2012 – August 2013. 1 = Very Poor, 2 = Poor 3 = Average, 4 = Good, 5 = Excellent. The two seasons are significantly different. Bison endoparasite load as determined by helminth egg counts for four habitat types (burn, chaining, closed, and open) and 2 seasons (early: January – June, and late: July – December) in the Henry Mountains of S. Utah, as determined from 150 fecal samples collected from 40 different groups of bison from May 2012 – April 2013. Chained habitat is significantly higher than the other three habitat types, which are statistically indistinguishable. Early season is significantly higher than late season. Box plot shows quartiles, median, and 1.5x interquartile range. Circles show outliers beyond 1.5x interquartile range.
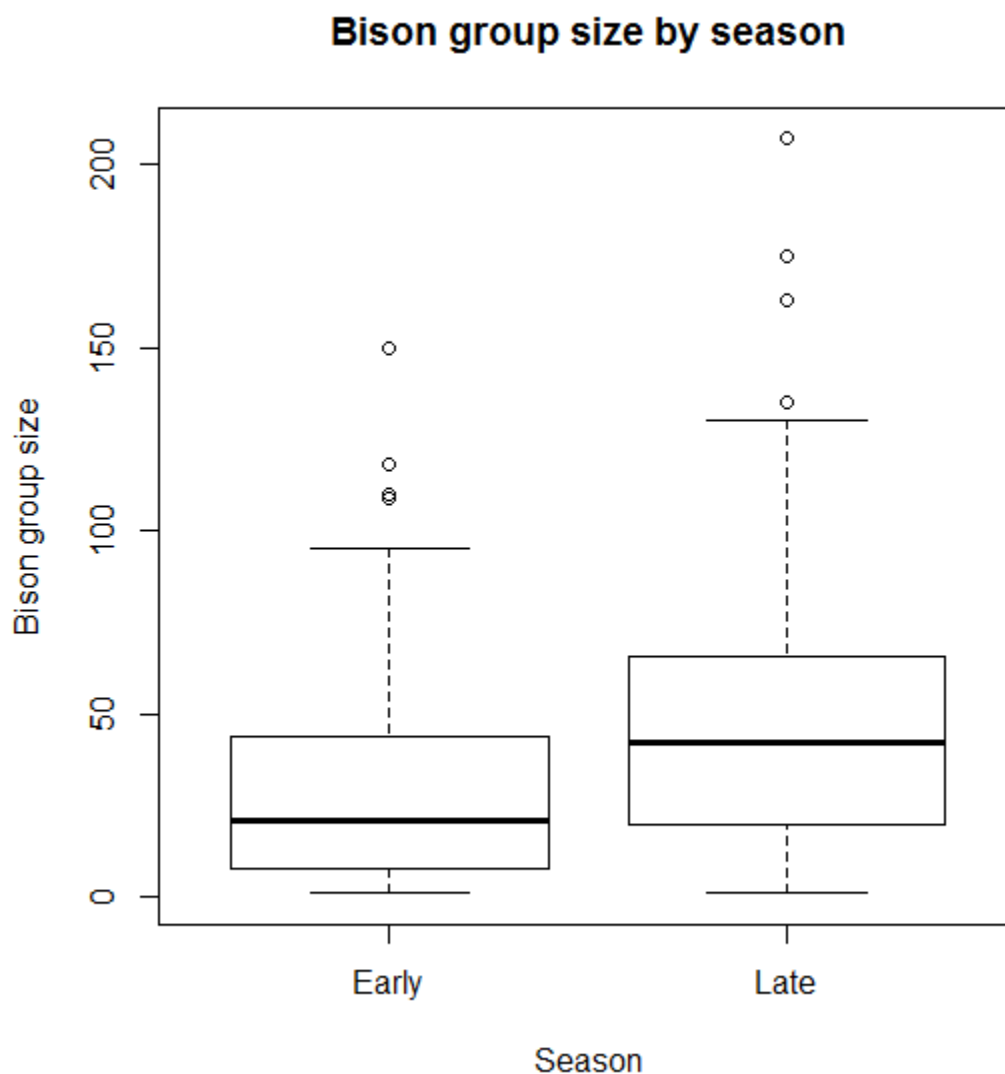
Figure 4-3. Bison group size in the Henry Mountains of S. Utah by season, early (January – June) and late (July – December), as determined through herd size counts of 110 groups from May 2011 – August 2013. The two seasons are significantly different. Box plot shows quartiles, median, and 1.5x interquartile range. Circles show outliers beyond 1.5x interquartile range.
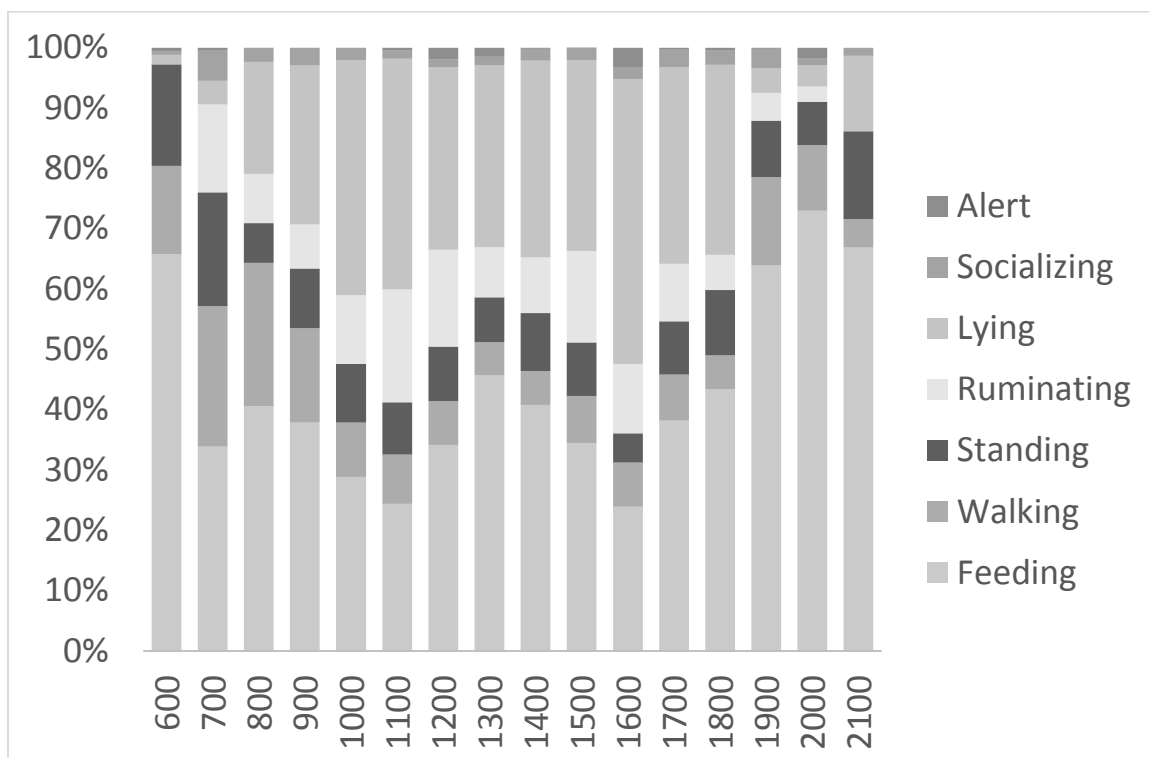
Figure 4-4. Diurnal bison activity pattern as determined by herd activity scans from ~170 hours of observation of 125 different bison groups in the Henry Mountains of S. Utah. The percentage of the herd engaged in each of the seven activity types is indicated by the relative size of each colored bar.

