

Competition on the range: science vs. perception in a bison–cattle conflict in the western USA

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Summary

1. Competition between livestock and wild ungulates is commonly perceived to occur on shared rangelands. 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 also abundant in this area. 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 m²) in the conflict area: 20 excluded bison + cattle (‘partial’) and 20 excluded bison + cattle + lagomorphs (‘full’). All exclosures, each with a paired open reference plot, were monitored for 1 year, and above-ground plant production was measured. GPS telemetry (bison) and scheduled grazing (cattle) allowed visitation to be quantified for each ungulate species based on the number of ‘animal days’ in the area. Rancher perceptions of wildlife–cattle interactions were recorded in a questionnaire survey.

3. Ranchers perceived bison as a high-level competitor with cattle, whereas lagomorphs were 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 large herbivores 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.* Cattle face a greater competitive challenge from lagomorphs than from bison in the study area. This case study illustrates the need for science-based management of social–ecological systems in which even long-term resource users might underestimate the complexities of trophic interactions. Attention should be redirected at the lagomorphs and their main predators, coyotes *Canis latrans*, which are currently subject to population control. To reduce negative perceptions among local ranchers, options should be explored to incorporate benefit-sharing into the management of the bison population.

Key-words: adaptive management, exclosure, grazing, lagomorphs, local ecological knowledge, predator control, rangeland, social–ecological systems

Introduction

Natural resource management is increasingly being conducted within a social–ecological framework with the views and knowledge of local peoples being integrated into man-

agement 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

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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 pastoralists 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 co-mingle 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 *c.* 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 below-average rainfall in the HM. The main concerns expressed by the grazing permit holders 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 man-

aged 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 = grazing resources for 1 cow + 1 calf for 1 month), and there are *c.* 25 600 AUMs permitted on the HM rangeland during the winter and *c.* 2600 during the summer. This is the equivalent of *c.* 4200 cattle present at any given time in the winter and *c.* 800 cattle present at any given time in the summer, mixed in with 350–400 bison all 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 behaviour, 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 (i) 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 (ii) 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 *c.* 160 km² 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.

Materials and methods

STUDY AREA

The Henry Mountains (HM) study area (Fig. 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

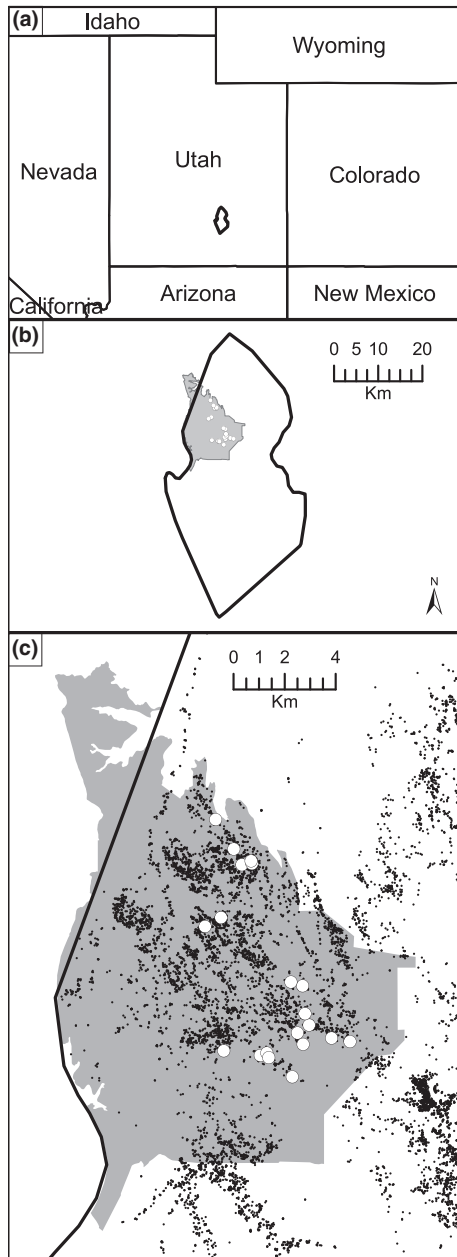


Fig. 1. Location of the Henry Mountain (HM) rangeland in the state of Utah (a); the Steele Butte North grazing allotment (grey), upon which the study was conducted, in relation to the HM, with the enclosure sites represented by white circles (b); the grazing allotment (grey), enclosure sites (white circles) and the bison GPS locations (black dots) collected during the enclosure study period (c).

