DIET, GUT MICROBIOTA, AND MANAGEMENT OF AMERICAN BISON (*Bison bison*) IN CONSERVATION AND COMMERCIAL HERDS OF THE GREAT PLAINS

by

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Thesis directed by Associate Professor Noah Fierer

ABSTRACT

Because American bison (*Bison bison*) are important to both conservation and ranching, I inquired as to the diet and gut microbiota of these animals, and the implications of these factors for sound management. I found that bison in Kansas browsed more in spring and fall, and consumed more forbs during summer, but graminoids formed a consistently low proportion of the diet. In Colorado, the bison diet was dominated by graminoids, followed by forbs, then browse. This pattern remained consistent for 18 months, despite a brief increase in forbs and decrease in graminoids when the herd's pasture was enlarged. Comparisons among sites from May-August showed significant differences, with bison in Montana and Kansas consuming more forbs and browse than those in Colorado during certain months. Thus, the diet of bison was temporospatially variable and sometimes deviated significantly from grazing, possibly due to 1) plants that are high in protein and low in toxins; 2) large body size dictating less forage selectivity; 3) a lack migration; and 4) broad niche breadth. The present study suggests that bison may benefit from access to forbs and browse in addition to grasses. I also compared gut microbiota along the digestive tract between grass-finished and grain-finished bison. Location had the greatest effect, with sections of the foregut, the hindgut, and to a lesser degree the midgut being statistically similar. I also found a significant effect of diet on gut microbiota throughout the digestive tract, with the grain-finished bison exhibiting higher relative abundances of the bacterial phyla Firmicutes and Proteobacteria. Finally, my analysis of the natural and human history of the Great Plains shows that bison and other animals, as well as new energy sources, have the potential to foster both ecological and economic sustainability in the region to a greater degree than the system currently in place.

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CHAPTER I

Seasonal shifts in diet and gut microbiota of the American bison (*Bison bison*)

Abstract

North American bison (*Bison bison*) are becoming increasingly important to both grassland management and commercial ranching. However, a lack of quantitative data on their diet constrains conservation efforts and the ability to predict bison effects on grasslands. In particular, we know little about the seasonality of the bison diet, the degree to which bison supplement their diet with eudicots, and how changes in diet influence gut microbial communities, all of which play important roles in ungulate performance. To address these knowledge gaps, we quantified seasonal patterns in bison diet and gut microbial community composition for a bison herd in Kansas using DNA sequencing-based analyses of both chloroplast and microbial DNA contained in fecal matter. Across the 11 sampling dates that spanned 166 days, we found that diet shifted continuously over the growing season, allowing bison to take advantage of the seasonal availability of high-protein plant species. Bison consumed more woody shrubs in spring and fall than in summer, when forb and grass intake predominated. In examining gut microbiota, the bacterial phylum *Tenericutes* shifted significantly in relative abundance over the growing season. This work suggests that North American bison can continuously adjust their diet with a high reliance on non-grasses throughout the year. In addition, we find evidence for seasonal patterns in gut community composition that are likely driven by the observed dietary changes.

Introduction

North American bison (*Bison bison*) are a keystone species in the grasslands of the Great Plains, where their feeding, migration, and wallowing activities promote plant diversity (Knapp et al. 1999). Bison are considered primarily grazers, meaning they consume mostly graminoids (grasses and sedges) (Peden et al. 1974; Reynolds et al. 1978; Coppedge et al. 1998; Van Soest 1994). The bison diet varies across different geographic regions, depending on the type and abundance of potential forage available. For example, in northern habitats, bison diets are dominated by cool-season graminoids (H. Reynolds, Hansen, and Peden 1978). Yet bison may also browse, feeding on shrubs such as *Salix* as their primary forage when graminoids are scarce (Waggoner and Hinkes 1986; Painter and Ripple 2012).

In general, herbivores have been shown to prefer fresh shoots, because they are often lower in plant secondary compounds and richer in protein, making such plants more palatable, easier to digest, and more nourishing (Albon and Langvatn 1992; Villalba, Provenza, and Bryant 2002; Villalba et al. 2004). Phenologically driven pursuit of new growth was first observed in geese (R. Drent, Ebbinge, and Weijand 1978; RH Drent et al. 2007; Graaf et al. 2006; van Wijk et al. 2012), and then in deer (Smallidge et al. 2010; Sawyer and Kauffman 2011; Bischof et al. 2012; Albon and Langvatn 1992). Bison prefer newly produced shoots as well, including those on mowed areas (Larson and Murdock 1989), burned areas (Coppock and Detling 1986; Coppedge and Shaw 1998; Schuler et al. 2006; Biondini et al. 2013), and prairie dog towns (Coppock et al. 1983; Coppock et al. 1983; Krueger 1986). Despite their historic keystone role in North American grasslands, little is known about how the bison diet changes seasonally. Bison have been observed exhibiting seasonal variation in diet, continuing to feed on graminoids (Reynolds et al. 1978; Fortin et al. 2002), but also incorporating forbs, woody plants, and even lichen into their diet (Larter and Gates 1991). These temporal shifts in the bison diet are likely due to the changing nutritional quality of plants, and likely important to understanding the health of bison, as well as the impacts of bison on grassland ecosystems.

Along with our poor understanding of the seasonal patterns of bison diet, we do not know if bison gut microbial communities shift in response to changes in diet. Like all ruminants, bison rely on symbiotic microbes to help them digest vegetation (Varel and Dehority 1989). Digestion begins in the reticulorumen, and continues in other parts of the digestive tract, concluding in the colon (Van Soest 1994). Domestic cattle (*Bos taurus*) on pasture or forage retain a diverse, benign gut microbiota associated with a healthy digestive tract. The few studies on the seasonal patterns of gut microbiota in wild herbivores have found changes in gut community composition that are associated with changes in diet (Schwab et al. 2011; Dittmer et al. 2012). If changes in gut microbial communities are associated with dietary shifts in bison, this would suggest that microbes respond to changes in nutritional quality, antinutritional secondary metabolites, or plant species composition of the diet (de Menezes et al. 2011; K. D. Kohl and Dearing 2012; McCann, Wickersham, and Loor 2014).

Understanding seasonal variation in plant consumption will increase our understanding of bison’s dietary needs. Documenting concurrent shifts in gut microbiota will help us establish baseline rates of change in gut community composition throughout the year, and assess whether microbial shifts are associated with dietary changes. In order to better understand seasonal patterns of diet and gut microbial community composition, bison fecal material was collected from adult and subadult bison in a Kansas prairie approximately every 14 d during the growing season. An herbivore’s diet is affected by both plant availability and forager preference for different plant species (White and Trudell 1980; Odo, Omeje, and Okwor 2001; Udeh, Isikwenu, and Obika 2013), so both plant availability and the preferences of bison will affect the amounts of different plants ultimately consumed by bison. However, computing preference indices requires assessing plant abundance and dispersion in the environment (W. C. Krueger 1972; Vreede et al. 1989). Diet and gut microbial community changes over time were reconstructed using DNA sequencing-based analyses of both plant chloroplast DNA and the 16S rRNA gene of bacteria and archaea. These data were used to address two main questions: to what degree does the bison diet change throughout the growing season, and do temporal changes in diet drive corresponding shifts in gut microbial community composition?

Materials and Methods

Study design

The Konza Prairie Biological Station is a private 3,487-ha native tallgrass prairie preserve in the Flint Hills of northeastern Kansas (39.08 N, 96.57 W). American bison (*Bison bison*) were reintroduced to the preserve in 1987, and now about 300 of them live in a fenced range of about 970 ha. To study their diet and gut microbiota, fecal samples were collected every other week from adult and subadult bison (three male and three female) during the period of April 17 – September 30, 2011. Samples were collected from the first individuals observed to defecate during each collection trip, which may or may not have been the same individuals from one trip to the next. Fecal samples were sampled 48 times and divided into two demographic groups: 24 adult or subadult males, and 24 adult or subadult females. Collectors waited at a distance for the bison to defecate, and once they moved away, fresh fecal material was sampled with an inverted plastic bag, taking care to avoid contamination from soil underneath. Fecal samples were transported on ice, and stored at -20°C. Because only bison fecal material and vegetation were collected for the present study, no Institutional Animal Care and Use Committee (IACUC) approval was required. John Briggs, Director of Konza Prairie Biological Station, was the authority who reviewed our procedures and granted us permission to collect samples.

Diet analyses

We used analyses of plant chloroplast DNA in feces to infer which plant species the bison had consumed, and to track changes in these plants' relative abundance in the diet over time. This method, known as the *trn*L approach (Valentini et al. 2009), uses the P6 loop of the *trn*L (UAA) intron to assay diet in herbivores (Kowalczyk et al. 2011). We used the *trn*L g-h primer pair, whose targeted gene region is only 10-146 bp long, making it likely that the gene region can be amplified and sequenced from feces after passage of the plant material through the bison gut. The amplified region is also highly variable, so it can be used to differentiate many plant species (Taberlet et al. 2007). An identical approach has been used previously for non-invasive analysis of herbivore diet (Frey et al. 2010; Romero-Pérez et al. 2011; de Oliveira et al. 2013).

To match the *trn*L sequences to plant species, we created a *trn*L reference library for the site by acquiring representative samples of 73 plant species to which the bison had access. Single specimens of plants were collected in the field and placed in sealable plastic bags. They were identified and stored in the freezer at -20°C. To extract DNA from plants, vegetation samples were finely chopped with a sterile razor prior to DNA extraction. To extract DNA from bison feces, sterile swabs were dipped in thawed fecal samples before also being placed in reaction wells. For both sample types, DNA was extracted using the MO BIO PowerSoil®-htp 96 Well Soil DNA Isolation Kit (Lauber et al. 2008).

To amplify the *trn*L fragment from the plants and fecal samples for barcoded pyrosequencing, we followed (Lauber et al. 2009), except with the primer pair g-forward/h-reverse, which targets the *trn*L fragment (Taberlet et al. 2007). The forward primers included the Roche 454-B pyrosequencing adapter, while the reverse primers included the Roche 454-A sequencing adapter and a 12-bp barcode that was unique to each sample. Amplicons from the triplicate reactions were combined, cleaned, quantified, and pooled in equimolar concentrations. The pooled sample was sent to the University of South Carolina for sequencing on a Roche 454 automated sequencer.

Sequence data were processed using the QIIME pipeline (Caporaso et al. 2010). Sequences were assigned to specific plant samples based on their unique barcodes, and sequences were clustered at 100% similarity for each plant species. A reference library of *trn*L sequences was constructed using consensus sequences from identified plant specimens. For plants with at least 10 representative sequences, the consensus sequence was the one that made up at least 40% of sequences in a given sample, and was at least 30% more abundant than the second-most common sequence. As some of the plant species shared identical *trn*L sequences, our collection of 73 plant species was represented by 44 *trn*L sequences, with 32 species (44%) having unique representative sequences. For the remaining 41 plants (56%), two or more species shared sequences, meaning they could not be distinguished if detected (Valentini et al. 2009). The *trn*L sequences from fecal samples were matched against this *trn*L reference database using the BLAST algorithm at ≥ 98% similarity over the entire length of the reference sequence (Altschul et al. 1990).

Because different fecal samples have different *trn*L sequence counts, we rarefied down to 50 sequences, to compare all samples at an equivalent sequencing depth. Chloroplast *trn*L sequences in feces might be affected not only by the abundance of plants from which they came, but also by chloroplast and gene copy number in living plants, and by the digestibility of plants in the herbivore digestive tract. Thus, the sequence of *trn*L genes in feces depends not only on the plant species consumed, but also on the density of chloroplasts in the plant biomass, and the degree to which chloroplasts of different species are digested. One feeding trial demonstrated no consistent bias between the percentage intake of biomass and percentage of sequences in fecal matter of sheep (Willerslev et al. 2014). Given that *trn*L is a chloroplast gene with no known variation in copy number in the chloroplast genome, we assume for the purposes of the present study that the percent of sequences recovered from fecal matter is proportional to the relative intake of chloroplasts from the different plant taxa. Thus, although the proportions of different plants in the diet may not correspond perfectly to proportions of different *trn*L sequences in feces, the *trn*L approach allows us to document relative changes in the composition of specific plant taxa over time (Willerslev et al. 2014).

Microbial analyses

We also used the collected fecal samples to track shifts in gut microbiota across the sampling period, and to assess if the changes in gut microbial communities are associated with temporal shifts in diet. We sequenced a portion of the 16S rRNA gene from bison fecal DNA to study bacterial and archaeal community composition in the colon. Fecal DNA was extracted as described above. Amplification and sequencing followed the approach used previously (Lauber et al. 2009). Briefly, we used the 515F/806R primer pair containing Illumina adapters, with a 12-bp error-correcting barcode unique to each sample on the reverse primer. The V4–V5 region of the 16S rRNA gene amplified by this primer set is well-suited to accurate phylogenetic placement of bacterial and archaeal sequences (Liu et al. 2007). Together, these primers are expected to amplify nearly all bacterial and archaeal taxa with few biases (Bergmann et al. 2011).

After quantification and pooling, the amplicons were sequenced on an Illumina MiSeq instrument at the University of Colorado Genomics Core Facility with the 2 × 100 bp paired-end protocol (Caporaso et al. 2011). We used the QIIME pipeline for data analysis on the forward reads only (Werner et al. 2012). Quality filtering and processing of reads was performed following (Caporaso et al. 2011). Bacterial 16S rRNA sequences were clustered at 97% similarity, and a representative sequence from each OTU was classified against the RDPII database (Cole et al. 2007). Due to unequal numbers of 16S rRNA sequences in each fecal sample, we rarefied down to a depth of 15,000 sequences to compare all samples at an equivalent sequencing depth.

Statistical analysis

To test the effect of time on diet, plants were grouped into three functional groups, corresponding to the following growth habits: graminoids (grasses and sedges), forbs (non-graminoid herbaceous plants), and woody vegetation (shrubs and trees). A small number of *trn*L sequences (≤ 2%) could not be distinguished between forbs and graminoids, and were not included in downstream analysis. OTU tables for both *trn*L data and the 16S rRNA data were square root-transformed, and the Bray-Curtis method was used to generate distance matrices for multivariate statistical analysis, namely principal coordinates analysis (PCoA) and PERMANOVA in the PRIMER 6.1.12 & PERMANOVA + 1.0.2 software package (Leff and Fierer 2013). PERMANOVA indicated that diet and gut community composition were not significantly different between the sexes or between adults and subadults (P = 0.53), so we combined all these non-calf bison prior to further analysis. We used repeated measures ANOVA with Bonferroni correction to test for the effect of time on the relative abundance of the three plant functional groups, the ten most abundant plant species, and the three most abundant microbial phyla using the Tukey's Honest Significant Difference (HSD) post-hoc test (R. H. Green 1993; Zar 2009). We used linear regression to test the relationship between the proportions of plant functional groups and microbial phyla. Finally, we fit quadratic curves to the mean proportions of each plant growth habit over the growing season in the bison diet. Repeated measures ANOVA, Tukey's HSD, linear regression, and quadratic fitting were all conducted in the R statistical package (R Core Team 2014).