CHAPTER 5

BISON WITH BENEFITS: TOWARD INTEGRATING WILDLIFE AND RANCHING

SECTORS ON A PUBLIC RANGELAND IN THE WESTERN USA[4]

Abstract

The North American model of wildlife conservation, based on the Public Trust Doctrine, is credited for the recovery of several charismatic wildlife species including the plains bison. In that model, wildlife is a public resource for the benefit of all, but any negative impacts from wildlife are felt by a small number of individuals in local communities. In recent years however, resilience thinking is pushing for changes in the traditional state-run wildlife management model to allow for integrated multi-sector approaches at the landscape scale. A free-ranging bison herd on public land in the Henry Mountains (HM) of Utah is used as a case study to consider if and how a community-based conservation program could be developed for a state-managed wildlife resource to benefit all stakeholders. The HM bison, which are disease-free, share the rangeland with cattle that are privately owned by individual ranchers and corporations with various economic goals and environmental values. The ranchers currently derive no specific benefits from the bison and have concerns regarding competition between bison and cattle. However, a threshold harvesting strategy with community participation could generate revenue to offset the competition concern. It could also provide benefits to the local community, increase state revenue, and increase the bison population size while securing its long-term genetic viability. Implementation would initially require

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facilitation by policy specialists, after which we suggest an HM bison partnership could serve as a model for bison recovery efforts elsewhere in North America.

Introduction

The North American model of wildlife conservation (Geist et al. 2001) is based on the doctrine that wildlife resources are held in the public trust and managed by government agencies according to the law. This Public Trust Doctrine, which is rooted in Roman law and was first invoked by the USA Supreme Court in the mid-19th century, is now represented in laws that differ among states (in the USA) and provinces (in Canada) but which all preclude personal or communal profit from wildlife (Organ & Mahoney 2007). Implementation of management and enforcement of laws by state and provincial wildlife agencies is funded to a greater or lesser extent by license revenue, and so while the model's purpose is to protect wildlife from over-exploitation, it is also dependent upon state-regulated hunting and angling. As a consequence, populations of wildlife species are typically managed to maximize hunting opportunities, subject to resistance from other local land users. This traditional, command-and-control, top-down management approach is credited for having brought several iconic wildlife species back from the brink of extinction, but it represents the species-focused 'Maximum Sustained Yield (MSY) paradigm' of wildlife management, which is now being challenged by the 'resilience paradigm' of the 21st century (Chapin et al. 2009; Allen et al. 2011; Curtin & Parker 2014). Resilience thinking conceptualizes multiple linkages between social and ecological systems that enhance the resilience of the coupled system against shocks and disturbances, which are naturally inherent in global change (Walker & Salt 2006).

Reconciling conservation, agriculture, and other competing land uses within a resilience framework involves changing the culture of the relevant management agencies - rather than replacing them – and calls for an integrated approach at the landscape scale (Sayer et al. 2013).

Lessons in integrating community participation into wildlife management can be learned from the developing world (Hill 2009) where experience has shown that conservation efforts generally fail if local communities are denied access to, or benefits from, their traditional resources (Newmark & Hough 2000). In such situations, community-based conservation approaches have sought to incentivize local communities to become active participants in conservation by enabling them to directly derive sustainable benefits in the process (Spiteri & Nepal 2006). For decades now, integrated conservation and development projects (ICDPs) have been advocated, funded, and technically supported by foreign aid agencies and international NGOs that are slow to bring back and apply the best ICDP practices in developed countries (Garnett et al. 2007). Case-studies are few and far between and so here we suggest how cattle ranching on public rangeland might be at least partially integrated with the management of American bison (*Bison bison*), the iconic species of the North American model (Organ et al. 2010).

Once numbering in the millions, bison populations across North America plummeted due to over-harvesting to less than 100 wild bison by the late 1800s (Hedrick 2009). Private individuals led the charge for bison conservation with coordination by the American Bison Society (Boyd 2003). Early bison managers around the beginning of the 20th century interbred bison with cattle for commercial purposes, leading to introgression

of cattle genes into much of the bison genome. 'Wild' bison were only found in small groups in Yellowstone National Park, Banff National Park, and near Winnipeg, Canada. Most of the existing bison were held in private conservation and commercial herds (Boyd & Gates 2006). This gave rise to an interesting problem, as bison became legally classified as both wildlife and livestock depending on the state. Currently, bison are only considered to be a wildlife species in four Canadian provinces, ten US states, and one Mexican state and are considered to be livestock in all others (Aune & Wallen 2010). Of the ~500,000 bison in North America, only ~20,000 are found in conservation herds while the others are all private commercial herds (Freese et al. 2007).

