Wild bison as ecological indicators of the effectiveness of management practices to increase forage quality on open rangeland

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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 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 the foraging parameters of free-ranging bison are effective ecological indicators of rangeland quality for both bison and cattle.

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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 (Aro, 1971; Ansley and Castellano, 2006; Ansley et al., 2006). 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 consider using the foraging parameters of wild, free-ranging grazing herbivores as ecological indicators of habitat quality on open rangeland. 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 that spatially explicit variations in their foraging parameters should indicate the success (or not) of habitat manipulations intended to improve rangeland conditions for both bison and 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

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and Zollner, 1996; Wallis De Vries, 1996). Optimal foraging theory predicts that higher quality resource patches lead to larger group sizes (Schoener, 1971; Hirth, 1977) 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 Neuhaus, 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 and Lucas, 1970; Fretwell, 1972).

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, with fire return interval estimates ranging from every 8 years to no fire depending on the site (Anderson, 2002). In general, the fire return interval was likely <35 years (Paysen et al., 2000). These periodic fires 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 (Popov and Low, 1950; Nelson, 1965), the HM bison herd now numbers ~325 adults (post-hunt) and is controlled primarily by sport hunting. Bison hunting is typically broken into multiple seasons running from Nov. 1 to Jan. 31, such that there are no more than 20 hunters permitted to hunt in each season. There are both "hunter's choice" and "cow only" tags that specify what sex may be taken by the hunter. They may hunt anywhere within the HM hunting unit, though there are several areas that receive little to no hunting pressure due to limited access, effectively acting as refuges for the bison. 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 (~12% of the habitat available to bison) 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 (~2% of the habitat available to bison) 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.

BLM cattle grazing permits in the HM are quantified in AUMs (animal unit months; 1 AUM = grazing resources for 1 cow + 1 calf for one month) and there are ~25,600 AUMs permitted on the HM rangeland during the winter and ~2600 during the summer. This is the equivalent of ~4200 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.

2.2. Data collection

Satellite-download GPS telemetry collars were 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). 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. An additional 35 females were fitted with a traditional VHF collar in January 2011, bringing the total sample of monitored bison to 63 females and 19 males, or roughly 25% of the adult bison population. Effort was taken to ensure that the collars were distributed representatively among groups throughout the HM area. Both types of telemetry (VHF and GPS) were 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 min 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). Standing alert behavior was indicated by upright ears and eyes, while standing resting was the absence of either alert or ruminating behavior. Scans were conducted for up to 5 h, 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 subsamples 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 3 h of collection, whereas the endoparasite load sub-sample was refrigerated until analysis could be completed in the field, generally within 5 h 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 root 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).

To determine the effects of habitat selection in relation to habitat availability and the potential influence of roads on bison distribution, we used a resource selection function framework (Manly et al., 2002) with aspect, elevation, slope, distance to road, distance to water, and landcover type as covariates. A generalized linear mixed model (GLMM) with a random effect for individual allowed for interpretation of selection between sexes (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. All statistical analyses were performed in R version 3.0.2. (2013), with 'vegan' version 2.0-10 (2013) used for MRPP.

3. Results

A total of 198 bison groups were observed during the study period (Table 1). Of those, complete herd composition was obtained for 110 groups. Approximately 170 h of behavioral observations were obtained from 125 groups. BC was determined for 63 groups.
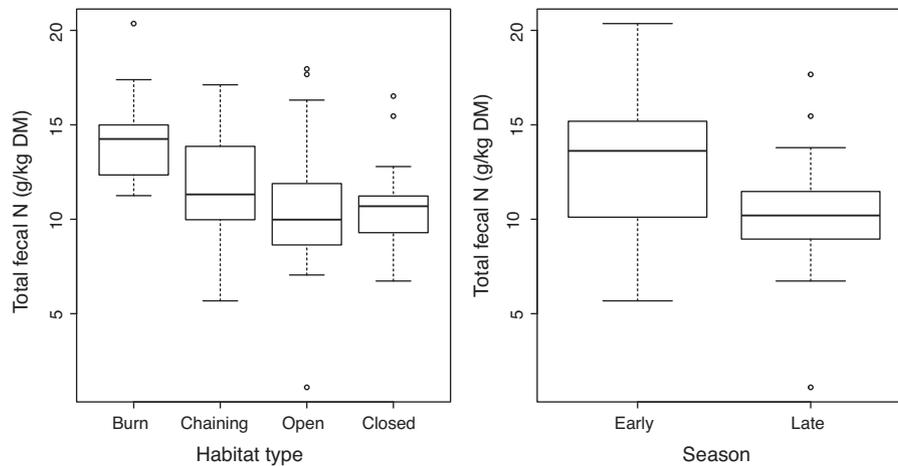
Fig. 1. Bison total fecal N (g kg^{-1} dry matter) for four habitat types (burn, chaining, closed, and open) and 2 seasons (early: January–June, and late: July–December) in the Henry Mountains of S. Utah, as determined from 126 fecal samples collected from 39 different groups of bison from May 2012–April 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 median, quartiles, and 1.5× interquartile range. Circles show outliers beyond 1.5× interquartile range.