Results

Diet

Across 11 sampling dates spanning 166 days, analysis of bison feces revealed 44 unique *trn*L sequences, representing up to 73 different plant species in the bison diet. Dietary composition varied seasonally ($P < 0.001$, Figure 1.1). The four most abundant clusters (groups of species with a single *trn*L sequence) were the *Achillea* forb cluster (*Achillea millefolium, Chloris verticillata*), the *Ageratina* forb cluster (*Ageratina altissima, Ambrosia artemisiifolia, Ambrosia psilostachya, Ambrosia trifida, Antennaria neglecta, Echinacea angustifolia, Helianthus maximiliani, Helianthus tuberosus, Ratibida pinnata, Silphium laciniatum, Taraxacum officinale*, and *Euphorbia corollata*), the *Andropogon* graminoid cluster (*Andropogon gerardii, Bothriochloa bladhii, Bothriochloa laguroides*, and *Schizachyrium scoparium*), and the *Oligoneuron* forb cluster (*Oligoneuron rigidum, Solidago canadensis,* *Solidago missouriensis*, *Solidago speciosa*, *Symphyotrichum ericoides*, and *Symphyotrichum laeve*). Plotting the relative abundance of plants by growth habit over time (Figure 1.2), bison consumption of woody vegetation was greater early and late in the growing season than in mid-season ($P < 0.001$, quadratic fit: $y = 0.55 - 0.0025*DOY + 7.31*10^{-5}*(DOY-178.2)^2$; DOY = Day of Year). *Ceanothus herbaceus,* an actinorhizal N_2-fixing shrub, was the primary woody species consumed. This species exhibited a significant change in proportion over the growing season ($P < 0.001$), contributing on average as many as 56% of the sequences in the spring and 60% in the fall.

Consumption of herbaceous species peaked in the middle of the season (Figure 1.2, $y = 0.44 + 0.0024*DOY – 7.3*10^{-5}*(DOY-178.2)^2$; $P < 0.05$). At their greatest relative abundance, 84% of the sequences on average could come from forbs. *Lespedeza violacea,* a legume, was the most abundant forb during the summer. Its proportion in the diet also changed significantly over time ($P < 0.05$), with as many as 77% of the dietary sequences on average coming from this species. The *Oligoneuron* cluster was another predominant group of forbs to exhibit significant temporal change ($P < 0.05$). The percentage of sequences derived from grasses was never higher than 12% on average, and grasses were consumed more in summer than in spring or fall ($P < 0.001$, Figure 1.3). The *Andropogon* cluster was the most abundant of the graminoid *trn*L clusters, but individually it did not show significant change over time ($P > 0.1$).

Gut microbiota

Using 16S rRNA gene sequence data, we identified 46,061 bacterial species, 355 archaeal species, and 7 unclassified microbial species in the sampled bison during the growing season. Gut microbial community composition varied over time ($P < 0.001$, Table 1.1 and Figure

1.1). The three most abundant microbial phyla were *Firmicutes* (53% of sequences on average), *Bacteroidetes* (33%) and *Tenericutes* (4%). The *Firmicutes* phylum was dominated by taxa within the *Clostridiales* order, while taxa within the *Bacteroidetes* order were the dominant *Bacteroidales*. Finally, *Tenericutes* consisted entirely of taxa within the *Mollicutes* class, which was comprised entirely of the putative order RF39 (Table 1.1). Although there was no significant relationship between the proportion of sequences from graminoid, forb, or woody plants and the relative abundance of *Firmicutes*, *Bacteroidetes*, or *Tenericutes* ($P > 0.05$), the phylum *Tenericutes* exhibited significant temporal change in relative abundance over the growing season, increasing more than twofold from about 2% of the gut microbial community in April to about 5% in May ($P < 0.001$, Table 1.1 and Figure 1.4).

Discussion

Diet

Bison are considered to be primarily grazers (Peden et al. 1974; Reynolds et al. 1978; Coppedge et al. 1998), but in this study the proportion of grass chloroplast sequences recovered from fecal samples was relatively low during the summer. This could imply that the proportion of chloroplasts ingested from grass biomass was relatively low. The present study did not quantify forage availability or compute preference indices, but previous research has shown good correspondence between the relative amounts of biomass and sequence abundances in feeding trials (Willerslev et al. 2014). However, the relatively low percentage of grass *trn*L sequences could be due to preferential degradation of grass DNA during passage through the gastrointestinal tract. Alternatively, differences in protein concentration among plants are likely to be associated with differences in chloroplast density, so high-protein plants could be overrepresented in the *trn*L libraries relative to biomass intake. Further research is needed to determine if the proportion of *trn*L sequences in fecal material accurately reflects the consumption of the respective plants. Because some plant species could not be distinguished using the current method, future work could improve taxonomic resolution by using a different *trn*L primer pair than g-h, such as c-h or c-d, which produce longer sequences (Taberlet et al. 2007), or by incorporating additional loci, such as *rbc*L, into the identification system (Jurado-Rivera et al. 2009; García-Robledo et al. 2013). Nevertheless, we can use the data presented here to assess changes in the relative intake of plant taxa over time.

Our results from *trn*L sequencing indicate that plains bison at Konza shift their diet among high-protein plant species seasonally. In the spring and fall, intake of *Ceanothus herbaceus*, an N_2-fixing shrub, is relatively high. During the summer, bison consumption of N_2-fixing legumes like *Lespedeza violacea* and *Mimosa nuttallii* peaks (Figure 1.3). This pattern may be driven by plant phenology, as changes in the inferred diet of the bison roughly corresponded to plant phenology at this site (Craine et al. 2012). Herbivores generally prefer to feed on new growth, because fresh shoots of a given type of plant are higher in moisture and nutrient content (including protein), and lower in fiber and secondary metabolites, making them both more palatable and more nutritious, even for grazers (Craine 2009). The bison's diet was likely influenced by both the availability of and preference for nutritious vegetation (Fortin, Fryxell, and Pilote 2002; Fortin et al. 2003), with the bison appearing to favor high-protein plant species and life stages (D. Coppock et al. 1983; Larter and Gates 1991; Willerslev et al. 2014).

Many ruminants in both the Afrotropic and Holarctic ecozones exhibit seasonal variation in plant consumption (Watson and Owen-smith 2002; Tshabalala, Dube, and Lent 2009; Van Der Merwe and Marshal 2012; Hjeljord et al. 1990), and ruminant species that do not change diet with the seasons change location instead (Bischof et al. 2012; John F. Wilmshurst et al. 1999; J F Wilmshurst, Fryxell, and Bergman 2000; Pettorelli et al. 2005). Domestic cattle (Ganskopp and Cruz 1999), European wisent (*Bison bonasus*) (Mysterud et al. 2007), and North American bison (Schuler et al. 2006; Fortin and Fortin 2009) are all among the temperate ruminants that take advantage of preferred vegetation during the summer, and tolerate suboptimal vegetation during the winter. Our results appear to corroborate this pattern in bison. Fresh shoots of forbs and graminoids in summer are likely relatively high in protein and relatively low in secondary metabolites (Craine 2009; Glasby 1991; Palo and Robbins 1991). Woody shrubs selected in spring and fall, such as *Ceanothus*, are potentially high in secondary metabolites (Glasby 1991; Palo and Robbins 1991; Kie 1986), but also high in protein (Ahmed E Sidahmed, Morris, and Radosevich 1981; A E Sidahmed et al. 1983; Beck and Peek 2005). Thus, like other ruminants (Christianson and Creel 2013; Gad and Soorambail 2011; Renecker and Hudson 1986), bison appear to exploit more nutritious forage during the growing season, but still accept less nutritious forage outside the growing season (Fortin et al. 2003; Larter and Gates 1991).

The relative abundance of eudicots in the bison diet raises questions about the degree to which bison should be considered obligate grazers (Hofmann 1989; Coppedge et al. 1998; Coppedge et al. 1998). Their broad mouth, massive shoulders, and low-slung head allow them to crop vegetation close to the ground (Shrader, Owen-Smith, and Ogutu 2006; Waldram, Bond, and Stock 2007; Steuer et al. 2010), and their large reticulorumen facilitates digesting large amounts of low-nutrient graminoids (Hudson and Frank 1987). However, our work shows that North American bison, like wisent and cattle, supplement their diet with more nutritious forbs and woody species throughout the growing season. *Bison* and *Bos* species, like their common ancestor *Leptobos*, have adaptations for grazing (Palmqvist et al. 2003). However, today’s plains bison subspecies (*B. bison bison*) is thought to have a more grass-dominated diet than fossil *Bison* populations (Feranec 2004; Widga 2006), the contemporary wood bison subspecies (*B. bison athabascae*) (Rivals, Solounias, and Mihlbachler 2007), and European wisent (the closest living relative of the American bison species). Yet this does not mean that plains bison do not browse or utilize non-graminoids (Kowalczyk et al. 2011). The molecular evidence presented here suggests that the dependence of *Bison* species on grasses might be more labile than previously thought.

Microbiota

As in other mammals, *Firmicutes* and *Bacteroidetes* were the most abundant bacterial phyla in the bison digestive tract (De Filippo et al. 2010; Abdallah Ismail et al. 2011; Tilg and Kaser 2011). As in other studies showing that gut microbial community composition can be structured by diet (Ley, Hamady, et al. 2008; Ley, Lozupone, et al. 2008; Muegge et al. 2011; Yatsunenko et al. 2012), we found correspondence between major microbial phyla and dietary composition. In the change from spring to summer, *Tenericutes* became significantly more abundant ($P < 0.05$, Table 1.1 and Figure 1.4). This increase may be driven by members of this phylum that preferentially metabolize simple sugars (Manurung 2012), which could have been associated with higher caloric and protein yields in the bison diet during summer and fall (Craine et al. 2013). Together, these results highlight that there are subtle but significant shifts in gut bacterial community composition that correspond to seasonal changes in the bison diet. The changes we observed are unlikely to be due to the influx of bacteria adhering to ingested plant matter, for although some microbes (and their DNA) can survive passage through the digestive tract (David et al. 2014), the vast majority of dominant bacterial taxa in fecal samples are rarely found in the phyllosphere (see (Ley, Lozupone, et al. 2008) and (Redford et al. 2010)). Factors contributing to this difference include the harsh environment of the stomach (von Rosenvinge et al. 2013), differences between the enteric and ambient environments (Costello et al. 2012), and strong competition from established members of the gut microbial community in mature animals (Dethlefsen, McFall-Ngai, and Relman 2007; Stecher and Hardt 2011; Kamada et al. 2013). Thus, the shift in microbial communities observed here are most likely to reflect shifts in enteric communities more than phyllosphere communities.

Although we do not know the impact of this microbial community shift on bison health, the results of the present study indicate that gut microbial communities are not static, and that even presumably healthy animals can experience significant temporal variability in gut microbial community composition.

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CHAPTER II

Variability in the diet of American bison (*Bison bison*) and implications for their management

Abstract

American bison (*Bison bison*) were once common throughout the Great Plains, but due to overhunting in the 19th Century, today they are near-threatened and conservation-dependent. Bison are considered grazers, but we wanted to know to what degree their diet varies temporospatially among three sites within their former range: a central tallgrass prairie (Konza Biological Station, KZA), a central shortgrass prairie (Rocky Mountain Arsenal National Wildlife Refuge, RMA), and a northern shortgrass prairie (American Prairie Reserve, APR). We studied RMA for a period of 18 months (May 2012 – October 2013), as well as KZA and APR from May-August (2011 and 2013, respectively). To characterize the bison diet, we collected bison dung, sequenced the *trn*L chloroplast intron, and compared these sequences to a database constructed from plants collected at these sites, as well as *trn*L sequences from GenBank. At RMA, the bison diet was dominated by graminoids, followed by forbs, and lastly woody vegetation, and did not vary significantly over time. Significant differences were observed among sites for each plant type in each month. Thus, the bison diet appears to be broader and more variable than expected. This may be due to: 1) the bison's need to supplement its bulk diet with young forbs and browse, 2) the bison's large size and need to maximize energy intake, 3) the sedentary existence of modern bison, which contrasts with their historically migratory existence, and finally 4) the relatively low diversity of the North America's herbivore guild, which may give bison greater niche breadth than ungulates elsewhere in the world. The ability of

bison to exploit a variety of plants may allow managers to make different types of vegetation available to these animals, so that they can more easily maintain optimal nutrition and condition.

Introduction

Like most members of the tribe *Bovini*, today's *Bison* species – American bison (*Bison bison*) and European bison or wisent (*B. bonasus*) – are considered bulk/roughage feeders that forage predominantly on groundcover, or graminoids (grasses and sedges) and forbs, based on the findings of microhistological studies (Peden et al. 1974; Reynolds et al. 1978; Coppedge et al. 1998; Van Soest, 1994). However, DNA sequencing studies indicate that both of the extant *Bison* species supplement their diet by browsing on woody vegetation, or shrubs and trees (Kowalczyk et al., 2011; Kerley et al., 2012; Bergmann et al., 2015; Bocherens et al., 2015). As in other ungulates, this behavior likely allows bison to increase consumption of moisture, protein, and digestible cellulose from young shoots, and to decrease consumption of toxic alkaloids, tannins, and indigestible lignin from mature plant matter (Albon and Langvatn, 1992; Villalba et al. 2002; Villalba et al. 2004; Craine, 2009).

Historically, the range of American bison included all of the Great Plains and beyond (Isenberg, 2000; Gates et al. 2010). These animals numbered 20-30 million until the overkill of the mid-19th Century, when their population was reduced to fewer than one hundred (Hedrick 2009). This peak distribution and abundance could have been greater than pre-Columbian levels, when human predation may have consistently kept the bison population as low as one million (Kay 1998). Restoration efforts helped the bison population reach 20,000, and bison in conservation herds still number about that many today. However, since the 1970s, commercial bison ranching has allowed the overall population to grow beyond that former plateau, bringing the total to about 500,000 (Freese et al., 2007; Sanderson et al., 2008; Hedrick, 2009).

Today, although their wanderings are restricted, free-ranging bison once more occupy a variety of habitats around the Great Plains, from the southern and central plains to the northern plains, and from the eastern tallgrass prairie to the western shortgrass prairie, or steppe, on the high plains (where their numbers were once greatest). These represent a range of abiotic conditions, with more southerly areas being hotter and having a longer growing season compared to more northerly areas, and with the tallgrass prairie being more mesic and supporting a different community than the more arid shortgrass prairie (Samson and Knopf, 1996). Today, when bison are kept in a variety of environments throughout the Great Plains, it is a partial reconstruction of their formerly large range. Because bison are important to both prairie restoration (Knapp et al., 1999; Truett et al. 2001; Kohl et al. 2013) and diversified ranching (Renecker & Kozak, 1987; Torbit & LaRose, 2001; Butler et al. 2005; Sayer et al. 2012), understanding the nutritional needs of these animals is essential to their management and husbandry. So, we wanted to take advantage of the widespread distribution of bison to observe how their diet varies over space. In addition, we wanted to study a Colorado shortgrass prairie bison herd over time to assess any seasonal changes in diet that exist, much as we had done over the growing season in a Kansas tallgrass prairie bison herd (Bergmann et al. 2015).