Despite the success of many conservation herds and the large number of commercial herds, the question of whether bison have recovered ecologically as a wildlife species is still without an answer (Freese et al. 2007). Most conservation bison herds are small, isolated, and intensively managed within fences where they exist without natural predators (Gates & Ellison 2010). While the number of conservation herds is growing, the total number of bison in conservation herds has remained relatively constant (Freese et al. 2007). Conflict exists between bison conservationists and livestock managers due to issues of competition and disease, leading to most bison herds being kept separate from cattle through fences and hazing practices (Meagher 1989). If, however, large-scale ecological restoration of bison is to take place, bison and cattle will likely be required to share rangelands. It therefore becomes imperative to learn how bison and cattle can coexist. Currently, the only place in the USA where free-ranging bison

share a public rangeland with cattle is in the Henry Mountains (HM) of southern Utah (Fig. 5-1).

Established in the early 1940s with 20 bison (15 females, 5 males) from Yellowstone National Park (Popov & Low 1950; Nelson 1965), the HM bison herd now numbers ~325 adults (post-hunt) and is controlled primarily by sport hunting. The presence of bison on public allotments leased for cattle grazing has become a source of contention between local cattle ranchers and the state and federal management agencies (UDWR 2007). A search for mentions of the HM bison in a major daily newspaper in Utah (*Deseret News*), together with the Utah Legislature archives, revealed an increase in the conflict with no mentions prior to 1991, eight mentions between 1991 and 1995, and 13 mentions in the 2000s of which all occurred during 2007-2012 (Fig. 5-2). This latter period coincides with below-average rainfall in the HM when the grazing permittees in that area began expressing doubt over the accuracy of official annual bison counts and concern that bison were reducing the standing crop of grass in summer on grazing allotments that were designated for cattle in winter. Early work discovered that bison and cattle have 91% dietary similarity in the HM, indicating a high potential for competition (van Vuren & Bray 1983). This, combined with their conspicuous presence on the landscape caused by their herding behavior, dust wallowing, trampling and large cattle-like dung pats, has led to a local perception that bison are important competitors with cattle for grazing resources.

To complicate the issue, the HM bison herd is a public resource managed by a state agency, the Utah Division of Wildlife Resources (UDWR), but the HM rangeland is

a checkerboard of primarily federal and state land with the federal Bureau of Land

Management (BLM) being responsible for regulating cattle grazing. BLM grazing

permits are quantified in AUMs (animal unit months), by which one AUM represents the

grazing resources required to support one cow with her calf for one month. For cattle,

there are ~25,600 AUMs permitted on the HM rangeland during the winter and ~2,600

during the summer. This is the equivalent of ~4,200 cattle present at any given time in the

winter and ~800 cattle present at any given time in the summer, mixed in with 350-400

bison year round. The cattle are privately owned by individual ranchers and corporations

with various economic goals and environmental values.

The current management objective for the HM bison is to maintain a stable

population size by harvesting with an escapement threshold (Lande et al. 1997) of 325

adult bison as agreed upon by state and federal agencies and the HM Grazing Association

(UDWR 2007). This threshold is also the maximum that the HM Grazing Association

will tolerate, while allowing a population size that meets the state's objectives for

conservation and licensed hunting. It is important, however, to consider the impacts that

small population sizes have on genetic diversity. For bison, the genetically viable

population size is estimated to be 1000 individuals (Gross & Wang 2005) but this would

not be practically achievable for the HM. A population of that size would likely damage

the resource base (Allen et al. 2011), increase conflict between local ranchers and state

wildlife managers, and restrict hunting opportunities as a consequence of strong density

dependence. Maintaining the population at less than half its genetically viable size

depends on meta-population management to exchange HM individuals with others from

genetically pure bison herds to overcome genetic diversity concerns (Boyd et al. 2010), but that has obvious cost implications.

The Henry Mountains lie within one of the most important conservation priority areas of the roadless BLM lands in the western USA (Dickson et al. 2014). Also, with the only free-ranging, disease free, genetically pure, and huntable wild bison herd in the world, the rugged HM environment offers a unique opportunity to sportsmen and so hunting permits ('tags') are in high demand. At the Western Hunt Expo in Salt Lake City in 2014, Sportsmen for Fish and Wildlife (SFW) sold two HM bison tags under the state's conservation permit program at auction for $19,000 and $18,500, with the funds going primarily to the state for use in projects that benefit bison, with input from SFW. In 2013, applications were submitted by 8135 prospective hunters (5618 Utah residents, 2517 non-residents) of bison on the HM, with a total of 95 permits being issued through a lottery system (86 reserved for residents, 9 for non-residents). Permit fees were $413 for residents and $1518 for non-residents, resulting in nearly $50,000 of license revenue to the state.

Our field research has found that, in one area of the HM, bison grazing accounts for 14% of the total grass biomass removed from the HM rangeland per year, whereas lagomorphs account for 34% and cattle 52% (Ranglack et al., in review). At current population size, the HM bison are neither major consumers of the forage resources used by cattle nor competitors for the habitats that local ranchers consider to be most important for their cattle (Ranglack and du Toit, in prep). Nevertheless, as long as they derive no benefits from the bison, local ranchers can be expected to continue using their contention

of bison-cattle competition to attract political attention to their ranching interests. Allowing a fair system for the local ranching community to benefit directly from the bison that share the public rangeland with their cattle, while also securing bison conservation, might be a solution. Implementation would require the negotiation of policy barriers but that process would be contingent upon an ecologically and economically feasible plan. Here we investigate the feasibility of incrementally raising the escapement threshold for the HM bison population, commensurately reducing the stocking rate of cattle, using benefits from bison hunting to compensate the affected ranchers, and providing a fund of bison benefits for community development. Our objective is to explore options for integrating bison conservation into the local ranching community to enhance the resilience of this unique social-ecological system.

Methods

Study Area

The Henry Mountains (HM) study area in south-central Utah [38°5' N, 100°50'W] includes arid, semi-arid, and subalpine habitats for bison, which migrate seasonally between northern (summer) and southern (winter) parts of the range and utilize almost all vegetation types and elevations in-between. Apart from bison, cattle are the only other large grazers in the region. Mule deer (*Odocoileus hemionus*) are present on the HM, but their preference for forbs would suggest negligible levels of competition with the grazers (van Vuren & Bray 1983). Black-tailed jackrabbits (*Lepus californicus*) and desert cottontail rabbits (*Sylvilagus audubonii*) are common in the low- and mid-elevations. The only large predators are mountain lions (*Puma concolor*) and coyotes, but

their population densities are limited by long-standing predator control efforts implemented by both government and private entities. For a description of the study area see Nelson (1965) and van Vuren and Bray (1986).