(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. Local state and federal biologists estimate that the lagomorph population in the HM during the time of this study was below the peak of the popula-

tion cycle. The only large predators are mountain lions *Puma concolor* and coyotes *Canis latrans*, 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 & Bray (1986).

This study focused on the Steele Butte North grazing allotment (c. 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–shrubbyland 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 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. We scored the ratings (low = 1; high = 3) and then identified the median score within each response category.

In late October 2011, 20 enclosure sites were systematically selected on the Steele Butte North cattle grazing allotment (Fig. 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 neighbouring 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-h intervals (00:00, 06:00, 12:00, 18:00). Location data from these collars were used to ensure that selected enclosure 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 enclosures and their adjacent grazed reference plot were identical in layout. Sites had to be relatively rock free to allow for the construction of grazing enclosures.

At each selected site, two enclosures (each 5.95 m², i.e. 8' × 8') and one equal-sized reference plot were constructed 10 m apart (Fig. 2). Both enclosures 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 or 15.2 cm). At each site, one of these enclosures was skirted with finer mesh (2.54 cm diameter) poultry wire such that it extended 60 cm vertically up the side of the enclosure 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' enclosure was intended to exclude lagomorphs in addition to all large herbivores, while the other 'partial' enclosure was to exclude only large herbivores. The overall design was thus

Table 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

How do bison interact with cattle?			
Competition for forage	Competition for water		
Aggression or disturbance	Other (Please explain)		
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		
How much might these wildlife species compete with cattle?			
Mule deer	Bison	Jackrabbit	Other (Please explain)
Should the coyote population be controlled in the HM?			
Yes	No		
Which species benefit from coyote control in the HM area?			
Mule deer	Livestock	Other (Please explain)	

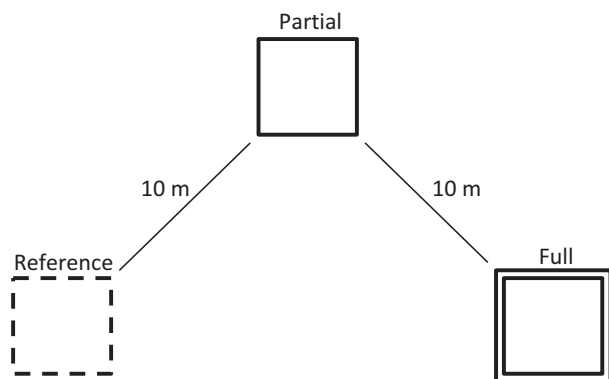


Fig. 2. The layout of each enclosure site is detailed with dashed squares representing open plots and solid squares representing excluded areas. All treatments, grazed reference plots or excluded areas, are 5.95 m² (i.e. 8' × 8'). The partial enclosure is designated by a single solid line and the full enclosure by a double solid line. All sites were erected in October 2011. The standing crop in both enclosures and the reference plot at each site were clipped in October 2012.

an experimental array of 20 study sites comprising a total of 40 enclosures (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 enclosures (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 km² 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 km² 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 enclosure was established and bison visitation at each site during the study period. RDI varies asymmetrically about 1, therefore log RDI was used in the statistical analysis. Given that >10% of the bison population was telemetered, we assumed the foraging patterns of these animals were representative of the bison population as a whole.

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 enclosure 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 enclosure types, with the response variable being the difference in clipped biomass between the enclosure plot and reference plot for each enclosure type. Given this response variable, the mean difference between full and partial enclosure types estimates the lagomorph impact on biomass, and the mean for the partial enclosure 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 (October 2011–April 2012 and May–October 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 $p_t N$ over the number of days d in the segment as follows (eqn 1):

$$BD = \sum_{t=1}^d p_t N \quad \text{eqn 1}$$

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 permit holders 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. The non-respondents included some cattle producers who are not resident in the HM area and so we assume they, together with some local ranchers with small herds, were comparatively less motivated to participate in the survey. Overall, bison were perceived by the respondents as a high-level competitor (median score = 3) against cattle in all seasons except winter, when they were perceived as a low-level competitor (median score = 1). The primary concern was over competition for forage (median score = 2.5), whereas competition for water and disturbance or aggression were of little concern (median score = 1). Lagomorphs were perceived as a low-level competitor (median score = 1) with cattle in all seasons. All respondents reported their perception that the coyote population should be controlled, as all believed it provides a high benefit to both mule deer and livestock, with one exception, who indicated the livestock benefit was medium.