Past research using microhistological methods has shown that bison are primarily grazers, with a diet that consists of about 98% graminoids (Coppedge et al. 1998). However, given our work at KZA (see Chapter I), which showed that bison may prefer forbs and browse for at least part of the year (Bergmann et al. 2015; Craine et al. 2015), we wanted to assess the diet of bison at other locations as well. Thus, we used three study sites with free-ranging bison. These were the Rocky Mountain Arsenal National Wildlife Refuge (RMA), a central shortgrass prairie site in Colorado (39.81 N, 104.88 W); the American Prairie Reserve (APR), a northern shortgrass prairie site in Montana (47.95 N, 107.78 W); and the Konza Prairie Biological Station (KZA), a central tallgrass prairie site in Kansas (39.08 N, 96.57 W). The questions we posed were as follows. One, does the diet of free-ranging bison at RMA change significantly over time to include appreciable levels (more than 2%) of forbs and browse? And two, does the diet of free-ranging bison differ significantly among the three sites in a given month, with bison consuming appreciably elevated levels (more than 2%) of forbs and browse in at least one site for at least part of the growing season? With respect to the temporal component of this study, we hypothesized that bison at RMA would exhibit a seasonal shift in diet. Specifically, we expected bison to graze more during the growing season, and to browse more during the winter. With respect to the spatial component of the study, we expected significant differences in diet over the growing season, with the bison diet including appreciable levels (more than 2%) of forbs or browse in at least one site for at least part of the growing season.

Materials and Methods

Sample collection

We collected bison fecal samples from the three study sites: the Rocky Mountain Arsenal National Wildlife Refuge in Colorado (RMA), the American Prairie Reserve in Montana (APR), and the Konza Prairie Biological Station in Kansas (KZA). For an earlier study, plant and fecal samples from KZA had been initially sequenced using the 454 GS FLX system. The present study used the Illumina MiSeq system (see “Sample processing” section below) to sequence plant and fecal samples from RMA and APR, so fecal samples from KZA were likewise re-sequenced using this same system for the sake of uniformity.

RMA is located near Denver, Colorado (39.82 N, 104.88 W). It is a Superfund cleanup site, having been converted from a chemical weapons manufacturing facility to a 6,470-ha federal wildlife refuge during the period of 1992-2010. In 2007, sixteen bison were introduced to a 567-ha fenced portion of the refuge. The herd had grown to more 80 animals by February 2013, at which time their pasture was enlarged to 1,295 ha. This adjustment took place about halfway through our study, and gave us the opportunity to look for any changes in the bison's diet as they began to occupy a new area. RMA is a shortgrass prairie undergoing restoration, with significant coverage of nonindigenous vegetation like field bindweed (*Convolvulus arvensis*) under grazing pressure from black-tailed prairie dogs (*Cynomys ludovicianus*), whose density at RMA was high during this study. We collected representative vegetation samples, as well as feces from free-ranging adult and subadult bison of both sexes. We sampled from May 10, 2012 to October 25, 2013 – a period of 532 days spanning 18 months – sampling once per month outside the growing season (November 2012-March 2013), and every other week in the growing season (all other months). This sampling duration is of value, because it spans two growing seasons. During each visit, we collected dung from at least four males and four females, observing the animals as they defecated, and then waiting until they moved away to sample their dung with a clean, inverted plastic bag, taking care to avoid contamination. Samples were collected from the first individuals observed to defecate during each collection trip, and it is not known whether these were the same or different individuals from one trip to the next. Fecal samples were transported on ice, and stored frozen at -20°C.

APR is located in northeastern Montana (47.81 N, 107.77 W). As of this writing, APR owns or leases over 123,000 ha of deeded and public land, with grazing privileges on over 25,000 ha in the adjacent Charles M. Russell National Wildlife Refuge – a total of more than 148,000 ha accessible for prairie restoration. Sixteen American bison (*Bison bison*) were reintroduced to APR in 2005, and the herd has since grown to about 500 individuals. To study their diet, fecal samples were collected every few weeks from May 5 – August 13, 2013 (six dates spanning 101 days). Fecal samples came from adult and subadult bison (up to eight male and eight female per day), and stored frozen. Only those fecal samples for which all metadata were complete were analyzed.

KZA is a private 3,487-ha native tallgrass prairie preserve in the Flint Hills of northeastern Kansas (39.08 N, 96.57 W). For KZA, we reanalyzed fecal samples from our previous study (Bergmann et al. 2015), in which samples had been collected every other week during the period of May – August 2011 from adult and subadult bison (three male and three female).

Fecal sample processing

Thawed fecal samples were swabbed for use in the DNA extraction protocol. We then performed DNA extractions on all samples, using the MO BIO PowerSoil®-htp 96 Well Soil DNA Isolation Kit, according to the method in (Lauber et al. 2008). Fecal plant chloroplast DNA was used to infer which species of vegetation the bison had eaten, and to track changes in their dietary relative abundance over the growing season. To amplify the *trn*L fragment from the plants and fecal samples for barcoded sequencing, we followed (Lauber et al. 2009) modified for the *trn*L approach (Valentini et al. 2009), which uses the P6 loop of the *trn*L (UAA) chloroplast intron to assay the diet of free-ranging bison (Kowalczyk et al. 2011), using the primer pair g-forward/h-reverse, which targets the *trn*L fragment (Taberlet et al. 2007). The targeted gene region is short (only 10-146 bp long), making it likely that it can be amplified and sequenced after passage through the digestive tract. The amplified region is highly variable, so it can be used to differentiate many plant species (Taberlet et al. 2007). However, differentiating among species is problematic within the grass family (*Poaceae*), as well as the sunflower family (*Asteraceae*). The forward primers included the Illumina pyrosequencing adapter, while the reverse primers included the Illumina sequencing adapter and a 12-bp error-correcting barcode unique to each sample on the reverse primer. Amplicons from triplicate reactions were combined, cleaned, and pooled in equimolar concentrations using the Invitrogen SequalPrep™ Normalization Plate Kit (96-well). The composite sample was taken to the University of Colorado Genomics Core Facility for sequencing on an Illumina MiSeq machine with the 2 × 100 bp paired-end protocol (Caporaso et al. 2011). We used the UPARSE pipeline for data analysis (Edgar 2013). Quality filtering and processing of reads were performed following (Caporaso et al. 2011).

Plant database

We used chloroplast *trn*L DNA sequencing to build a reference library of sequences of plants against which to match sequences from fecal samples to characterize the diet of the bison over the course of this study. Single specimens of plants were collected in the field and stored either frozen or air-dried, then finely chopped to release cell contents prior to use. As with the fecal samples, DNA was extracted from plant samples using the MO BIO PowerSoil®-htp 96

Well Soil DNA Isolation Kit (Lauber et al. 2008) and pooled using the Invitrogen SequalPrep™ Normalization Plate Kit (96-well).

We created a *trn*L reference database with 190 sequences representing 275 sampled plant species – some of which shared the same sequence with other species in the same genus or family – to which the bison had access at any of the three sites (KZA, RMA, and APR), as well as 77,254 sequences from GenBank (Altschul et al. 1990). Sequences were assigned to plant samples based on their unique barcodes, and sequences were clustered at 100% similarity for each plant species. Sequence data were processed using the UPARSE pipeline (Edgar 2013).

Statistical analysis

The relative read abundance (RRA) table of *trn*L functional taxa (individual plant species, or those that are congeneric or confamilial and share the same sequence) was square root-transformed, and the Bray-Curtis method was used to generate a distance matrix for multivariate statistical analysis, namely principle coordinates analysis (PCoA) and PERMANOVA in the PRIMER 6.1.12 & PERMANOVA + 1.0.2 software package (Leff and Fierer 2013). At RMA, PERMANOVA indicated that dietary composition was not significantly different between males and females ($P = 0.918$) nor between adults and subadults ($P = 0.544$). In comparing sites, we likewise found no effect of sex ($P = 0.928$) or age for a given site ($P = 0.294$). Therefore, all samples were combined for analysis. We used PCoA to assess segregation of samples by date in the RMA only time series, and to assess segregation among four months (May-August) for KZA.2011, RMA.2012, RMA.2013, and APR.2013. Months were chosen as independent variables because they are an arbitrary division of time that allowed us to compare sites using the same units.

We also used PERMANOVA to test for the effect of time on diet composition in our RMA time series, for the effect of time on diet in each of our sites, and for the effect of site during a given month. With the R statistical language, we used repeated measures (RM) ANOVA with the Tukey HSD post-hoc test to compare time points (dates or months) in the RMA time series, which spanned 18 months. Finally, we also used RM-ANOVA with Tukey HSD to compare months of May-August within each of the sites, and among these sites for each of these months.

Results

Sequencing

For our plant reference database we used 190 unique *trn*L sequences, representing 275 plant species at KZA, RMA, and APR. Of these, 147 (77.4%) were species-specific, while the remaining 43 (22.6%) were clusters of related species in the same genus or family that could not be distinguished by the *trn*L method. Analysis of bison feces revealed 419 functional taxa in the bison diet. Overall, most abundant plant family was grasses (*Poaceae*) making up on average 52.8% of the sequences, with a range of 0-100%. The second most abundant plant family overall in the bison diet was composites (*Asteraceae*), with an average relative abundance of 11.7% (0-87.6%). The third most abundant plant family overall was legumes (*Fabaceae*), whose average relative abundance was 6.1% (0-91.1%). Graminoid was the most abundant growth habit, with a mean of 53.7% of sequences overall (0-100%). Forb was the second-most abundant growth habit, with a mean of 29.25% of sequences overall (0-93.7%). Finally, browse (woody plants) was the least-abundant growth habit, with a mean of 15.88% of sequences overall (2-94.3%).

Rocky Mountain Arsenal

From June 20012 – October 2013, we monitored the relative abundance of plant functional taxa, and combined them into three growth habit categories in the diet of bison at RMA: forbs, graminoids, and browse (woody plants). We found that bison grazed more than they browsed, with graminoids on average making up 60.12% of the diet, forbs 27.88%, and woody plants 10.62%. PCoA showed no great segregation of the data, with most points falling within a large cluster. However, months common to both growing seasons did exhibit some overlap, especially in June. PERMANOVA indicated no significant differences between sexes or age classes (adults and subadults). RM-ANOVA testing for diet composition as a function of time by date, month, and year were all significant (Figure 2.1). Most nonadjacent dates were significantly different from one another, as were most nonadjacent months. Between years, similarly timed dates or months were often but not always significantly different. RM-ANOVA showed significant differences among times ($P < 0.001$), but no clear trend was visible from this analysis, as linear regressions for all plant types were significant but not highly correlated ($P < 0.05$, $R^2 < 0.05$), although a brief increase in forbs and decrease in graminoids was detected at the time the bison's pasture was enlarged in February 2013. As a measure of alpha diversity, we used the Shannon index. Again, although RM-ANOVA indicated significant differences among dates ($P < 0.001$), these data exhibited a mean value of 2.09 ± 0.52, with likewise no clear change over time ($P > 0.05$, $R^2 < 0.05$). No significant changes in diet were observed in February 2013 when the bison's pasture was enlarged, giving them access to a new area. It seems the bison continued to feed in much the way throughout the study, with groundcover making up the majority of the diet, and browse making up only the minority.

Site comparisons

We compared the bison diet during the growing season (May – August) of three years (2011, 2012, and 2013) at three sites (KZA, RMA, and APR) (Figure 2.2). PCoA showed rather distinct segregation among the three sites, with the two years of RMA clustering together, and receiving a small amount of overlap from APR (Figure 2.3). PERMANOVA indicated that there were significant differences among all sites in each month ($P < 0.001$). Repeated measures ANOVA showed a number of significant differences among sites each plant type in each month ($P < 0.001$). Forbs were significantly higher at APR in May and August. Graminoids were lowest at APR in each month and highest at RMA in May and June. Browse was variable, but often lowest at RMA. Shannon diversity was also variable, but often lowest at APR.

Discussion

Our estimates of diet composition are influenced by a number of factors. One is the relative read abundance (RRA) of certain plant taxa, but another is the proportion of chloroplasts ingested from certain plant taxa. Measuring forage availability and preference was beyond the scope of this study, but earlier studies have shown a strong relationship between biomass and sequence abundance for particular types of plants (Willerslev et al. 2014). Nevertheless, it is possible that the results of the present study were influenced by differential degradation rates of DNA from different plants in the bison digestive tract. Earlier microhistologically based studies may have also been biased, with less degraded plants being overrepresented upon microscopic viewing compared to more degraded plants. Moreover, protein concentration in plants may be related to chloroplast density, so our results could over-estimate the intake of high-protein plants like legumes. To improve the accuracy of sequencing-based herbivory studies, more research is needed to assess the relationship between actual plant biomass ingestion and *trn*L sequence RRA in dung. Some plant species could not be distinguished using the *trn*L method. In the future, taxonomic resolution could be improved by using a longer *trn*L primer pair (Taberlet et al. 2007), or by including other genes, such as *rbc*L, into the identification scheme (García-Robledo et al. 2013; Jurado-Rivera et al. 2009).

We were surprised by how relatively consistent diet was over time at RMA, and by how divergent diets were among the three sites of RMA, KZA, and APR. Our hypotheses were informed by our earlier work with bison at KZA, in which bison varied their diet during the growing season by grazing more during summer – consuming not only graminoids but also more forbs than expected – and browsing more during spring and autumn (Bergmann et al. 2015). Based on this result in Kansas, we expected to find a similar pattern in Colorado, but this was not the case. Instead, we found that the diet of bison at RMA changed very little over the course of 18 months. Diet diversity, as measured by the Shannon index, may have been somewhat lower during the winter, but there was no significant trend in graminoid, forb, or woody plant consumption. Bison at RMA grazed more than they browsed, with the diet dominated on average by graminoids (53.72%), followed by forbs (29.25%), and finally woody plants (15.88%). In this way, RMA bison conform to our historical understanding of this species as a year-round grazer (Peden et al., 1974; Reynolds et al., 1978; Van Soest, 1994; Coppedge et al., 1998). However, the percentage of graminoid in this study (about 54%) is much lower than that detected in earlier, microhistologically based studies (about 98%). For this reason, it may be reasonable to think of bison not so much as grazers, but rather as “adaptive specialist” grazers (Cannon 2001), or perhaps even mixed feeders for at least part of the year.

We also compared bison diet among sites during the months of May-August. Although some differences existed, diet was similar between years at RMA, again with bison primarily grazing. As in our earlier study (Bergmann et al. 2015), bison at KZA browsed more earlier in the season, then increased their grazing in the following months. The greater consumption of forbs at APR in May and August was unexpected, as bison are thought to select more forbs in warmer, southern locations like KZA (Craine et al. 2015). Bison at RMA often consumed more graminoids and less browse than those at the other two sites, and diet diversity was often lowest at APR. Like bison at KZA, the bison at APR showed changes in grazing and browsing over the growing season in 2011 and 2013, respectively, while those at RMA in both 2012 and 2013 did not.

Whereas the bison at KZA and APR went through periods in which consumption of forbs and browse increased, the bison at RMA maintained a graminoid-dominated diet for most of the 18 months they were studied. Forage availability may have contributed to this pattern, as bison at RMA had access to few woody plants (*Yucca*, *Populus*, *Salix*, *Celtis*, *Rhus*, and *Elaeagnus*). Black-tailed prairie dogs (*Cynomys ludovicianus*) were of high population density at RMA during this study, and in many areas converted ground cover from grasses to forbs – a common outcome of their foraging and habit modification (Archer, Garrett, and Detling 1987). However, many of these forbs may have been unpalatable to prairie dogs and bison alike. We occasionally observed the bison feeding on exotic field bindweed (*Convolvulus arvensis*), although this plant contains tropane alkaloids and is mildly toxic (Todd et al. 1995). Bison have been shown to prefer feeding near prairie dog towns, but on grasses and not necessarily forbs (Coppock et al. 1983; Krueger 1986; Chipault & Detling 2013). When the bison's pasture was enlarged in February 2013, the bison's consumption of graminoids decreased and their consumption of forbs increased, but this effect was temporary. Thus, forbs and browse may not have been as readily available to bison at RMA as at KZA and APR.