Current research in the HM has focused on determining the relative impacts of both bison and cattle on forage resources, as well as identifying seasons and habitats in which bison and cattle are most likely to come into competition (Ware et al. 2014; Ranglack et al., in review; Ranglack & du Toit, in prep). HM bison and cattle differ in their space use, as bison use areas at greater distances (horizontal and vertical) to water (van Vuren 2001), likely minimizing spatial overlap and thus potential competition between the two species.

Historical data

The HM bison population has been surveyed by the UDWR annually (in July or August) each year since 1949, initially involving a team of 12 or more people working on the ground (on foot, horseback and vehicle) to count animals in specific areas. Since 1990 the entire HM bison range has been surveyed by helicopter to derive an annual total count, to which a correction factor has been applied (assuming 90% sightability) to estimate the pre-hunt population size (N). Since 1983 the population has been harvested according to a fixed escapement strategy with the escapement threshold (c) adjusted several times by agreement among representatives of the UDWR, BLM, and HM Grazing Association. The number of animals harvested (H) each year was the number killed by hunters in addition to live removals by UDWR for translocations (Fig. 5-3).

Harvesting calculations

We performed a hypothetical exercise in which we allowed the pre-hunt bison population to increase above the level at which it is held by the current escapement threshold ($c = 325$), considering incremental escapement thresholds up until $c = 500$. To quantify the actual harvesting rate (h) that had been applied to the population during its harvested history, we calculated $h = H/N$ and then averaged h over the 30 years (1983-2012) in which an escapement threshold strategy has been in place. That resulted in $h = 0.20$ (SE $= 0.015$), or 20% of the adult population harvested, on average, each year. By comparison, the maximum intrinsic population growth rate (r_{max}) for bison can be estimated from mean adult body mass (M in kg) as $r_{max} = 1.5M^{-0.36}$ (Caughley & Krebs 1983) and by using $M = 500$ kg (estimated average from Reynolds et al. 2003) this results in $r_{max} = 0.16$. Therefore, annually applying the historical harvesting rate ($h = 0.20$) would be unsustainable in the long term and so we conservatively made $h = r_{max}$ and used this theoretical value ($h = 0.16$) for our calculations of future potential harvesting. With a fixed harvesting rate (h) and a series of incremental values of escapement threshold (c) the hypothetical pre-hunt population size (N) was calculated for each threshold as $N = c/(1 - h)$ and the annual potential yield (H) with that threshold as $H = N - c$.

Financial calculations

With the current escapement threshold ($c = 325$) holding the bison population at the maximum size tolerated by the HM Grazing Association due to concerns of competition with cattle (the veracity of which is immaterial to this exercise), we assumed that any raising of the threshold ($c > 325$) would have to be accompanied by destocking

of cattle, for which the respective ranchers would have to be compensated. For simplicity
we also assumed, following the BLM standard for the area, that bison and cattle are
equivalent animal units and so one bison on the HM rangeland for one year is equivalent
to 12 AUMs in terms of grazing effect. Thus, each additional bison allowed to remain on
the HM rangeland for one year would require 12 AUMs to be released from cattle
grazing and those AUMs would have to be purchased elsewhere to maintain the rancher's
level of animal production. We assumed those AUMs would be purchased on the open
market from private landowners and so we used the 2013 market rate of $14.50 per AUM
for Utah (NASS 2014), which would be generous because the HM area is drier than most
rangelands under commercial cattle production in Utah. To provide the revenue to
compensate for moving destocked cattle off the HM rangeland, we arbitrarily allocated
one bison tag for auction each year if the escapement threshold was raised to $c = 350$ and
then one additional tag per year for each increment of 50 above that (0 tags for $c = 325$, 1
tag for $c = 350$, 4 tags for $c = 500$). We used the 2014 auction value of $19,000 per tag.
As a notional benefit distribution scheme, we assumed all of the auction proceeds would
go to the HM Grazing Association, from where it would be distributed on a pro rata basis
to affected permittees as direct compensation in market terms for the AUMs they gave
up, with the remaining funds going into a community fund such that no individual derives
personal profit.

Results

      Allowing the bison population to increase by raising the escapement threshold
and commensurately reducing the number of cattle on the rangeland could ultimately

provide a larger annual yield of bison. This could financially compensate affected ranchers and also provide an annual community dividend (Table 5-1). Once the bison population has become regulated by a new escapement threshold, and assuming current market conditions prevail, the local community could derive a minimum net benefit of $10,300 annually (after compensating ranchers for AUM reductions) for every increment of 50 bison in the escapement threshold. The state wildlife management agency could also increase its annual offtake of bison through any combination of hunting and live removal. Because we conservatively allocated just one bison tag to the community for each threshold increment, the community dividend could be increased through negotiation.

Discussion

Even with a more conservative harvesting rate than has historically been applied in the HM, each increase of 50 bison in the escapement threshold could result in nine more bison harvested each year. Of those, at least one could be allocated to the community for auction and up to eight could be added to those available for the state wildlife management agency to allocate to hunters in their lottery system or remove for metapopulation management. With the HM bison population currently being <10% of the size of the permitted cattle population on the HM rangeland, and with each increase in the bison escapement threshold matched with a commensurate decrease in the cattle population, we are assuming no density dependent effects. As with all harvesting strategies involving community-based wildlife management, the initial calculations are purely to establish a starting point from where adaptive management would proceed (du

Toit 2002). Nevertheless, our conservative calculations demonstrate that a policy change could enable a win-win situation for both the local community and the state wildlife management agency.

From a conservation perspective the implications are that the HM bison population could be increased to at least reduce the risk of small population syndrome. Also, additional animals could become available for translocation as founders in other suitable habitats, to augment existing subpopulations, as exchange for a few genetically pure bison from elsewhere (metapopulation management), or as exchange for batches of animals from other species of concern. Genetically-pure, disease-free bison, such as those in the HM, are valuable to conservation, with few other populations meeting those requirements (Halbert & Derr 2007; Aune & Gates 2010).