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 enclosures and 43.7 (\pm 7.61) g m⁻² in the full enclosures (Fig. 3). The regression model found no evidence of the expected positive relationship between

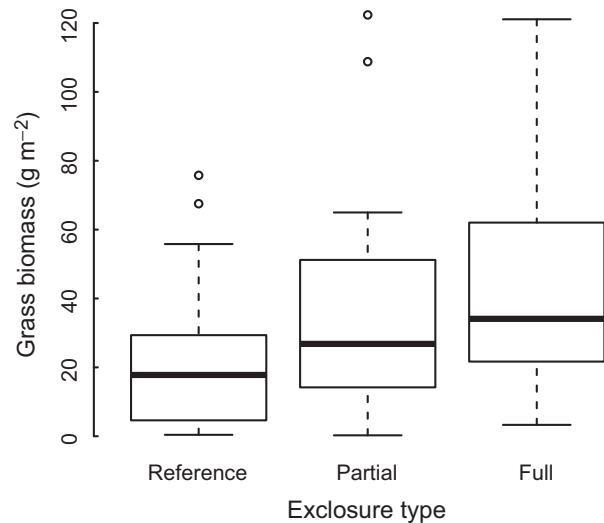


Fig. 3. Boxplots of grass biomass clipped to measure standing crop after 1 year for each of the treatment types ($n = 20$ per type): grazed reference plot; partial enclosure (cattle + bison out); and full enclosure (cattle + bison + lagomorphs out). Significant differences were found among all three 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 median, quartiles and $1.5 \times$ interquartile range. Circles show outliers beyond $1.5 \times$ interquartile range.

bison RDI and grass depletion across sites. Instead, a slight negative relationship was discovered, though not statistically significant ($P = 0.17$; Fig. 4), indicating the possibility of sward stimulation through a grazing-lawn effect. These results fail to support our *a priori* prediction (i) that site-specific bison visitation (RDI) should drive the variation in grass depletion across sites.

The exclusion of only large herbivores (partial enclosure) resulted in a 13.9 g m⁻² increase in grass biomass relative to the reference plots ($t_{19} = 2.93$, one-tailed, $\mu_{\text{partial}} > \mu_{\text{reference}}$, $P = 0.004$), with the additional exclusion of lagomorphs (full enclosure) resulting in a further increase of 7.18 g m⁻² of grass biomass (Table 2) relative to the partial enclosures ($t_{19} = 1.75$, one-tailed, $\mu_{\text{full}} > \mu_{\text{partial}}$, $P = 0.048$). Grass biomass in reference plots and both enclosure 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 ($R^2 = 0.53$) enclosures (Fig. 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 one 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

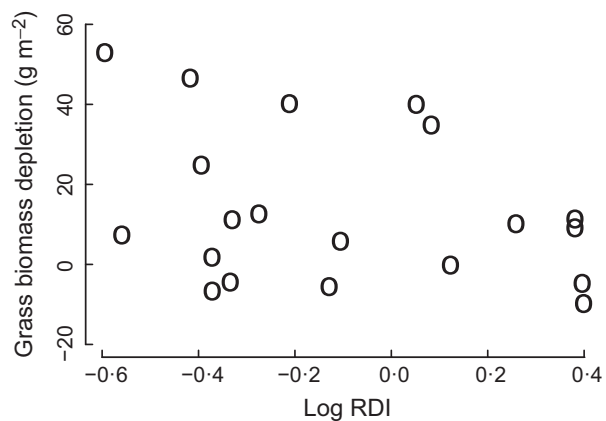


Fig. 4. Variation in site-specific grass depletion (difference in grass dry mass between reference plot and the partial enclosure at each site) is not explained by variation in bison visitation (log RDI) across sites ($P = 0.17$), contrary to the positive relationship expected by Prediction (i). Data points represent the difference in grass biomass (partial – reference) for each site.