Climatic differences may have contributed to the differences we observed in foraging patterns among the three sites (Samson et al. 2004). The bison may have preferentially selected forbs, much as their relatives, cattle (*Bos taurus*) do (Plumb and Dodd, 1994; Steuter and Hidinger, 1999), because of the relatively high protein and low toxin levels of this herbaceous ground cover. They may have also accepted browse outside the growing season when it was still palatable (Larter and Gates, 1991; Fortin et al. 2003; Christianson and Creel, 2013). The bison may be selecting graminoids – a much more common form of ground cover – as an abundant and palatable, but less nutritious form of forage, to which bison are adapted to digest (Van Soest 1994).

Early in the season, bison appear to consume more forbs in the north than they do in the south. Young forbs tend to contain more protein than graminoids (Albon and Langvatn, 1992; Villalba et al. 2002; Villalba et al. 2004), as well as lower levels of secondary metabolites than their later maturational stages do (Glasby, 1991; Palo and Robbins, 1991; Craine, 2009), so bison and other grazers seem to prefer them (Coppock and Detling, 1986; Coppedge and Shaw, 1998; Schuler et al. 2006; Biondini et al. 2013). Bison in the south may be more nutritionally stressed during hot summers, while those in the north may be more metabolically stressed during cold winters, despite undergoing a 25% reduction in basal metabolic rate, or BMR (Craine et al. 2009; Craine et al. 2013; Craine et al. 2015; Craine 2013). In the present study, higher forb and browse intake by the herd at APR may be attributable to a greater need for high quality forage after a harsher winter than that experienced by those of more southerly herds at RMA and KZA, although they may be more susceptible to heat stress (Craine et al. 2015). Northern bison also appear to encounter a reduced diet diversity compared to their more southerly counterparts. This could be due to a generally less diverse flora from which to feed, or reliance on a smaller selection of preferred forage plants. The bison may then have selected browse during certain times of the year, or in certain environments, when ground cover was not readily available, or when the woody plants' leaves were new and contained less lignin or toxins (Searle and Shipley, 2008).

All of these findings indicate that the American bison has a more variable diet than previously thought. Earlier work has shown that, although primarily a grazer like other bovines, American bison (*Bison bison*) can also browse (Waggoner and Hinkes, 1986; Painter and Ripple, 2012), as can their European congener, the wisent (*B. bonasus*) (Gębczyńska et al. 1991; Kowalczyk et al., 2011), and their common ancestor the steppe bison (*B. priscus*) (Rivals et al. 2007). However, whereas assessments of temporal and spatial variability in the diets of all three species have yet to be performed, we here present the results of research on at least the American representative of this Holarctic genus.

Looking at the temporal component of diet variability, we see that at RMA, diet changes little over the course of two growing seasons and the winter in between, with the diet being dominated by graminoids and to a lesser extent forbs, as well as supplemented with browse. However, this does not appear to be the case at other sites (KZA and APR) where diet was observed during a single growing season. At KZA, the bison browsed heavily in the spring, transitioning to grazing later on in the summer. At APR, the bison consumed grass at a consistently low level, consuming forbs both early and late in the growing season, and browsing more heavily in June. Thus, depending on their location and the time of year, bison appear to be able to expand their diet beyond mere grazing to browse as well, sometimes to a large degree.

As large herbivores, optimal foraging theory predicts that bison may need to be relatively unselective to obtain enough energy, especially during certain times of the year when forage quality may be compromised, or if predation pressure constrains their foraging time (Senft et al., 1987; Vivas and Saether, 1987; Du Toit and Cumming, 1999; Kie, 1999). However, such a comparatively generalized diet may seem surprising when one considers that most ungulates are relatively specialized for the browsing, grazing, or mixed feeding niche (Van Soest 1994). African bovids are adapted to exploit certain types of vegetation more than others. Such specialization is a form of species packing, in which a relatively large number of species avoid competition by narrowing their resource use (Prins and Olff, 1998). The tribe *Bovini* arose in the woodlands of Asia some 8 million years ago during the late Miocene, where it diverged from a browsing, frugivorous, or generalized ancestor similar to today's tribe *Boselaphini* into grazers that can take advantage of ground cover in more open country (Pitra et al. 1997; Bibi, 2007; MacEachern et al. 2009; Bibi & Vrba, 2010). Why, then, would American bison not be similarly specialized?

The answer may be related to the diversity of the assemblage in which North American bison have found themselves since the Pleistocene extinction event (Martin 2005). For most of its half-million years in North America, the genus *Bison* belonged to a diverse guild of herbivores, comparable to those found elsewhere on Earth (Macfadden, 1997; Peek et al. 1987). Only for the past 10,000 have bison been part of a small community of ungulates. Although some resource partitioning exists, these relatively few species comprise a much less diverse assemblage than that of African ungulates, which likely exhibit less niche overlap than their North American counterparts (Owen-Smith 1982). Thus, unlike African bovids, American bison, despite being characterized as grazers, may be more adaptive specialists than has previously been recognized (Cannon 2001). This degree of generalized feeding may allow them to take advantage of the abundant resources in the North American landscape – ground cover as well as browse – that is not being fully exploited by other herbivores in their guild. This finding has implications for the management of American bison conservation and commercial herds, which if given the opportunity, might supplement their diet with shrubs and trees in addition to grazing.

Until the late 19th Century, bison were a migratory temperate ungulate, whose mass movements may have once been akin to those of saiga antelope (*Saiga tatarica*) and Mongolian gazelle (*Procapra gutturosa*) in temperate Eurasia (Bekenov et al. 1998; Olson et al., 2011); the guanaco (*Lama guanicoe*) in Andean South America (Raedeke 1979); blue wildebeest (*Connochaetes taurinus*) in tropical East Africa (Holdo et al. 2011); or reindeer (*Rangifer tarandus*) in the circumpolar Arctic (Forbes and Kumpula 2009). Little information is available from this earlier period, but migratory bison may have been able to specialize as grazers, following a “green wave” of fresh ground cover, much as other migratory ungulates still do today (Bischof et al. 2012). However, given the dietary plasticity of the ancestor of modern bison, *B. (bison) antiquus* (Rivals and Semprebon 2011), bison may have had a relatively broad diet for much of their evolution and into historically recent times. Even since their recovery from near-extinction in the 1880s, the American bison has been a largely sedentary species, so allowing them to browse and forage beyond their typical grazing niche could be an important part of their management. This practice has the potential to improve the overall condition of bison with minimal intervention or cost, possibly obviating the provisioning of these animals, and indeed may even help restore their landscape to a sustainable form consistent with historical baselines. Further research into the feasibility and effectiveness of such a management strategy is warranted.

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CHAPTER III

Microbial community composition along the digestive tract in forage- and grain-fed bison

Abstract

We compared the diversity and composition of microbial communities across the 13 major sections of the digestive tract in two captive populations of American bison (*Bison bison*), one of which was finished on forage, the other on grain. We found that microbial diversity fell to its lowest levels in the small intestine, with *Bacteroidetes* reaching their lowest relative abundance in that region, while *Firmicutes* and *Euryarchaeota* attained their highest relative abundances there; *Gammaproteobacteria* were most abundant in the esophagus, small intestine, and colon. Microbial community composition shifted with diet in the rectum as it did elsewhere in the digestive tract. Fecal sampling is a convenient, noninvasive, and informative method for studying gut microbial communities. However, because rectal (fecal) community composition was not directly indicative of those in other sections, fecal sampling did not replace sampling other parts of the digestive tract. The forage-finished bison population exhibited higher overall levels of diversity, as well as a higher relative abundance of *Bacteroidetes* in most gut sections. The grain-finished bison population exhibited elevated levels of *Firmicutes* and *Gammaproteobacteria*, both of which have been linked to host obesity and pathogen-shedding in other studies. The clinical condition of the animals used in the present study was not evaluated, so further research is needed to establish whether the microbial profiles of some bison in this study are indeed indicative of dysbiosis, a predisposing factor to ruminal acidosis and its sequelae.

Introduction

Ruminants, like all vertebrate herbivores, rely on vegetation for nourishment, but are unable to digest plant fibers without the aid of symbiotic microbes in their digestive tract (Van Soest 1994). Bacteria and protozoa are predominant, accounting for 40-60% of microbial biomass (Hobson and Stewart 1997). As in other mammals, the ruminant gut microbiota is dominated by the bacterial phyla *Firmicutes*, *Bacteroidetes*, *Actinobacteria*, *Proteobacteria* (especially in the class *Gammaproteobacteria*) and *Verrucomicrobia* (Ley et al. 2008a; Ley et al. 2008b; De Filippo et al. 2010; Muegge et al. 2011). Protists, found mostly in the foregut, are dominated by the phylum *Ciliophora*, which may specialize in digesting storage carbohydrates or proteins, preying on other microbes, or harboring other microbes as symbionts within symbionts (Belzecki et al. 2013; Gürelli 2014). Fungi, dominated by the phylum *Neocallimastigomycota*, constitute a much smaller fraction of the microbial biomass (only 5-10%), and like fungi in the ambient environment, specialize in degrading recalcitrant lignocellulosic fibers (Teunissen et al. 1991; Gordon and Phillips 1998; Liggenstoffer et al. 2010). Finally, most archaea are methanogens in the phylum *Euryarchaeota* (Hobson and Stewart 1997; Janssen and Kirs 2008; Hook et al. 2010; Singh et al. 2011).

Most of the ruminant digestive system is a favorable environment for microbes, as body temperature is warm and stable at around 39°C (Lenz et al. 1983). However, the digestive tract is also a challenging environment for microbes given that they must compete for space and nutrients (Flint et al. 2007). Moreover, although ruminants provide their symbionts with abundant resources, most are in the form of cellulose, which is difficult to break down (Morrison et al. 2009). The reticulorumen and omasum are weakly acidic with a pH of 5.5-6.5, which is favorable for many microbes (Frey et al. 2010). These sections house most of the ruminant’s symbiotic microbiota. Bacteria and protozoa are predominant, accounting for 40-60% of microbial biomass (Hobson and Stewart 1997). Bacteria fermenting this material release the volatile fatty acids (VFAs) acetic, propionic, and butyric acid, which the host absorbs and metabolizes (Van Soest 1994).

Because the different sections of the ruminant gut present different environmental conditions, the composition of the gut microbiota changes from one section to another. The first region (a functional grouping of sections) is the foregut, which houses several common fibrolytic species (Morrison and Miron 2000; Devillard et al. 2004; Suen et al. 2011), as well as amolytic, saccharolytic, lactolytic, and proteolytic species (Chistoserdova et al. 2004; Forano et al. 2008; Marx et al. 2011; Jiao et al. 2014). Second, the abomasum has a pH of 2-4, which kills and digests many of the microbes entering from the omasum, supplying the host with 60-90% of its amino acids, which are in turn absorbed in the small intestine (Asplund 1994; Stevens and Hume 1995; Stevens and Hume 1998; von Rosenvinge et al. 2013). Third, the small intestine is responsible for neutralizing acid from the stomach, breaking down macromolecules with enzymes, and absorbing nutrients. Microbial biomass drops sharply between the foregut and small intestine because of the acidity of the abomasum, but then increases caudally as pH rises again from 2-4 in the duodenum, to 4-7 in the jejunum, and finally to 7-8 in the ileum (Frey et al. 2010). Finally, the hindgut is the last site for salt and water balance. In ruminants, this region is second to the foregut in microbial biomass. Microbiota in the cecum, colon, and rectum ferment remaining fiber and produce a variety of vitamins for their host (Van Soest 1994; Hobson and Stewart 1997).

We compared community composition along the entire digestive tract from two populations of captive plains bison (*Bison bison bison*). In domestic cattle (*Bos taurus*), gut microbiota have been explored in the reticulorumen and feces (Ozutsumi, Hayashi, et al. 2005; Patton et al. 2009; Shanks et al. 2011; Thoetkiattikul et al. 2013), as well as across the entire digestive tract (Frey et al. 2010; de Oliveira et al. 2013). Microbial diversity along the digestive tract has been researched in humans, rodents, and horses as well (Wang et al. 2005; Dougal et al. 2013; K. D. Kohl et al. 2014). However, studies of the gut microbiota of bison have been limited to the reticulorumen (Towne et al. 1988; Towne et al. 1989; Varel and Dehority 1989) and feces (Weese et al. 2014). The earlier research on ruminal microbiota predates high-throughput sequencing, so it relied on culture-dependent methods that could not detect much of the microbial diversity found in the gut. The study by (Weese et al. 2014) used culture-independent methods to characterize fecal microbiota among semi-free-ranging wood bison (*B. bison athabascae*) in Elk Island National Park near Edmonton, Alberta, Canada.

We wanted to know to what degree microbial community composition varies along the length of the digestive tract in plains bison, and to what degree fecal samples could be reflective of microbial community composition elsewhere in the digestive tract. In addition, we wanted to know whether or not the relative abundance of a given microbial taxon in a given gut section differs between two populations of bison. Finally, we wanted to compare the composition of microbial communities observed presently in plains bison to those observed previously in wood bison and domestic cattle. We hypothesized that different sections of the digestive tract would exhibit significant differences in microbial diversity and community composition, thereby making fecal samples not directly indicative of community composition higher in the digestive tract. Likewise, for a given digestive tract section, we hypothesized that microbial diversity and community composition would differ significantly between the two bison populations. Finally, we hypothesized that when compared to the present observations on microbial community composition in plains bison, earlier research in wood bison and domestic cattle would show similar community composition for a similar diet (forage vs. grain), or for a similar section of the digestive tract.

Materials and Methods

We identified 13 major sections of the alimentary canal for sampling. In anterocaudal order, they were the esophagus, reticulum, rumen, omasum, abomasum, duodenum, jejunum, ileum, cecum, ascending colon, transverse colon, descending colon, and rectum. We went to an abattoir to dissect four bison from one population on one day, and three from another population a week later, for a total of seven bison. On October 10, 2012, all four bison were grain-finished bulls, aged two-three years, from Colorado (Population B). On October 16, 2012, all three bison were forage-finished cows, aged four-fourteen years, from Nebraska (Population A). The forage-finished diet consisted of 100% roughage for the lifetime of the animals. In contrast, the grain-finished diet was 60% corn and 40% roughage from age six months, with the bison not being returned to forage prior to slaughter. For all seven individuals, we used double sterile cotton swabs to simultaneously sample the lumen and mucosa of each section in triplicate, yielding a total of 273 samples. These were transported on ice in a cooler, and stored frozen at -20°C until processing. We then performed DNA extractions on all four of the grain-fed bison, and on three of the forage-fed bison, using the MO BIO PowerSoil®-htp 96 Well Soil DNA Isolation Kit, according to the method in (Lauber et al. 2008).