If some financial benefits from the HM bison were allowed to flow directly to the local community then this might incentivize local ranchers to adjust their cattle management to improve conditions for the bison population. There might also be opportunities for the local community to diversify operations to protect against future changes in the livestock market or as a buffer against changing environmental conditions. For example, the community may stipulate that a hunter who purchases their tag(s) at auction must use one of the local ranchers as a guide. With the local knowledge the ranchers possess, an eco-tourism industry could be developed with the ranchers providing guided hunts, horse-packing trips, wildlife safaris, etc. Capitol Reef National Park is directly adjacent to the HM and so tourists are already frequenting the area. The Sturgeon River Ranch near Prince Albert National Park in Saskatchewan, Canada, is an example of

a ranching community taking advantage of such opportunities with bison (Esrock 2014).

The community fund could also be used for projects that benefit the entire community,

such as scholarships for local students, improving community infrastructure, etc. (Frost &

Bond 2008).

From global analyses it is clearly evident that conserving wildlife on rangelands

depends on the support and active involvement of local communities (Deutsch 2010).

Integrated science-based management planning that takes into account the complexities

of the social-ecological system is key for managing large ungulate populations on shared

ranges with domestic livestock (Weisberg et al. 2002). Also, although wildlife resources

are publicly owned, wildlife management planning can accommodate any negative

impacts that are generally felt by a relatively small segment of the public represented by

those local communities that live with, and therefore have influence on, the wildlife

resource (Madden 2004). Offsetting such negative impacts is best achieved with a direct

and tangible benefit that varies depending on the overall health or size of the wildlife

population(s) in question (Berkes 2007). Allowing a local community to become an

active partner in, and beneficiary of, a wildlife management program builds both the

adaptive capacity of the social-ecological system and also trust among all partners

(Berkes 2004).

Although this hypothetical example has shown the feasibility of a staggered

incentive system, we fully recognize the challenges to implementation within local, state,

and federal institutions. This represents a fairly dramatic change to the present

management system for wildlife resources on public lands in North America. Our

purpose is to explore and describe the possibilities so that representatives from the

community and state and federal agencies have a basis for ongoing dialogue and

planning. Management of the HM bison is a contentious issue (Fig. 5-2) that needs

additional inputs from policy specialists, resources economists and social scientists, but

our simple population analysis (Table 5-1) points to a solution. If an agreement were to

be reached for an increased escapement threshold then current hunting would have to be

reduced while the population grows to a size that could sustain the potential offtake we

have calculated. During that bison population adjustment, time would be available for

facilitated discussions leading to new agreements among all partners. It is crucial that

wildlife managers and cattle ranchers work together for American bison conservation

(Freese et al. 2007). The same applies for European bison (*Bison bonasus*), for which

there is abundant potential habitat outside of protected areas (Kuemmerle et al. 2011). In

broader context, we present the HM bison as a case-study of how wildlife management in

North America might begin adapting to the 'resilience paradigm' (Chapin et al. 2009;

Allen et al. 2011; Curtin & Parker 2014) in a time when the historically successful North

America Model is facing mounting challenges (Duda et al. 1998; Manfredo et al. 2003;

Teel & Manfredo 2009; Organ et al. 2010).

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Table 5-1. A proposed community-based wildlife management strategy for the Henry Mountains (HM) bison population is presented for several potential escapement thresholds using a conservative harvesting rate ($h = 0.16$).

Threshold	N^a	H^b	AUMs^c	Cost^d	Tags^e	Net benefit^f
325	387	62	0	$0	0	$0
350	417	67	300	$4,350	1	$14,650
400	476	76	900	$13,050	2	$24,950
450	536	86	1,500	$21,750	3	$35,250
500	595	95	2,100	$30,450	4	$45,550

[a] Hypothetical pre-hunt population size.

[b] Required harvest to maintain the HM bison population at the designated threshold.

[c] Commensurate reduction in cattle grazing.

[d] Cost of purchasing grazing rights elsewhere on the open market, calculated using 2013 average market rates for Utah. Compensation could be from the proceeds of an annual public auction of bison hunts (tags), which could be distributed on a pro-rata basis to affected ranchers, after which a net benefit could go to the community for local projects.

[e] An illustrative minimal number of tags for the community.

