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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.

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