study, 310 GPS locations out of 10 979 were located within the study area ($P = 0.028$). The 2012 segment had 5755 GPS locations out of 15 564 located within the study area ($P = 0.37$). Bison days (using eqn 1) were calculated as $BD = 21\,415$. Cattle days amounted to $CD = 81\,949$, as verified by the grazing permit holders 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 1 year. This result does not support our *a priori* prediction (ii) 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 estimate that the lagomorph population in the HM during the time of this study was in the low to 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, 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 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

Table 2. Mean increase in grass biomass (dry mass) relative to reference plots as a result of herbivore exclusion on the HM rangeland. Full enclosure 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

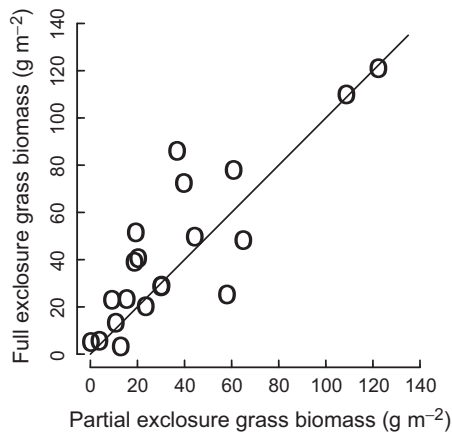


Fig. 5. Comparison of grass biomass (g m^{-2}) clipped in the partial and full exclosures for each of the 20 grazing exclosure sites plotted with a 1 : 1 reference line. Residuals above the line indicate the size of the lagomorph effect on grazing resources across exclosure sites.

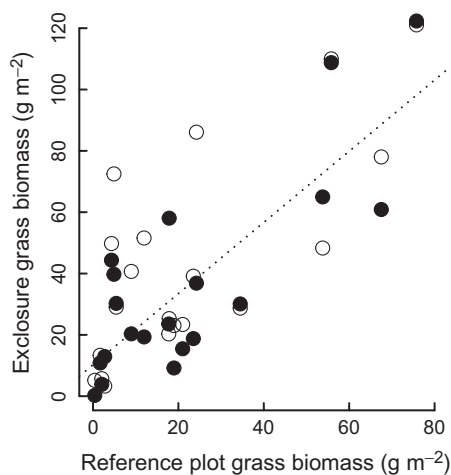


Fig. 6. Grass biomass (dry mass) clipped after 1 year in reference plots, plotted against partial exclosures (closed circles) and full exclosures (open circles). Values covaried across sites because of variation in site-specific productivity. Nevertheless, variation in grass biomass in reference plots 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.

reported. Lagomorphs represent one of the primary prey species for coyotes throughout the seasonal cycle (Rosen 2000; Bartel & Knowlton 2005); therefore, sustained suppression of the coyote population should increase jackrabbit densities (Henke & Bryant 1999). If predator removals were reduced or eliminated, lagomorph densities would 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 reductions in forage availability for cattle. Furthermore, they are not the predominant wildlife competitor with cattle for grazing resources. These results align with a concurrent study in the HM, which found that bison grazing caused no significant impacts on plant species composition (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). Bison and cattle exhibit spatial segregation on shared rangelands because bison range widely across the landscape, whereas cattle are central place foragers, usually focusing their grazing around water sources (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.

Acknowledgements

Funding was provided by the U.S. Fish and Wildlife Service and the Utah Division of Wildlife Resources with facilitation by Frank Howe. Field and logistical assistance was provided by Jake Thurston, Erin Wampole, Kent Hersey, Wade Paskett, Sue Fivecoat, David Cook, David Koons, and Pat Terletzky. David Koons, Peter Adler, Morgan Ernest and Frank Howe provided valuable comments on a previous draft.

Data accessibility

The data are available at the Utah State University research data repository: http://digitalcommons.usu.edu/all_datasets/6/.

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Received 28 July 2014; accepted 17 December 2014
Handling Editor: Matt Hayward