We PCR-amplified and sequenced a portion of the 16S rRNA gene to characterize bacterial and archaeal community composition in the bison digestive tract. To amplify these 16S rRNA genes for barcoded high throughput sequencing, we followed (Lauber et al. 2009). We used the primer pair 515F / 806R with Illumina adapters, and with a 12-bp error-correcting barcode unique to each sample on the reverse primer. The V4–V5 variable region amplified by this primer set is well-suited to accurate phylogenetic placement of bacterial sequences (Liu et al. 2007). Together, these primers form a good “universal” primer set that amplifies nearly all bacterial and archaeal taxa with few biases (Bergmann et al. 2011). Amplicons were cleaned using the MO BIO PowerClean® DNA Clean-Up Kit, and quantified using first the Quant-iT™ PicoGreen® dsDNA Assay Kit, and then the Thermo Scientific NanoDrop 1000, to determine the volume needed to produce a single composite sample with equal representation of each individual sample. The composite sample was taken to the University of Colorado Genomics Core Facility for sequencing on an Illumina MiSeq machine with the 2 × 150 bp paired-end protocol.

We used the QIIME pipeline for data analysis. Quality filtering and processing of reads was performed following (Caporaso et al. 2011). Only forward reads were used for downstream analyses (Werner et al. 2012). Bacterial 16S rRNA sequences were clustered into operational taxonomic units (OTUs) at the 97% similarity level using the RDPII taxonomy (Cole et al. 2007). We used parametric and nonparametric statistical approaches to determine if communities varied across gut sections within each population of bison, as well as for a given gut section between the two bison populations. The Shannon index was used to compare diversity levels among sections and between populations. Single-factor ANOVA with the Tukey HSD post-hoc test was used for comparisons among sections, while t-tests with Bonferroni corrections were used for comparisons between populations. Exploratory and multivariate statistics consisted of hierarchical cluster analysis, principal coordinates analysis (PCoA), and PERMANOVA. Relative abundance data were square root transformed, and then used to generate a Bray-Curtis similarity matrix, from which the PCoA ordination plot was produced. Using the Bray-Curtis distance matrices for microbiome and metagenome, we applied the Mantel test with Pearson product-moment correlation. These analyses were performed in the R programming language and in the PRIMER + PERMANOVA 6 software package.

Results

In the forage-finished population (Population A), diversity differed significantly among sections, and was lowest in the ileum ($P < 0.05$). Bison from the grain-finished population (Population B) also exhibited significant differences in diversity among sections ($P < 0.05$), but there was no clear trend (Figure 3.1). Population A tended to exhibit significantly higher levels of diversity for a given gut section. Shannon index values were higher for bison from Population A in the esophagus, rumen, and jejunum ($P < 0.004$ in all cases). The three most common OTUs detected were in the phyla *Bacteroidetes* and *Firmicutes*. *Paraprevotellaceae* (Phylum *Bacteroidetes*) was more abundant in the colon among bison from the forage-finished population, and was more abundant in the hindgut generally among bison from the grain-finished population. *Bacteroidales* (Phylum *Bacteroidetes*) was more abundant in the foregut among bison from both populations. Finally, *Peptostreptococcaceae* (Phylum *Firmicutes*) was more abundant in the ileum and cecum among bison from the forage-finished population, but more abundant in the jejunum and ileum among bison from the grain-finished population.

In each population, microbial community composition varied significantly by gut section, as indicated by PERMANOVA ($P < 0.05$), although not typically within the same gut region (Figure 3.2). Thus, for a given diet, the three main fermentation chambers of the foregut (reticulum, rumen, and omasum) had similar microbial communities, as did the five main sections of the hindgut (cecum, ascending colon, transverse colon, descending colon, and rectum). The forage-finished population also exhibited similarity in community composition between sections from two different regions of the digestive tract, namely the abomasum and duodenum ($P = 0.073$), and the jejunum and rectum ($P = 0.161$). No such extra-regional similarities were detected in the grain-finished population. *Bacteroidetes* were at their lowest relative abundance in the small intestine, specifically the ileum of bison from the forage-finished population ($P < 0.001$), and in the duodenum, jejunum, and ileum of bison from the grain-finished population ($P < 0.001$). In contrast, *Firmicutes* had their highest relative abundance in the small intestine, namely the ileum of bison from the forage-finished population ($P < 0.0001$), and the jejunum and ileum of bison from the grain-finished population ($P < 0.001$). *Proteobacteria* and *Tenericutes*, although the third and fourth most abundant phyla, respectively, exhibited no clear trend across the digestive tract in either population ($P > 0.05$).

Gut section had a greater effect on microbial community composition than population. Thus, foregut communities between the two populations were more similar to each other than they were to hindgut communities from the same population. Likewise, hindgut communities resembled each other more than either resembled corresponding foregut communities (Figure 3.3). However, for a given section, there was a significant effect of population as well, as indicated by PERMANOVA ($P < 0.05$). We used t-tests to compare bacterial relative abundance at a given taxonomic level between populations for each digestive tract section. Here we report sections with significantly different relative abundances of bacteria. Bacteria in the phylum *Bacteroidetes* were more abundant for the forage-finished population in the jejunum ($P < 0.001$) and ascending colon ($P < 0.001$). Bacteria in the phylum *Firmicutes* were more abundant for the grain-finished population in the jejunum ($P < 0.001$) and rectum ($P = 0.002$). Bacteria in the phylum *Proteobacteria* were more abundant for the grain-finished population in the omasum (*P* = 0.003), and those in Class *Gammaproteobacteria* were more abundant for the grain-finished population in the reticulum (*P* = 0.001), abomasum (*P* < 0.001), duodenum (*P* = 0.007), and descending colon (*P* = 0.003).

Discussion

In each population, microbial community composition was significantly different among gut sections from different regions, but similar among those within the same region, namely the multi-chambered stomach and large intestine. This is probably because, although anatomically partitioned, each of these two regions probably functions as a unit (de Oliveira et al. 2013). For both bison populations studied, diversity as indicated by the Shannon index appears to be lowest in the small intestine, and for bison from Population A (forage-finished), diversity was lowest in the ileum specifically, although the other sections showed no clear trend. We found that the two dominant bacterial phyla in the digestive tract were the *Bacteroidetes* and *Firmicutes*, as is the case in all known mammals (Ley et al. 2008; Muegge et al. 2011). *Bacteroidetes* exhibited their lowest relative abundance in the small intestine, while *Firmicutes* reached their highest relative abundance there.

Earlier research has shown that, despite high resource availability, the small intestine tends to harbor the lowest levels of microbial biomass and diversity of any gastrointestinal section, for two main reasons (Gerritsen et al. 2011). The first is that digesta have a relatively short retention time in the small intestine (3–5 hours) due to peristaltic movement, which gives microbes less time to proliferate there (Booijink et al. 2007). The second is the influence of the section just anterior to the small intestine, the abomasum (true stomach). While the pH of most gut sections ranges from 5-7, the abomasum has pH levels of 2-4, the lowest of the ruminant digestive tract (W. E. Wheeler and Noller 1977; Hobson and Stewart 1997; Booyse and Dehority 2012). Although the small intestine receives this gastric acid and begins buffering it, that takes time. Digesta pass through the long ruminant small intestine, which is about 20 times the length of the animal, or some 40 meters long in bison and cattle. During this time, pH remains relatively low in the duodenum and jejunum, and does not return to near neutral levels until the ileum. In addition to acid, the small intestine also receives bile from the gall bladder and enzymatic secretions from the pancreas. Together, these three inputs create a relatively harsh environment for most microbes (Booijink et al. 2007). In this environment, the Gram- *Bacteroidetes* could be at a disadvantage compared to the *Firmicutes*, which have a thick peptidoglycan Gram+ cell wall (Vos et al. 2009).

The effect of gut region on community composition was stronger than that of population, as microbial communities were more similar in the same region between populations, than to another region within the same population (Figure 3.3). Nevertheless, the bison from Population A (forage-finished) appeared to support greater microbial diversity in most sections of the digestive tract, except the ileum. In the present study, we compare two bison populations that differed in four ways: sex, age, location, and diet. Population A consisted of female bison aged four-fourteen years from Nebraska that were forage-finished, while Population B consisted of male bison aged two-three years from Colorado that were grain-finished. Thus, diet was not the only factor to differ between these populations. Nevertheless, it is reasonable to infer that diet was the most important factor, because diet has many times been shown to be the most important factor affecting microbial community composition, because it most strongly affects resource throughput in the digestive tract. Previous work with captive domestic cattle has shown that age, sex, and location have less of an effect on microbial community composition than diet (Shanks et al. 2011; Kim et al. 2014). The same likely applies to captive bison. Thus, differences in community composition between the two populations for a given gut section may be due to forage-finishing in Population A and grain-finishing in Population B. Specifically, the present study suggests that a forage-based diet may be associated with overall greater gut microbial diversity in bison (Figure 3.1).

In many gut sections, *Bacteroidetes* were more abundant with a forage diet, while *Firmicutes* were more abundant with a grain diet. This mirrors what has been found in studies on obesity in humans and mice, where a more natural, less calorific diet that is rich in protein and fiber seems to favor *Bacteroidetes,* while an artificial, energy-rich diet of starch and fats seems to favor *Firmicutes* (Turnbaugh et al. 2006; Guo et al. 2008a; Guo et al. 2008b; Costello et al. 2010; Thomas et al. 2011). Thus, the gut microbiota of grain-fed bison appears to resemble those of other animals fed a diet high in starchy, processed foods. At the phylum level, *Proteobacteria* were more abundant with a grain diet only in the omasum. Moreover, at the class level, a higher relative abundance of *Gammaproteobacteria* was associated with the grain diet throughout much of the digestive tract. It is noteworthy that certain bacterial groups exhibit differences in relative abundance between the rectum and elsewhere in the GI tract. Thus, one must be cautious when inferring abundances of bacteria elsewhere in the alimentary canal (de Oliveira et al. 2013). Fecal sampling is convenient, noninvasive, and informative, but it does not replace sampling of other sections of the digestive tract when direct knowledge of them is needed.

Finally, we compared the present study's findings on the gut microbiota of commercial plains bison (*Bison bison bison*) to those of our study on free-ranging bison at the Konza Prairie Biological Station in Chapter I (Bergmann et al. 2015), as well as earlier studies on semi-free-ranging wood bison (*B. bison athabascae*) (Weese et al. 2014) and commercial domestic cattle (*Bos taurus*) (Ozutsumi et al. 2005a; Ozutsumi et al. 2005b; Patton et al. 2009; Shanks et al. 2011; de Oliveira et al. 2013; Thoetkiattikul et al. 2013). All of these studies and the present study showed that *Firmicutes* and *Bacteroidetes* were the two dominant bacterial phyla, as in most mammals (Ley et al. 2008; Muegge et al. 2011). Although relative abundances varied considerably, among cattle *Bacteroidetes* generally dominated the foregut (33-72%), while *Firmicutes* generally dominated the midgut and hindgut (42-81%).

Proteobacteria were on average the third-most abundant phylum, especially in (Patton et al. 2009) and (Weese, Shury, and Jelinski 2014). *Tenericutes* were the fourth-most abundant phylum on average. In cattle but not bison, *Spirochaetes* were the fifth-most abundant phylum, generally in the foregut, although (Ozutsumi et al. 2005b) and (Shanks et al. 2011) reported them as abundant in fecal matter. *Fibrobacteres* were the sixth-most abundant phylum on average in (de Oliveira et al. 2013) and (Thoetkiattikul et al. 2013), again in the foregut of cattle but not bison. Finally, *Actinobacteria* and *Verrucomicrobia* were the next most abundant phylum on average, found variously in the foregut, midgut, and hindgut of both species.

Some differences were also apparent between the fecal microbial communities from conservation wood bison in (Weese et al. 2014) and the hindgut microbial communities from commercial plains bison in the present study, as well as fecal microbial communities from Konza Biological Station described in Chapter I (Bergmann et al. 2015). The wood bison fecal samples were strongly dominated by *Firmicutes* (39% in one enterotype and 71% in the other), but had a lower relative abundance of *Bacteroidetes* (0% and 1%, respectively). The fecal microbial community from bison at Konza Biological Station also exhibited dominance of *Firmicutes* over *Bacteroidetes*, but to a lesser degree (53% and 33%, respectively). However, the plains bison hindgut in the present study overall showed a more even relative abundance of *Firmicutes* (29-51%) and *Bacteroidetes* (37-50%). The wood bison also exhibited a high relative abundance of *Proteobacteria* (19% and 43%, respectively), similar to that of the two groups of cattle in (Patton et al. 2009), whose relative abundances were 13% and 17%. In contrast, the relative abundance of *Proteobacteria* at Konza Prairie Biological Station (1%) and that observed in the present study (1-11%) were similar to levels observed in most of the cattle studies (1-7%).

The comparison of the gut microbiota in plains bison, wood bison, and domestic cattle presented here is preliminary, and many factors – such as animal age, condition, location, and diet – remain uncontrolled. Nevertheless, the gut microbiota of cattle appears to support more dominant phyla, including *Spirochaetes* and *Fibrobacteres*, when compared to that of bison. In addition, the gut microbiota of semi-free-ranging wood bison in (Weese et al. 2014) stands out for having a lower relative abundance of *Bacteroidetes* than that of the free-ranging bison at Konza Biological Station, the commercial plains bison in the present study, or the commercial cattle in the other studies. The reason for this difference is not known, but it is possible that these wood bison, which live in Elk Island National Park, may have a diet or be in a condition that is sufficiently different to foster a divergent gut microbial community from the other bison and cattle populations.

In summary, the present study found microbial community compositional differences in the digestive tracts of two bison populations, possibly due to differences in diet (forage- vs. grain-finished). Given previous research on grain-fed cattle and bison, as well as on obese mice and humans, it is possible that the higher levels of *Firmicutes* and *Gammaproteobacteria* found in the grain-finished bison represented dysbiosis (Krause and Oetzel 2006; Nagaraja and Titgemeyer 2007; Plaizier et al. 2008). However, the bison in this study were not assessed for ruminal acidosis, anorexia, or the shedding of enterohemorrhagic bacteria to their environment. Additional research is needed to evaluate the clinical relevance of symbiotic communities brought about by artificial feeding methods in bison.

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CHAPTER IV

Wildlife livestock: conservation as a consequence of better agriculture

Abstract

The Great Plains supported tremendous biodiversity during the Pleistocene Epoch, comparable to the ecological communities of Africa and Asia today. Megafaunal extinctions about 10,000 years ago, likely due at least in part to human activity, left the Great Plains depauperate, although some species remained to repopulate the region. These included herbivores like bison, elk, pronghorn, deer, and prairie dogs, as well as carnivores like wolves, bears, cougars, and jaguars, constituting an ecosystem that has been dubbed the "American Serengeti." However, during the 19th Century, Westward Expansion of the United States resulted in the displacement of indigenous people and the extirpation of many animals. Today, the Great Plains provide the critical function of providing food, but via intensive methods such as monocultures for crops and feedlots for livestock, which may not be sustainable in semi-arid grasslands, and which introduce other problems, such as reduced food quality, preventable disease, and inadequate animal welfare. The Great Plains have been largely overlooked for conservation, despite having been repeatedly recommended for such treatment since 1841. However, there has been increased interest in prairie conservation since the 1980s from various fields. Moreover, five additional, complementary developments have emerged that together could sway policy and management in the Great Plains. One is the practice of wild game ranching, which began some 2,000 years ago in Eurasia, but has seen a worldwide resurgence since the 1970s. Another is a growing interest in sustainable, low-impact agriculture with both plants and animals, focusing on free-ranging elk or wapiti (*Cervus canadensis*) and especially

bison (*Bison bison*) as hardy, low-input alternatives to domestic cattle in feedlots. The third is large-scale conservation, known as rewilding, which involves preserves with core and buffer zones, as well as corridors to connect preserves, and carnivores for top-down ecosystem regulation. A variant of this approach is Pleistocene rewilding, which acknowledges the cascading effects of megafaunal absences, and that humans have been affecting ecosystems for millennia. For this reason, Pleistocene rewilding sets baselines for restoration or intervention (Hobbs et al. 2011) to not just pre-colonial, but pre-human conditions altogether, and allows for the reintroduction of extirpated animals, or the substitution of related and similar proxies for extinct animals, to achieve restoration or intervention goals. A fourth development is the advent of energy sources on the Great Plains, such as wind and solar power, to which rural and indigenous communities can add sustainable, diversified ranching and ecotourism as part of a profitable milieu of renewable industries. The fifth and final development is a shift in how nature is regarded, as not only a treasure to be protected from people, but also as a system to which people belong, and in which they can participate if they are responsible. Each of these perspectives is ethically justified as benefiting people, animals, and environments. The confluence of these six streams may now justify and bring about comprehensive prairie conservation. A network of preserves and ranches could be put into place that would not only restore the vibrant landscapes and megafaunal assemblages of the Great Plains, but would also make commercial interests in the region sustainable and economically viable.