[f] Annual community benefit calculated assuming the 2014 auction value of $19,000 per tag.
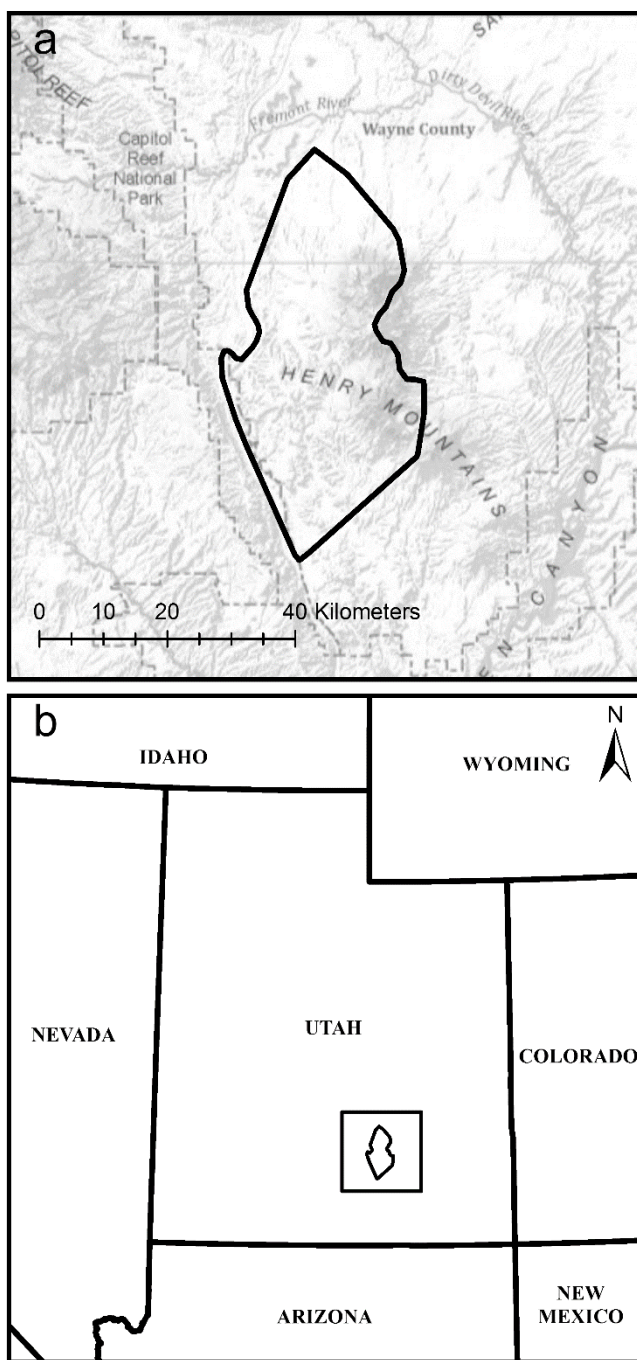
Fig. 5-1. The Henry Mountains area of southern Utah (a) with the area used by the bison herd designated by the black line; the location of the Henry Mountain (HM) rangeland (b) in the state of Utah.
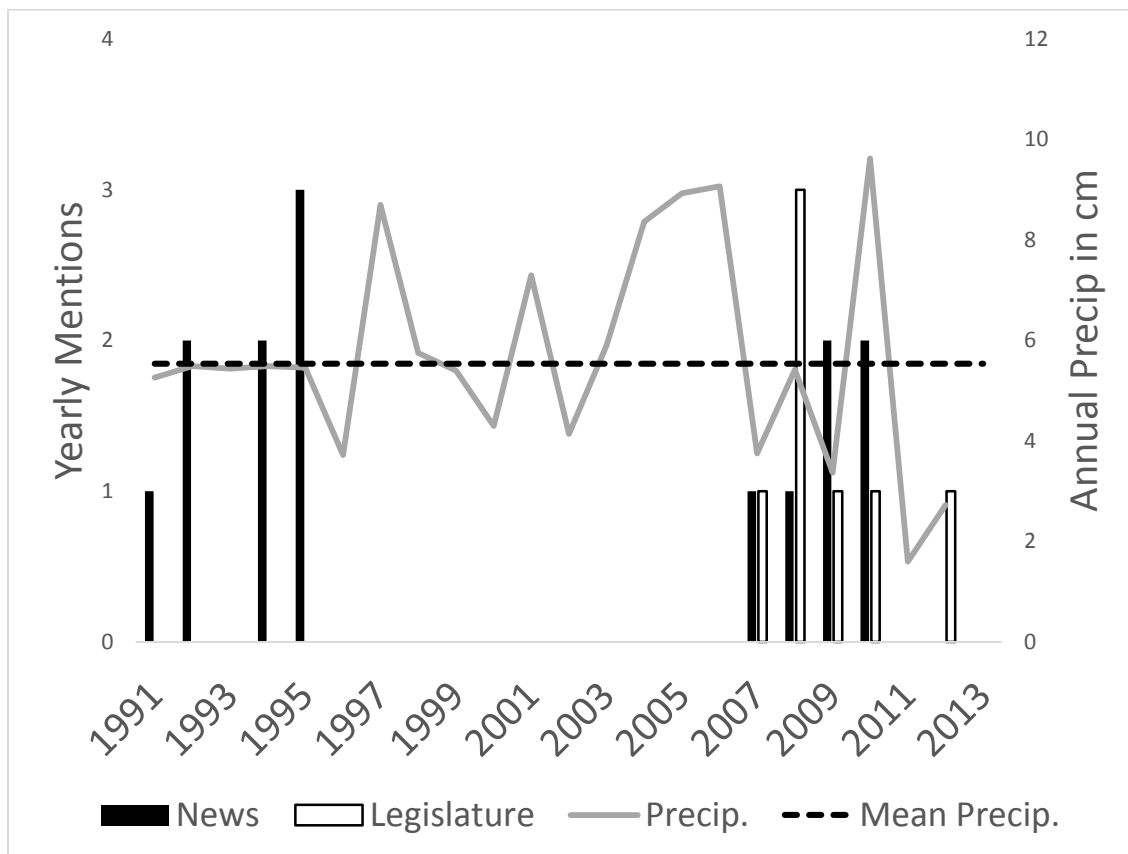
Fig. 5-2. The yearly number of mentions of the HM bison conflict in a major Salt Lake City newspaper (*Deseret News*) and the Utah State Legislature plotted with annual precipitation and mean annual precipitation at the nearby Hanksville airport. The two peaks in conflict correspond to periods of below average rainfall in the area.
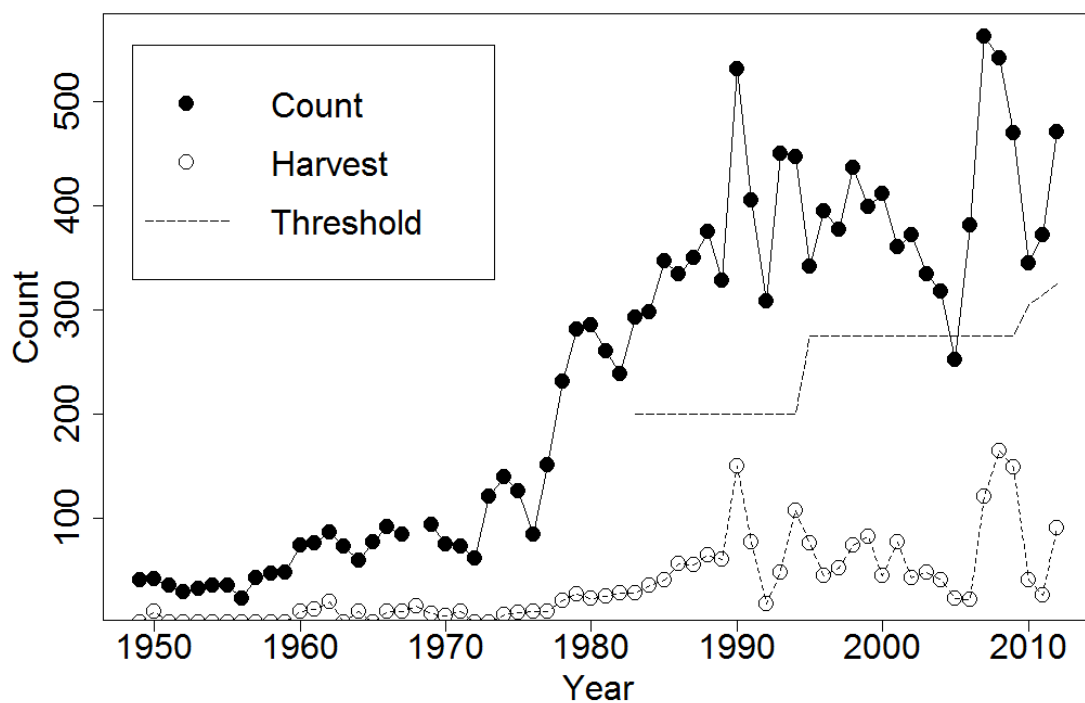
Fig. 5-3. The HM bison population trajectory from 1949-2012, including the total pre-hunt population count (*N*) is from UDWR summer bison surveys compared to the total harvest (*H*) through hunting and live removals and the escapement threshold (*c*) shown as it went through adjustments from 1983-2012.