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 ± SE) was higher (12.8 g kg^{-1} ± 0.50) than in the late season (10.2 g kg^{-1} ± 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 (Fig. 1). Burned habitats showed the highest (mean ± SE) fecal N concentrations (14.4 g kg^{-1} ± 0.81), followed by chainings (11.7 g kg^{-1} ± 0.49), closed (10.6 g kg^{-1} ± 0.44) and open (10.5 g kg^{-1} ± 0.37) habitat types.

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

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. 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 (mean ± SE = 67.4% ± 6.79%) devoted to feeding compared to chained (75.5% ± 3.75%), open (78.8% ± 2.80%), and burned (91.6% ± 4.07%), 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. 2). 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.

The resource selection functions indicated that, when controlling for habitat type, elevation, slope, aspect, and distance to water,

Table 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.

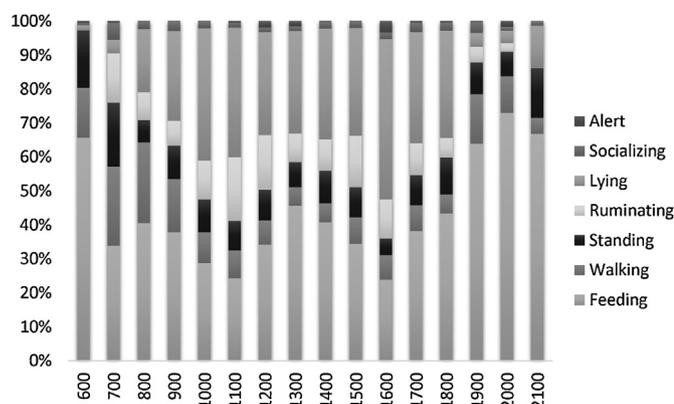| Bison variable	Season		Habitat				Total
	Early	Late	Burn	Chaining	Open	Closed	
Group size	62	136	10	56	96	36	198
Group composition	30	80	2	39	56	13	110
Activity	33	92	5	39	64	17	125
Fecal N	45 (18)	81 (22)	11 (4)	32 (16)	58 (14)	25 (6)	126 (40)
Fecal parasite load	53 (17)	97 (22)	10 (3)	53 (16)	62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

Fig. 2. Diurnal bison activity pattern as determined by herd activity scans from ~170 h 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.

bison showed a significant ($p < 0.001$) preference for areas further from roads. However, this did not seem to influence the types of habitat used. Burned and chained habitats were preferred by bison above all other habitat types.

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 (Krasinski and Krasinska, 1992; Krasinska and Krasinski, 2007). 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 (Krasinski and Krasinska, 1992; Krasinska and Krasinski, 1995).

African buffalo (*S. 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). 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 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. This was mirrored in the rankings of the resource selection functions at the habitat scale.

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. 1), but lower body condition and higher parasite load, with smaller and more sexually segregated groups compared with the larger and more mixed groups in the late season. The mixed message from the physiological indicators in the early season likely reflects 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.) also influence 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, and the higher preference we detected at the habitat scale from the resource selection functions, are 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 foraging parameters can serve as ecological indicators of where grazing conditions are better, which is ultimately what rangeland managers need to know. Sampling by humans is unlikely to target the same plants and

plant parts selected by wild, free-ranging, locally adapted grazers, thus highlighting the value of using bison foraging parameters to indicate areas of high forage quality.

Bison in the HM meet the main assumptions of the ideal free distribution 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 (Popov and Low, 1950; Nelson, 1965); are sexually size-dimorphic and thus have different dietary tolerances, but little sexual segregation is observed in the HM (Ranglack and du Toit, in review), 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 ecological indicator 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 ecological indicator 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).

These results are also useful for creating management plans for bison in areas where they are being restored, such as the Book Cliffs (Utah), Badlands National Park (South Dakota), and various Indian reservations and private lands (e.g. in Montana). We have shown that burning creates higher quality foraging areas than mechanical treatments, and that bison can continue to respond to such habitat enhancement for at least 10 years post-burn. A pyric-herbivory management construct (Fuhlendorf et al., 2008) could be used to attract bison to certain foraging areas and away from others. This offers the potential to minimize conflict between reintroduced bison and other interests such as cattle grazing, which is spatially constrained by proximity to water. These treatments are expected to increase landscape heterogeneity, thereby increasing biodiversity and conserving ecosystem function (McGranahan et al., 2012). The conservation value of such treatments have been demonstrated for cattle (Limb et al., 2011), macroinvertebrates (Doxon et al., 2011) and small mammal communities (Fuhlendorf et al., 2010), showing that these practices have broader applicability and conservation value than to just bison grazing systems.

Acknowledgements

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