A brief history of the Great Plains

The Great Plains of North America is a vast region of semi-arid grassland known as prairie, similar in some respects to the temperate steppes of Eurasia (Bredenkamp et al. 2002;

Bai et al. 2007). Once occupying 1.3 million km^2, the prairie is now the most fragmented and endangered habitat in the United States (Samson and Knopf 1996). At the end of the Pleistocene Epoch about 10,000 years ago, the prairie underwent a massive extinction, in which 33 genera of megafauna (animals 45 kg or larger) disappeared, including herbivores such as horses, camels, and elephants (mammoths and mastodons), as well as carnivores like lions and cheetahs, at least partly due to human hunting and burning activities (Barnosky et al. 2004; Koch and Barnosky 2006). In the 19th Century, continued over-hunting and habitat loss led to the further extirpation of native prairie plants and animals, namely herbivores like bison (*Bison bison*), elk or wapiti (*Cervus canadensis*), pronghorn (*Antilocapra americana*), deer (*Odocoileus* spp.), and black-tailed prairie dogs (*Cynomys ludovicianus*), as well as carnivores like wolves (*Canis lupus*), cougars (*Puma concolor*), jaguars (*Panthera onca*), black bears (*Ursus americanus*), and grizzly brown bears (*Ursus arctos*) (Isenberg 2000; Laliberte and Ripple 2003). Today, the prairie (sometimes known disparagingly as “flyover country”) is used primarily for the valuable function of food production. However, this sector is dominated by subsidized, industrial monoculture crops and feedlots for livestock, also known as factory farms or concentrated animal feeding operations (CAFOs), as more natural agricultural operations have been bought up by agribusinesses (Popper and Popper 2006).

Since the Great Depression, the Great Plains has seen the establishment of a few National Grasslands and other non-governmental preserves, but these are not interconnected to allow migration. Unlike comparable ecosystems with megafaunal umbrella species in Africa and Eurasia, these existing areas are relatively small and do not support high levels of prairie biodiversity. Thus, in a phenomenon known as the “Rocks and Ice Syndrome,” or monumentalism (Terborgh and van Schaik 2002), and despite the National Park Service’s success elsewhere, there is no national park or conservation network dedicated to protecting and showcasing the diverse wildlife of America's Great Plains. Yet, the first proposal for a national park of any kind was put forth in 1841 by painter George Catlin, whose experiences among the bison-hunting Plains Indians inspired him to conceive of a place that would protect the Great Plains, its wildlife, and the people who relied on it (Flores 1996; Isenberg 2000; Lott 2002).

Since Catlin's time, calls for prairie conservation have surfaced time and again. In his classic book, *The Extermination of the American Bison* (1889), William Temple Hornaday presciently appealed to Americans' sense of both nature preservation and economic utility, arguing that the great herds of bison need not be eradicated, for in addition to being appreciated as native wildlife, they could also be used as livestock (Hornaday 1889). By 1902, the Boone and Crockett Club was working to establish big game preserves in the Great Plains (Brinkley 2009). In the 1920s, ecologist Victor Shelford worked toward federal protection for Great Plains ecosystems, but was turned down. The 1930s saw some increased protection for grasslands, as the Great Depression and its Dust Bowl led to the Bankhead-Jones Farm Tenant Act of 1937, creating the National Grasslands system. The National Park Service acquired South Dakota's Badlands in 1939, and North Dakota's Little Missouri Badlands in 1947; both became national parks in 1978 as Badlands National Park and Theodore Roosevelt National Park, respectively (Flores 1996). In the 1960s, zoologist Eugene Raymond Hall proposed a Prairie National Park in the tallgrass prairie region of northeastern Kansas, but the federal government took no action (E. R. Hall 1962).

Since the 1980s, however, there has been some increased interest in restoring Great Plains ecosystems for both sustainable use and conservation. Daniel Licht's prescriptions for reforming the way prairie is managed have yet to be followed (Licht 1994a; Licht 1994b;

Armstrong 1997; Licht 1997). However, The Land Institute, founded by Wes Jackson, has identified soil erosion from annual crops as a major obstacle to sustainability in agriculture, and has been developing perennial grains like Kernza™ (*Thinopyrum intermedium*) to address this problem (Jackson 1980; Crews et al. 2014). Geographer Bret Wallach has argued for a system that would convert defunct farms into restored prairies, rather than allowing them to become abandoned and neglected (Wallach 1985). And geographers Frank and Deborah Popper proposed an idea that came to be known as the Buffalo Commons, which would be debated vociferously over the coming decades (Matthews 1992).

The Poppers recalled historian Frederick Jackson Turner's taxonomy, which divided the United States into wilderness, frontier, and settled areas, defined as 0-2, 2-6, and ≥ 6 people/mi^2, respectively. They pointed out that, although it is said the West was won by the early 20th Century (Turner 1920), most of the Great Plains is far from settled, and has remained or reverted to frontier or wilderness, based on the above thresholds. Thus, the region has been in environmental, economic, and population decline since the early 1900s (Popper and Popper 1987; Lang 1997). This phenomenon may be attributable to the Great Plain's semi-arid climate, which receives ≤ 20 inches of rain/year, and necessitates the depletion of large but finite stores of well water, such as the Ogallala Aquifer (Sophocleous 2000; Allen et al. 2008). A solution to this problem is to let bison and other wildlife return. Rather than using intensive, industrial forms of farming and ranching, the land can be restored to a sustainable system of ranches, commons, and refuges with native prairie vegetation and native herbivores, such as bison, elk, pronghorn, and more. This comprehensive network of preserves and pastures would be implemented in areas where people are currently sparse or absent, restoring the native ecosystems of Middle America and bringing new opportunities to the rural and native people of the Great Plains.

The Great Plains now supports some conservation areas for native prairie vegetation and wildlife. Several of these belong at least in part to The Nature Conservancy, such as the Tallgrass Prairie Reserve in Oklahoma, and the Konza Prairie in the Flint Hills of Kansas. Other Kansas parks dedicated to grassland communities include the Tallgrass Prairie National Preserve (also in the Flint Hills), and the Big Basin Prairie Preserve in the Red Hills. In Colorado, The Nature Conservancy holds the Zapata Ranch, a preserve with 2,000 bison. There are also several state and federal lands that protect prairie ecosystems and megafauna, including the Rocky Mountain Arsenal National Wildlife Refuge, a Superfund cleanup site in Colorado that is now managed as a native shortgrass steppe with bison and other prairie wildlife (Jones and Cushman 2004). In addition, organizations have arisen to facilitate education and involvement with prairie conservation. The Texas-based Great Plains Restoration Council works with local people to restore prairies and build community. There are several other such groups in the region as well.

With fewer human inhabitants, the Northern Great Plains has received the most attention for prairie restoration. Beginning with the Big Open Project in 1986 (Coffman, Jonkel, and Scott 1990; B. Scott 1992), Montana is now home to the American Prairie Reserve (APR), a joint effort by The Nature Conservancy, World Wildlife Fund, and other nongovernmental organizations. The APR was featured in a National Geographic documentary entitled *American Serengeti*, which showcased the preserve’s steppe landscape and native wildlife (Mitchell 2010). The APR currently consists of over 100,000 ha, and is working to connect a total of 1.2 million ha, encompassing both private and existing public lands, including the more than 445,000 ha of the Charles M. Russell (CMR) National Wildlife Refuge (Manning 2009; Henwood 2010). The National Wildlife Federation also works in this area, seeking to restore bison to CMR and the Fort Belknap and Fort Peck Indian Reservations. Thus, there has been progress since the early

20th Century in the realm of prairie conservation. However, there is still no park with a full complement of North American grassland flora and fauna, and resource use in the Great Plains remains unsustainable.

Woodlands have higher overall plant biomass than grasslands, and support browsing herbivores, which feed on the leaves of woody vegetation. With food being spread out and shelter abundant, woodland herbivores and carnivores often live alone or in small groups. In contrast, grasslands have a higher percent edible plant biomass than woodlands, and support grazers that feed on graminoids and forbs (Bodmer 1990; Van Soest 1994). With more food but a dearth of shelter, grassland herbivores and carnivores are often highly gregarious (McNaughton 1984). For this reason, grasslands are renowned for some of the greatest spectacles in the natural world.

Much of the public seems to have forgotten just how plentiful megafauna and other wildlife once were, a phenomenon first identified in fisheries as the shifting baseline syndrome (Pauly 1995; Papworth and Rist 2009). Reindeer or caribou (*Rangifer tarandus*) remain abundant, with a world population of some 5 million (Forbes and Kumpula 2009). Over a million blue wildebeest (*Connochaetes taurinus*) still migrate in East Africa (Holdo et al. 2011), and the Mongolian gazelle (*Procapra gutturosa*) population of the Eurasian steppe has rebounded to over a million as well (Olson et al. 2011). However, other temperate ruminants, such as the saiga antelope (*Saiga tatarica*) and goitered gazelle (*Gazella subgutturosa*) have fallen precipitously from such numbers (Kingswood and Blank 1996; Bekenov et al. 1998). In South Africa, springbok (*Antidorcas marsupialis*) remain safe at about 2 million, but until the end of the 19th Century, they numbered some 8 million, occasionally forming huge migratory herds known as “treks” in response to drought (Bigalke et al. 1993; J.D. Skinner 1993; Spinage 2012). South

America is home of the greater rhea (*Rhea americana*) and Darwin's rhea (*Pterocnemia pennata*), two large ratite birds related to the ostrich and emu. They once numbered in the millions, forming huge flocks on the Pampas grasslands of South America, but today they are near-threatened due to overhunting and habitat loss (Conway 2005). The Pampas deer (*Ozotoceros bezoarticus*) of South America's plains once numbered over a million, but hunting and habitat loss have reduced them to mere tens of thousands (González et al. 1998). South America also once supported an estimated 30-50 million guanacos (*Lama guanicoe*) (Raedeke 1979), as well as millions of vicuñas (*Vicugna vicugna*), domestic llamas (*L. guanicoe glama*), and alpacas (*V. pacos*). Today, there are still millions of llamas and alpacas, but wild guanacos and vicuñas number only in the hundreds of thousands (Coates and Ayerza 2004).

During pre-Columbian times, the American bison population may have been around one million due to human predation (Kay 1998), rising to 20-30 million during post-Columbian times. Overhunting during the 19th Century nearly caused the extinction of the American bison, reducing them to fewer than 100, although their ongoing recovery since then has become legendary (Freese et al. 2007; Sanderson et al. 2008; Hedrick 2009). The bison's rapid decline was due to unregulated market hunting during drought years. Mounted Plains Indian hunters took their toll, but traders from the East Coast were more destructive. Their unfettered killing was openly encouraged by Generals William T. Sherman and Philip Sheridan, who saw it as a tool to deplete the resource base of American Indians and facilitate their conquest, a strategy that ultimately resulted in the genocide and dispossession of the Great Plains' indigenous population (Payne 1989; Smits 1994; Isenberg 2000). Prior to these changes, the prairie's abundant herbivores supported some 1.5 million plains wolves (*Canis lupus nubilus*) (Isenberg 2000), while today there are only about 9,000 gray wolves of any subspecies in the whole United States

(Mech and Boitani 2003). Furthermore, other North American ungulates, despite their currently secure conservation status, have decreased in abundance as well. Today there are about a million elk and pronghorn each, but elk once numbered 10 million (Payne 1989; Polziehn et al. 2000), and pronghorn some 35 million (Cohn 2010). These declines in wildlife populations and their associated losses in ecosystem functioning could be reversed if species were reintroduced and utilized sustainably (Luxmoore 1989). This does not mean we should be careless about intervention, but neither should we be puristic, either (Marris 2011). The thoughts and behaviors found in the human species are remarkably plastic and diverse – much more so than in other animals. We are capable of reflection and self-control to a degree far greater than that of other species, which is why discussion on environmental policy is possible. However, this does not mean that we are not part of nature. It only means that we can evaluate which of our thoughts and behaviors allow us to live in a thriving ecosystem, and which of them allow us to live by quelling other species and landscapes around us (Callicott 2003). Being pragmatic and including responsible human activity as part of ecosystems creates economically viable opportunities for intervention.

Another development since the 1980s is the concept of rewilding, including Pleistocene rewilding. Simply put, rewilding refers to the restoration of wilderness areas, their flora and fauna, and their natural processes using core and buffer zones, corridors, and carnivores (Quammen 1996; Soulé and Noss 1998; Soulé and Terborgh 1999; Foreman 2004). A new version of this large-scale approach to conservation is Pleistocene rewilding, which uses pre-human levels of biodiversity as a reference for intervention (Galetti 2004). This proposal rests on the hypotheses that human overhunting and habitat alteration have been factors in animal extinctions, not only during historical times, but during prehistoric times as well (Martin 1966;

Martin 1984; P. D. Ward 1997; Levy 2011), and that in the absence of megafaunal species, many important ecological processes, such as predation, herbivory, frugivory, and soil fertilization go unperformed (Janzen and Martin 1982; Catling 2001; Johnson 2009). Proponents of Pleistocene rewilding propose that wherever possible, animals should be reintroduced into areas where they have been extirpated, even if a relatively long time has passed. If extinct altogether, ecologically similar and closely related proxy species should be introduced instead.

Reintroduction of megafauna like bison, elk, and grizzly brown bear, as well as smaller animals like black-tailed prairie dog, black-footed ferret (*Mustela nigripes*), greater prairie chicken (*Tympanuchus cupido*), and peregrine falcon (*Falco peregrinus*) constitutes Pleistocene rewilding. Moreover, the Spanish release of horses (*Equus ferus*) in North America more than 400 years ago is also Pleistocene rewilding, because today's feral mustangs are of the same species as the wild horse that went extinct in North America as recently as 7,600 years ago (Vilà et al. 2001; Weinstock et al. 2005; Haile et al. 2009). As reintroduced megafauna, horses should therefore be included in Great Plains conservation efforts. The Wild and Free-Roaming Horses and Burros Act of 1971 was a valuable step in protecting North America's reintroduced horses, but it was not enough. Today the Bureau of Land Management (BLM) oversees 33,000 mustangs on public lands (about 10,000 over the 23,622 considered sustainable), and in feedlots an additional 45,000, whose fate is uncertain. Without a change in policy, many of America's wild mustangs could overrun their habitat's carrying capacity and face dehydration or starvation. By the year 2030, the United States' cumulative feral horse management costs are projected to surpass $1 billion, 60% of which would go toward maintaining captive horses, whose numbers by then will exceed 60,000 (Garrott et al. 1992; Garrott and Oli 2013). This situation is reminiscent of surpluses in large herbivore populations, which are often culled, such as bison in

Yellowstone National Park (Plumb et al. 2009), elk in Yellowstone and Rocky Mountain National Parks (Ripple et al. 2010), and African bush elephants (*Loxodonta africana*) in Kruger National Park (Shannon et al. 2013). As more land has become available for conservation in the Great Plains, the culling of elk, bison, and horses can be replaced with reintroducing them to their native prairie landscape.