CHAPTER 6

CONCLUSIONS

In Chapter 2, contrary to my *a priori* predictions, at current population densities, the bison impact on the grazing resource in HM is minor in comparison to lagomorph and cattle impacts. These findings are surprising and demonstrate that the local ranchers' perceptions were either based on a misunderstanding of the ecological interactions in this system or were reported with bias to suit their political stance in the HM bison controversy. Thus, while the integration of local ecological knowledge is important and valuable for management strategies, it is important to use science to validate those perceptions (Davis & Ruddle 2010). In the HM, given that lagomorphs consume more than twice the forage used by bison, there is a greater potential to reduce competition with cattle by reducing lagomorph abundances than by attempting to manage bison habitat use (through hazing, fencing, etc.) or population size (with hunting and live removals).

These results align with a concurrent study on grazing impacts on plant community composition in the HM that also found no significant impacts due to bison grazing (Ware et al. 2014). In contrast, grazing effects of small herbivores are commonly underestimated but must be accounted for as a potential driver of grassland structure and diversity (Rebollo et al. 2013). Because bison range widely across the landscape whereas cattle are central place foragers, usually focusing their grazing around water sources, bison and cattle exhibit spatial segregation on shared rangelands (van Vuren 2001, Allred

et al. 2011). Thus the purported negative impacts of bison on cattle have been overstated, at least in the HM.

Continued monitoring of the permanent exclosure sites used in Chapter 2, partnered with direct measurement of lagomorph abundance, is needed to determine the long-term effects of lagomorphs on the HM rangeland. Future studies should also include further study of the impact of coyote population control on lagomorph population densities. My study serves to illustrate why caution should be used when integrating local ecological knowledge into natural resource management (Krupnik & Jolly 2002; Gilchrist, Mallory & Merkel 2005; Ruddle & Davis 2009). The perceived knowledge base of local communities might not match current ecological realities, or might become biased by political pressures to misrepresent the complexities of the system. Scientific verification of local ecological knowledge is thus crucial (Raymond et al. 2010), but should not discount the importance of local stakeholders as active participants in management planning.

In Chapter 3, I found that annual rank profiles of bison habitat preferences, as determined through RSF analysis, and rancher-reported cattle habitat scores were marginally correlated (Prediction 1). I also found evidence from bison (some sexual segregation, more focused habitat selection) that winter is the most limiting season on the HM rangeland, as expected, but no evidence that bison and cattle compete at the habitat scale during that season (contrary to Prediction 2). Additionally, no correlation was found between summertime grazing by bison and rancher-reported winter habitat needs for cattle (contrary to Prediction 3), which was a particular concern among ranchers. These

results do not support the contention that bison and cattle (as reported by rancher knowledge) are competing at the habitat scale on the HM range, even with temporal separation in habitat use. My findings should hopefully ease tensions between the local ranching community and the state and federal government agencies regarding the potential impact of bison on cattle grazing.

While these findings are somewhat surprising, they are not entirely unexpected. Bison in the HM are large, generalist feeders and are generally in good body condition, indicating that food quality is not a limiting factor. When resources are not limiting, competition is unlikely to occur (Putnam 1996, Sale 1974). Despite this apparent lack of competition, bison might still reduce forage availability for cattle. Bison grazing is permanent and free-ranging across the HM rangeland, whereas cattle grazing is temporally and spatially constrained by the specific details of the grazing permit. Additionally, rancher knowledge of cattle habitat needs could be imperfect and, although it was impossible in our study, GPS data from cattle might have revealed different patterns.

On a broader scale, my results show that despite similarities in body size and diet, differences between bison habitat preferences (RSF analysis) and cattle habitat needs (rancher-reported) should allow for the coexistence of both species on the same rangeland. Concerns of disease transmission and property damage by bison need special consideration (Freese et al. 2007), but interspecific competition for forage has been overstated.

In Chapter 4, following my assumption that habitats and seasons with higher levels of fecal N are of higher quality in terms of grazing resources, I classify burned habitats as highest in quality, with mechanically manipulated (i.e., chained) habitats being similar to open habitats, in partial support of Prediction 1. My results reflect that chaining transforms closed habitats into open habitats, increasing habitat quality. Burning does the same while also pulsing nutrients into the system and thereby further improving grazing conditions (Eby et al. 2014). Whereas bison group dynamics and activity in general (F:M being a possible exception) did not respond to within-season differences in habitat quality at the spatial scale of our study (contrary to Prediction 2), they did respond to seasonal variations in overall environmental conditions.

Mechanical treatments are often used as fire surrogates (Kennedy & Fontaine 2009) but my results for bison show that burned areas offer significantly higher quality forage (based on fecal N) than other habitat types (supporting Prediction 3) despite only a weak signal of improved foraging efficiency and no detectable effect on aggregation (contrary to Prediction 3). It is important to note that the burned areas on the HM rangeland were ~10 years old and the higher quality forage we observed may not be the direct result of a post-fire nutrient pulse, but a community-level, indirect response. As the burned area was reseeded, it is possible that more nutritious plant species were able to establish given the lack of competition and the nutrient pulse from the fire, leading to an overall more nutritious plant community that was able to persist beyond the initial post-fire nutrient pulse. Our ability to detect a bison response was likely limited by sample

size for the burned areas, as most bison burn use occurred during the winter months when access was problematic.