Pleistocene rewilding of carnivores is also possible (J. Donlan et al. 2005; C. J. Donlan et al. 2006). Today's Old World lions (*Panthera leo*) are of the same species as the extinct American lion (*P. leo atrox*), although as with most widely distributed mammals, temperate lion subspecies like this one were likely more cold-tolerant than their tropical conspecifics (Burger et al. 2004; Barnett et al. 2009). Such disparity in habitat preference can make transplantation challenging (Whiting et al. 2011), although the climate of the Southern Great Plains may be suitable for modern lions (Richmond et al. 2010). However, given the conflict over reintroducing recently extirpated large carnivores, or indeed protecting modern carnivores in their present range, reintroducing pantherine lions to North America may be difficult.

A grand-scale system is needed to help the region as a whole thrive. A rewilding system could be set up that facilitates just such a practice. It would consist of cores, buffers, corridors, and land use reform (Soulé and Noss 1998; Soulé and Terborgh 1999; Foreman 2004). The core areas would consist of national parks, grasslands, and wildlife refuges, as well as privately or tribally owned preserves where hunting would be prohibited. Surrounding these cores would be buffer zones: areas of less control where wildlife would still be allowed to wander, but where recreational activities such as camping and hunting, as well as remote or tribal residence would be permitted. Because these core-buffer areas could be widely spaced, there would be corridors of natural habitat connecting them, so that wildlife would be able to migrate between them.

Outside of these core-buffer-corridor zones, other activities would be permitted, including regular traffic, residence, and industry. However, legislation would offer new and different economic incentives for more sustainable industries. Operations, such as windmill farms and solar panels would not be required, but would be encouraged. Wind and solar energy have yet to become widespread, and are not incompatible with bison ranching, as bison and other animals do not disturb and are not disturbed by windmill towers or enclosed solar panel arrays (Callenbach 1996).

The Great Plains today

For over a half a century, the American Midwest has been growing grains, legumes, and livestock on an industrial scale. Many methods of mass food production, including monoculture and feedlots, are praised as a boon to humanity for helping relieve hunger and labor, but they are also criticized for contributing to environmental nutrient pollution (Howarth, Sharpley, and Walker 2002), and for a lack of concern for the welfare of wild and domestic animals (Licht 1994a; Licht 1994b; Rollin 1995; Licht 1997). The widespread use of pesticides on plants has caused cascading ecological effects (Pimentel 2005), and antibiotics and hormones used on animals can lead to antibiotic resistant bacteria and a reduction in meat quality (Pruden et al. 2006; Landers et al. 2012; Duckenfield 2013). In addition, although food production is important, exhausting the environment's capacity for food production could lead to food shortages in the future. Furthermore, a landscape harnessed purely for commercial gain often loses its aesthetic and spiritual appeal. For all these reasons, the current means of harvesting resources from the Great Plains are untenable in the long run.

It is not feasible to simply quit farming and ranching, for such a move could result in unemployment, food shortage, and conflict. However, instead of staying the present intensive course, the United States could allow the Great Plains to return to a more natural state: a network of native prairie preserves, commons, and ranches supporting bison, elk, pronghorn, and other wildlife, to be visited and sustainably used by people in the region (Popper et al. 1987; Popper and Popper 2006; Popper and Popper 2006). This proposal, known as the Buffalo Commons, was praised by some as farsighted, but local farming and ranching communities, who valued independence and private property, were concerned that it jeopardized their way of life. In contrast, conservation biologists view this proposal as a means for restoring ecosystem processes that have been absent for over a century, and as an opportunity for restoring bison and other grassland animals (Freese et al. 2007; Sanderson et al. 2008). This conflict need not exist. Bison can be understood not just as a conservation imposition, but as an agricultural option, offering a more sustainable way to live with the land. Conservation would follow as a byproduct of such a practice, rather than as an exclusionary goal.

Agriculture is often viewed as a great threat to ecosystems because it requires large amounts of land that replace natural habitat, and because strict control of cultivated property interferes with the functioning of many wild species (Lemly, Kingsford, and Thompson 2000). Agriculture also utilizes a select suite of domesticated plants and animals, most of which are exotic. Nonnative species on wild lands are often considered invasive weeds or pests, but on cultivated lands they are desirable while native wildlife are not. These native weeds and pests can be anything from locusts and nematodes to magpies and prairie dogs, whether they are truly vermin or not (Miller et al. 2007).

In many parts of the world, wildlife is not only threatened by agriculture and development, it is also a limited source of food for growing populations. Empty forests resulting from the bushmeat crisis, most notorious in West and Central Africa, highlight this concern (Davies 2002). A grander, but similar, situation is occurring in the ocean. Fisheries, the world's last great wild food source, are being harvested beyond sustainable rates. Some predict their global collapse by as soon as 2050 (Worm et al. 2006). A seemingly obvious solution has arisen in response to all these concerns, namely wildlife farming, of which the Buffalo Commons is a prime example.

A brief natural history of bovines

Bovines are ruminants both adapted and bred for a variety of environments across the world. Southern Asia's water buffalo (*Bubalus bubalis*) are one of the world's few amphibious ruminants (FAO 1977). Their cousins, Sub-Saharan Africa's Cape buffalo (*Syncerus caffer*) are adapted to the drier conditions of open woodlands (Estes 1991; Ryan, Knechtel, and Getz 2006). The aurochs (*Bos taurus primigenius*) once lived in Eurasia's woodlands and lowlands, Asia's savannas and shrublands, and North Africa's deserts (S. J. G. Hall 2008; Lynch, Hamilton, and Hedges 2008). This species went extinct in the wild in 1627 (Mona et al. 2010), but was domesticated about 10,000 years ago, and became the Western, Indian, and African cattle of today (Beja-Pereira et al. 2006; Ajmone-marsan, Garcia, and Lenstra 2010; S. Chen et al. 2010). Western breeds, such as Angus and Highland cattle, inherited their western ancestors' fitness for cold, moist woodland (van Vuure 2002; van Vuure 2005; Gander 2003; Kaufmann et al. 2013). Indian and African breeds, such as Brahman and Ankole cattle, inherited their ancestors' greater disease resistance and adaptation to hot, open habitats that are either dry or humid (Hanotte et al.

2000; Huber et al. 2008; Desta, Ayalew, and Hegde 2011). Breeds of mixed ancestry, such as Iberian and Texas Longhorn cattle, are also suited to warm climates (McTavish et al. 2013). However, outside of these environments for which they are adapted, cattle struggle.

The American bison (*Bison bison*) evolved in North America's Great Plains, and thrives in its semi-arid grasslands (Lewis et al. 2007; Rivals, Solounias, and Mihlbachler 2007; Hill, Hill, and Widga 2008; Widga, Walker, and Stockli 2010). The Great Plains supported a population of 20-30 million bovines until 1885, when that number fell sharply to fewer than 100 (Isenberg 2000; Freese et al. 2007; Sanderson et al. 2008; Hedrick 2009). Since 1950, the number of bovines in North America has risen to 100 million, about 30 million of which live in the bison's historic range … only now it is domestic cattle (*Bos taurus taurus*) that graze on rangeland once occupied by plains bison (*Bison bison bison)* (Kelliher and Clark 2010; Kohl et al. 2013). Swapping the native wild bovine for an exotic domestic led to many problems. Unlike their native cousin, these exotic cattle have relied on human provisioning to survive the sporadic droughts and snowy winters that the Great Plains can bring. From the 1880s until today, countless cattle have died of thirst or hunger when conditions became too much to bear and people were unable to provide for them.

After near extinction in the 1880s, the bison population gradually grew to 20,000 by the 1930s. The population remained static until the 1970s, when it began to grow again (Freese et al. 2007). As of 2010, it stands at 500,000 (Gates et al. 2010). About 20,000 of these bison, or 4%, remain in conservation herds, but most of the growth has been in commercial herds, making up the other 480,000, or 96% of the world's North American bison. Such numbers are much improved from the mere one hundred bison left at the turn of the 20th Century, but still a far cry from what the plains ecosystem once supported. While the American West supported millions of bison for many thousands of years, it is not clear that it can support more cattle for just a few hundred.

Argument from sustainability

The Eastern United States is moderately to strongly mesic, supporting tallgrass prairie and woodlands (Ricklefs 1993). This part of the country is conducive to agriculture, because with all the moisture, crops grow more readily and animals can be fed and watered relatively easily. This environment also more closely mimics the European environment conducive to western cattle (Roever et al. 2015; Shabtay 2015). The shortgrass prairie to the west, however, receives significantly less precipitation, and this presents a challenge for applying traditional Western agriculture, including the use of most breeds of cattle. However, rather than adapting ranching practices to suit this environment, modern pastoralists have bent the environment to their will instead.

The Great Plains now is not economically self-sufficient, and agribusiness as usual cannot go on like this indefinitely. Once the water in the Ogallala Aquifer has been depleted below usable levels, perhaps some 40 years from now, then it will be gone, and no amount of subsidy will overcome the physical limitations imposed on us by the environment (Sophocleous 2000; Allen et al. 2008). Then there would no longer be enough water to irrigate plant monocultures for industrial farming, or to sustain the region’s 30 million cattle in feedlots. Thus, not only is the current agricultural system on the Great Plains economically unviable and inefficient, but it is not even ecologically sustainable. What is to be done?

One solution is to phase out entitlement subsides, and to restore the Great Plains to its native plant communities, followed by bison and other native wildlife. Tussock grasses stabilize the soil with their strong, deep roots, and require less water than annual grasses (Samson and Knopf 1996; Samson et al. 2004). With forbs dispersed among them, they can support bison and other native game, such as elk and pronghorn. These animals are easy keepers, and can fend for themselves, obtaining food and water from their natural habitat. The females of these wild animals can give birth on their own, unlike highly derived domestic livestock breeds that require human aid during labor. In addition, all but the young, old, or sick of these species can defend themselves against predators by either fighting back or fleeing. Thus, they require little or no assistance from people (Yorks 1989).

A number of related industries can be modified or erected to gain financially from these animals. One is to transition from cattle ranching to bison ranching, a process that is already somewhat underway. The 500,000 bison on the plains today number less than 2% of the 30 million cattle that have taken their place, but they are poised to reclaim their former domain. Ranchers may be reluctant to switch to bison because cattle have more meat on their hindquarters than bison. However, the dressing percentage of bison is higher (Koch et al. 1995). Moreover, the meat of bison and other wild ruminants is leaner and healthier than that of highly derived cattle breeds, which is one reason there is demand for it (Driskell et al. 1997; Rule et al. 2002; McDaniel et al. 2013).

Cattle grow faster than bison, partly because the metabolic rate of bison decreases by about 25% during the winter months (Christopherson et al. 1978; Christopherson et al. 1979). In addition, like horses, wild Bactrian camels (*Camelus ferus*), and domestic Bactrian camels (*C. bactrianus*), bison are among the few mammals that can supplement their moisture intake by eating snow, and that have some ability to sweep away snow to feed on vegetation underneath (Daubenmire 1985; Van Vuren 1987; Walzer and Kaczensky 2005). In the wintertime, cattle stand facing away from storms, but bison face into them instead, presenting their thickest insulation to the wind and snow. They may also walk directly into snowstorms, perhaps to shorten the length of time they must tolerate such conditions. These adaptations in bison are advantageous to people, because they mean that bison require less fodder in the winter, and fewer provisions from people (Reynolds and Hawley 1987; Hawley 1989). Thus, bison stand to be profitable because they require fewer inputs (Hudson and Dezhkin 1989; Luxmoore 1989).

Domestic animals are those that have been artificially selected for certain traits, especially docility. Cattle are domestic animals, and bison are not (Hawley 1989). Cattle can be confined with simple barbed-wire fences, while bison ranching requires more robust fencing (Lueck 2002). In both cases, fences can easily be modified without losing function to allow wildlife, such as pronghorn, to cross them (Scott 1992; Harrington and Conover 2006; Poor et al. 2014). However, fencing in bison is the only aspect of bison ranching that is more expensive. Every other aspect calls for less input of capital. Abattoirs are the same for both species (Hawley 1989), but cattle need more water and shelter, and polled cattle breeds also require protection against predators. Meanwhile, bison can take care of themselves. Because bison are so self-sufficient, ranchers need not invest as much time or money into sustaining their herds. All they need do is leave their bison to pasture, and calmly round them up at harvest time (Hawley 1989; Grandin 2008).

Both cattle and bison can be finished with grain in a feedlot, but this practice poses multiple problems for both species. This discussion deals with substituting bison for beef, so we will focus on feedlots that contain cattle, although there are others for sheep, pigs, horses, turkeys, chickens, and ducks. In fact, there are now even feedlots for bison, but as we will show, they are not suitable for them, either. The undesirable consequences of intensive, industrial-scale animal husbandry in feedlots have been largely documented, but have yet to be alleviated (Lund 2006; Balcombe 2009). In the current system, feedlots seem somehow necessary, because cattle are so ill-equipped to survive the natural conditions of the Great Plains without human intervention. Not so, however, with their native cousins, the bison.

Modern feedlots rely on grain backgrounding and finishing to feed cattle. In the feedlot system, beef cattle are allowed to graze normally for their first year to year and a half of life, at which point the males are castrated. Now known as steers, they are transported to a CAFO, where they are kept at a much higher density than on pasture. Here, they are given a diet of 70-90% grain for the last three to six months of life to accelerate their growth and maximize meat production. However, ruminants like cattle and bison are adapted to a diet of grasses, forbs, and browse, not grain, the starches of which can abnormally alter these animals' gut microbiota and tissues (Waggoner and Hinkes 1986; Redburn et al. 2008; Painter and Ripple 2012).

The feedlot system arose in the 1950s to increase convenience, reduce costs, and make meat more readily available (Wagner, Archibeque, and Feuz 2014). The advantages of this intensive practice are an increase in the growth of the livestock, and a decrease in space needed to support them. However, the feedlot system entails the added expense of the grain. As long as grain costs are low, grain-feeding also saves on transportation costs (Russell and Rychlik 2001; Fernando et al. 2010; Chen et al. 2011). The feedlot system also calls for more fuel consumption and oversight, and creates unsafe, inhumane conditions for animals, as well as lower quality food for people. Although its products appear to be cheaper for the consumer than those from pastured animals, this perception is an illusion. Government subsidies are what keep CAFOs afloat, and without them, they would be unable to compete with free-range cattle and other livestock (Alston, Sumner, and Vosti 2008). These subsidies also do not account for externalities like animal waste, which on normal grazing pastures remains diffuse and serves as fertilizer. On feedlots, however, waste accumulates and becomes concentrated, turning into chemical and biological pollution that must be stored and transported away to avoid insect infestation and groundwater contamination. When it is not properly contained, waste from industrial farms and feedlots dumps some 4.6 million tons of pesticides and 38 billion tons of fertilizer worldwide each year (Pimentel et al. 1997; Pimentel 2005; Zhang, Jiang, and Ou 2011). However, instead of fertilizing the soil, this waste becomes runoff that pollutes the water table and rivers, traveling downstream to pollute far away areas as well. The Gulf of Mexico's infamous "Dead Zone" is caused by an excess of nitrogen and phosphorus released from the Mississippi River, leading to algal blooms and hypoxic waters where zooplankton, fish, and marine birds and mammals cannot survive (Hanley 1990; Novotny 1999; Sneeringer 2009).