For rangelands in North America, I thus recommend that maintaining bison with cattle, and monitoring bison habitat use and fecal indicators, provides a better method of monitoring spatial and temporal variation in rangeland quality than by monitoring the cattle themselves. This is in addition to the multiple other benefits to social-ecological systems that would accrue if bison populations were restored across more of their former range in North America (Freese et al. 2007).

Chapter 2 showed that negative impacts of bison on cattle in the HM are smaller than perceived by the rancher community. Furthermore, in Chapter 3, little overlap was found between bison habitat preference and rankings of cattle habitat needs, as reported through a survey of local rancher knowledge, indicating that competition is minimal. Despite this, negative effects of bison will likely continue to be claimed by the ranching community so long as they derive no benefit from sharing their grazing allotments with bison. Allowing a fair system for the ranching community to obtain direct benefit from the bison, while also securing bison conservation, could be a solution to this socio-ecologic problem.

In Chapter 5, I suggest creating a partnership, with the local community taking an active part in the management and conservation of bison, may be one such solution to this problem. An integrated management plan that is science-based and takes into account the complexities of the socio-ecological system is key for managing large ungulate populations on shared ranges with domestic livestock (Weisberg et al. 2002).

Management plans also need to recognize that while wildlife are publicly owned, any negative impacts are generally felt only by a small segment of the overall population (Madden 2004). It therefore follows that these individuals should be involved in the wildlife management process and receive a direct and tangible benefit that varies depending on the overall health of the wildlife population (Berkes 2007). This creates a situation where the local community can actively participate as partners in a wildlife management program that builds the adaptive capacity of the socio-ecological system. By providing not only an economic incentive, but increased involvement in the wildlife conservation plan, trust is also gained among all parties (Berkes 2004), helping to align the goals of state and federal management agencies with the local community.

The original purpose of the North American model of wildlife conservation was to conserve game species and allow for continued hunting opportunity. It has served its course well and has done much to conserve wildlife in North American (Organ et al. 2010). It may be time however, to reconsider its value and make adjustments that reflect the ever-changing socio-ecological systems to which it is applied (Manfredo et al. 2003). That may allow for greater socio-ecological stability, leading to the protection of multiple species and ecosystem services with fewer management inputs and less conflict between management agencies and local communities. The system suggested for the management of bison on the HM (Chapter 5) is an example of this new direction and how it may be applied to take advantage of existing aspects of the North American model for wildlife conservation.

The HM rangeland serves as an example of a wild area where a free-ranging bison population can be maintained at low density by controlled hunting and coexist with cattle within a public grazing framework. Replicating this system across other public lands could allow for bison populations to be restored at ecologically meaningful scales, which to this point has only occurred in a few select places (Sanderson et al. 2008). As bison are considered to be the keystone species in North American grazing ecosystems (Knapp et al. 1999), expanding the practice of mixed bison-cattle grazing should also expand the cascading effects of bison grazing at the landscape-scale, thereby enhancing the biodiversity and conservation of rangelands.

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APPENDIX

September 9, 2014

I hereby give permission to Dustin Ranglack to reprint the following paper in his dissertation:

Competition on the range: science versus perception in a bison-cattle conflict in the western USA

Susan Durham Sep 9, 2014

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My research interests focus primarily on the ecology of large mammals in terrestrial ecosystems. More specifically, I am interested in animal space use, predator-prey interactions, and human-wildlife interactions. I am less interested in specific taxa than I am in working to solve real-life conservation problems. I am currently studying bison-cattle conflict on the Henry Mountains of S. Utah, focusing on identifying the timing, location, and intensity of competition between the two species, as well as developing a novel integrated management scheme that involves the local community.

TEACHING AND ADVISING

-Instructor for BIOL/NR 2220 General Ecology (Sp. 2015, 70-120 students)
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-TA for WILD 4880 Conservation Genetics (Fall 2010, 2011, Sp. 2013, ~30 students/semester)
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-EcoLunch Coordinator, Fall 2014
-Department of Wildland Resources Student Representative, Graduate Student Council, College of Natural Resources, Utah State University, 2013-2014
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-Stokes-Leopold Scholar, 2013, 2014
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-African Safari Club of Florida Scholarship, 2012, 2013, 2014
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-Department of Wildland Resources Senior of the Year, 2009
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PROFESSIONAL TRAINING
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Utah Division of Wildlife Resources, Fecal and genetic analyses of the Henry Mountains bison herd. J.T. du Toit and **D. H. Ranglack**. $30,000.

PUBLICATIONS
Ranglack, D. H., S. L. Durham and J. T. du Toit. Competition on the range: science *versus* perception in a bison-cattle conflict in the western USA. In review. Journal of Applied Ecology.
Ranglack, D. H. and J. T. du Toit. Testing a contention in public grazing: do bison prefer the same habitats perceived by ranchers as important for cattle? Submitted.
Ranglack, D. H. and J. T. du Toit. Bison as bio-indicators of the effects of habitat manipulation in a semiarid rangeland. In review. Ecological Indicators.
Ranglack, D. H. and J. T. du Toit. Bison with benefits: towards integrating wildlife and ranching sectors on a public rangeland in the western USA. Submitted.
Koons, D. N., P. Terletzky, P. B. Adler, M. L. Wolfe, **D. H. Ranglack**, F. P. Howe, K. Hersey, W. Paskett, and J. T. du Toit. 2012. Climate and density-dependent drivers of recruitment in plains bison. Journal of Mammalogy 93(2):475-481.

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GUEST SEMINARS

2014: Utah State University: Ecology Center Eco-lunch
    A discussion on comprehensive exams
2014: Utah State University: Animal Ecology Lab
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2013: Utah State University: Animal Ecology Lab
    Competition on the range: Perception versus reality
2013: Utah State University: Ecology Center Eco-lunch
    A discussion on comprehensive exams
2012: Utah State University: The Wildlife Society Student Chapter
    How do we use GPS and VHF telemetry in bison research?
2012: Utah State University: The Berryman Institute Student Group
    American bison ecology and bison-cattle interactions in an isolated montane environment
2012: Utah State University: College of Natural Resources: Panel Discussion
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COMMITTEES

- Organized the Biannual Berryman Institute Symposium, May 2010
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