Another problem is that feeding grain to herbivores can reduce the nutritional quality of their meat (Cordain et al. 2002). Grain-finished cattle have a less nutritious meat profile, with higher levels of fat and cholesterol, and lower levels of vitamins, antioxidants, omega-3 fatty acids, and conjugated linoleic acid than their grass-finished counterparts (Wood et al. 2004). This is to be expected, because not only does the ruminant digestive tract function better with herbivory than granivory, but ruminants (like most animals) also sequester nutrients from the organisms they eat in their tissues; the more nutritious their food, the more nutritious their flesh. The problem of lipid accumulation is exacerbated in derived breeds of cattle, which have been artificially selected for "marbling." This condition was developed to improve taste, but really results from abnormally high levels of intramuscular fat (Harper and Pethick 2004).

Finally, the risk of disease increases when cattle are not allowed to graze as they are adapted to do. Under artificial conditions, cattle are sometimes given high-protein feed that includes brain and spinal cord from other cattle. This practice has led to the prion-caused disease known as bovine spongiform encephalopathy (BSE, or mad cow disease) in cattle, and subsequently variant Creutzfeldt-Jakob disease in humans who have eaten contaminated beef (Kimberlin and Wilesmith 1994; Brown et al. 2001). Herbivores may occasionally eat some animal matter to supplement their protein intake, but they are not cannibals, and eating large amounts of muscle and nervous tissue from their own or related species is completely alien to them. Understanding and appreciating the niche of cattle as ruminant herbivores – not cannibalistic omnivores – could have prevented the rise of BSE, and will likely be the greatest factor in the eradication of this infectious disease, as well as the prevention of others.

Being ruminants, bovids like cattle and bison (as well as cervids like elk) have a four-chambered stomach that houses symbiotic bacteria to help them digest the tough, cellulosic fibers of plants (Van Soest 1994). Their diet naturally consists of a great deal of roughage, which the bacteria break down to simpler compounds that their host can use for nutrition (Waggoner and Hinkes 1986; Redburn et al. 2008; Painter and Ripple 2012). Giving these animals a diet of grain is known to wreak havoc on this delicate micro-ecosystem. The high starch content of grain promotes the growth of certain bacteria that are normally not especially abundant, creating an imbalance of the microbial community known as dysbiosis. In response to this new resource, *Gammaproteobacteria* in the reticulorumen become more abundant, causing the host to shed enterohemorrhagic bacteria like *Escherichia coli* O157:H7, which can cause disease in humans when they contaminate meat (Krause and Oetzel 2006; Nagaraja and Titgemeyer 2007; Plaizier et al. 2008). These *Gammaproteobacteria* ferment starch and cause the pH of the reticulorumen (normally neutral) to drop to 5.0 or lower. This condition, known as ruminal acidosis, can cause anorexia, and if left untreated, can erode the walls of the reticulorumen, leading to infection and even death of the ruminant host (Dyer and Newell 2002), (Greg Penner, personal communication).

Such infections may be avoided by putting cattle back on forage a few days prior to slaughter, a practice that allows ruminal pH to rise back to neutral levels, and bacterial community composition to return to normal. However, animals are often given antibiotics instead or in addition to a more natural diet. Antibiotics are given to feedlot animals because they live at abnormally high densities, in unsanitary and stressful conditions that promote the spread of disease from one individual to another. Feedlots also administer prophylactic antibiotics to apparently healthy animals, to prevent them from developing infections in the first place. This is the reason feedlots use 80% of the antibiotics in the United States, much more than any other sector, as they are where most of the sickness resides. The problem is that such frequent, indiscriminate use of antibiotics tends to lead to the development of antibiotic-resistant bacteria, which can and have created untreatable infections not only in animals, but in people as well (Heuer, Schmitt, and Smalla 2011; Jechalke et al. 2014; Woolhouse and Farrar 2014).

Being descended from the Eurasian aurochs, indicine and African cattle, such as Watusi, Brahman, and Iberian breeds do well in the deserts of the Southwest, while taurine cattle, like Angus, Hereford, and Holstein do well in the moist forests of the eastern United States. However, in the cold, semi-arid Great Plains, both lineages require assistance to survive and be of economic value. This is why taurine cattle prefer the cover of vegetation over open habitat, and loiter about streams, eroding the banks and clouding the water (Kohl et al. 2013). They must feed on forbs and drink frequently, for without this moisture, their health will decline (Fynn and O’Connor 2000). Cattle also eat nearly the same amount of food year round, and are unable to forage when the ground is covered in snow. In addition, the cows of highly derived breeds require human assistance during labor. Furthermore, polled (hornless) cattle cannot defend themselves against carnivores like wolves. For these reasons, it takes more time, money, and effort to ranch cattle in the semi-arid Midwest.

However, bison are superbly adapted to the grasslands of North America (Estes 1991). With their core range in the prairies, these animals can feed on perennial grasses, especially C_4 species (Vuren & Bray 1983; Damhoureyeh and Hartnett 1997; Towne et al. 2005), as well as forbs and browse (Waggoner and Hinkes 1986; Larter and Gates 1991; Painter and Ripple 2012; Bergmann et al. 2015), leading (Cannon 2001) to dub them “adaptive specialists.” In addition, bison do not spend much time near water. Although they usually need to drink daily, once they have had their fill, they leave the water behind (Allred et al. 2011; Kohl et al. 2013; Ranglack and du Toit 2015). For this reason, bison may be better able to adapt to climate change, which is expected to bring hotter temperatures and less precipitation to the Great Plains - changes that could lead to drought (Craine et al. 2015). A hotter, drier prairie would likely have a negative effect on many animals, including bison. However, bison would fare better under such conditions than woodland-adapted taurine cattle, while remaining more cold-tolerant than scrubland-adapted indicine and African cattle.

Unlike derived breeds, the cows of primitive cattle and bison do not require assistance in giving birth, and are able to defend themselves against carnivores unless they are very young, old, or sick. Finally, like other wild bovines, bison can use their horns or hooves to defend themselves. Those breeds of domestic cattle that still have their horns retain this ability, but those bred or altered to be hornless (polled) are more vulnerable to carnivores than their intact brethren.

Having evolved in the Great Plains, bison are able to live at equilibrium there. Indeed, like prairie dogs (*Cynomys* spp.), bison are considered a keystone species, because their activities have such a large effect on the structure and dynamics of prairie ecosystems (Knapp et al. 1999; Truett et al. 2001; Fahnestock and Detling 2002). Bison and cattle may be closely related, but their interactions with the prairie are not the same. Bison exhibit the behaviors of wallowing and horning, which are found in some other wild ungulates as well. Perhaps aurochs once performed these behaviors as well, but today, domestic cattle do not. When bison wallow, they rub their flank and belly on the earth, covering themselves in dust. This behavior probably serves to relieve itching, and the dust bath helps protect them against pests and parasites (Mooring and Samuel 1998). Wallowing can also serve as a social or agonistic display (McMillan et al. 2000; Trager et al. 2004). Bison also horn the ground, a behavior that likewise may be used for hygiene, communication, or relieving frustration (G. Bergmann, *personal observations*), but may also serve to expose soil minerals so they can be ingested (Beyer, Connor, and Gerould 1994). Mineral licks are an important resource for many herbivores, because they allow them to obtain nutrients lacking in their regular diet. Both wallowing and horning serve to create localized disturbances in the soil. These activities promote ecosystem diversity because they create gaps in stands of grass, as well as depressions where water can collect. This allows other types of vegetation to coexist with the dominant grasses, and this plant diversity in turn facilitates animal diversity.

If bison were to replace conventional sources of animal protein, our society could be better provided with a healthy form of meat at a fraction of the economic, environmental, and animal welfare cost. Bison are better equipped to deal with the elements of a Western environment, and suffer less than cattle in the winter. Their adaptations mean that bison ranchers do not have to force the animals into close quarters in winter, do not have to supply them with food to which they are not adapted to digest, and can essentially let the animals' natural life cycle dictate an appropriate harvest. Ruminal acidosis can occur in other ruminants besides cattle, including their close relatives, the bison (Dyer and Newell 2002). For this reason, it is both cheaper and more beneficial for human consumers to allow both cattle and bison to forage as they are adapted to do, with western cattle in the cool, mesic parts of North America in the East, indicine and African cattle in the hot, arid parts of North America in the Southwest, and bison in the cold, semi-arid parts of North America in the West and Midwest.

Thus, switching to bison and elk (indeed, *back* to bison and elk) solves multiple problems at once. By using native livestock that can graze in the open, we raise animals that are both healthier to eat and more benign for the environment. This benefit in turn allows ranchers and consumers alike to save money, because the main difference in investment for bison and elk as opposed to cattle is robust fencing. With such a system, little or nothing needs be spent on grain for fodder, environmental cleanup, or wildlife extermination. Moreover, because native ranching would take the place of monoculture where it is unsustainable, the government and the taxpayer would likewise save billions of dollars every year in fertilizer, pesticide, and herbicide costs. Bison are the native bovine of the Great Plains, and their presence is crucial to the resilience of the grassland ecosystem. In the long run bison can win, but cattle likely cannot. The Great Plains are not being managed in a sustainable manner, but bison conservation promotes the stability of prairie ecosystems, and bison ranching promotes the sustainable use of land for people as well. Protecting and utilizing bison are two sides of the same conservation coin.

Additional benefits to diversified ranching

Pastoral cultures have long used livestock as wealth (Fratkin 1989; Roth 1996; Reading, Bedunah, and Amgalanbaatar 2006). America could think of a great herd of bison in a similar way. The bison would be a gold standard; a hardy species able to handle the inclemency of the North American climate, a source of national pride, a reservoir of resources, and keepers of vast portions of our continent. Ranching bison and other livestock for meat, byproducts, and ecotourism on restored, diverse prairie habitat stands to serve as a major source of income for rural and native people in the Great Plains. Diversified ranching and tourism have the potential to join the milieu of Great Plains industries, and to help make the region's economy both prosperous and sustainable.

North America's indigenous peoples benefit greatly from bison ranching. Many American Indians lack a livelihood, relying instead on welfare. Unfortunately, much of the food they receive is of poor quality, being high in calories from fats and carbohydrates, but low in essential protein, vitamins, and minerals (Zontek 2007). Access to bison is important to American Indians, not only because the animals are of spiritual significance to them, but also because the meat is nutritious, especially for those with few other healthy foods. One non-profit organization, the InterTribal Buffalo Council (ITBC), serves 56 tribes in 19 states, and collectively owns more than 15,000 bison. The people affiliated with ITBC benefit from its administration, and many others stand to benefit as well. Many American Indian tribes are restoring bison to their reservations under the ITBC because they understand and appreciate the bison as part of their identity. Other Americans would be wise to follow their lead, and recognize the bounty of resources, both natural and cultural, that bison offer. A great herd of bison supports the pursuit of various aspects of American pride and identity; they can be hunted, they offer an environment that is both aesthetically and ecologically continuous, and they maintain their ecosystem. Bison literally define the landscape, both creating and representing a wild and abundant region.

Promoting animal welfare is another reason to switch from intensive industrial farming to sustainable diversified ranching. Regardless of one's ethical theory, causing suffering to sentient animals for no good reason will likely be seen as wrong (Callicott 1988; Sumner 1988; Russow 2002). The current norms of meat mass production necessitate that livestock, such as cows and chickens, will have horrible lives (Rushen and Passillé 1992). The philosophical discourse on animal welfare has presented many criticisms of this, ranging from utilitarian objections to the causing suffering, to deontological concerns for animal autonomy (Bennett et al. 2002; Broom 2008; Veissier and Forkman 2008). This debate is far from settled, but few would likely argue that, all else being equal, less animal suffering would be bad. Ordinary intuition suggests that if we did not need to make animals suffer to gain the instrumental value of meat consumption, then that would be a good thing (Gregory 1998). Unlike cattle, bison can live relatively natural lives in North America, unencumbered by humans, and with a high level of welfare. Bison ranching requires little human-inflicted suffering to give meat markets an equivalent amount of protein to what is currently provided through the needless torture of millions of similar animals.

With a conservation ethic, the prairie could be restored on a grand scale, but still harvested sustainably. Charismatic megafauna would allow for comprehensive conservation of wildlands, while also allowing for concurrent diversified ranching. This would be good for bison, elk, and other animals, and it would be good for people, too. The integrity of the ecosystem in which animals and people live is worthy of protection, for wildlife have intrinsic value as lifeforms with interests, and as sentient beings with the capacity to suffer (Leopold 1949; Varner 1998). Therefore, it is our moral imperative to support not only people in the Great Plains, but also the native animals there and the prairie they inhabit.

Wildlife Services (formerly Animal Damage Control, a program of USDA-APHIS) needlessly traps and poisons thousands of wild animals regarded as pests each year (Licht 1994a; Licht 1994b; Licht 1997). These include small herbivores like prairie dogs (*Cynomys* spp.). Although these animals do have significant niche overlap with larger grazers, at natural population densities prairie dogs can actually improve range quality for wild ungulates like bison, pronghorn, and elk (Coppock et al. 1983; Krueger 1986; Miller et al. 2007; Chipault and Detling 2013), and even for domestic livestock like cattle (O'Meilia, Knopf, and Lewis 1982; Miller et al. 2007; Sierra–Corona et al. 2015). However, most of the victims of Wildlife Services are carnivores, such as cougars, lynx, bobcat, black bears, grizzly bears, wolves, coyotes, red foxes, kit foxes, gray foxes, badgers, black-footed ferrets, and raccoons. Killing predators in defense of livestock is justifiable, but persecuting the carnivore guild in anticipation of predation is unnecessarily cruel, especially when most of these carnivores are too small to pose a threat to livestock, and are valuable in suppressing the populations of their prey animals (Korpimaki and Krebs 1996; Roemer et al. 2009; Elmhagen et al. 2010). Large carnivores (cougars, wolves, and bears) pose a greater threat to polled cattle than horned cattle (Goonewardene et al. 1999; Stankowich and Caro 2009; Knierim et al. 2015) or bison (Carbyn and Trottier 1988; Green and Rothstein 1993; Varley and Gunter 2002), both of which are better able to defend themselves against predators by virtue of their natural weaponry. Using naturally fit livestock not only makes ranching less labor-intensive, it also makes it more compatible with the surrounding ecosystem.

Bison and elk offer a path toward comprehensive prairie conservation. As both a keystone species and a charismatic umbrella species, bison can promote the protection of plains habitat and vegetation, as well as other important herbivores, such as prairie dogs, pronghorn, elk, mule deer, and whitetail deer. Moreover, relying on these robust animals would allow people to reduce or cease the extermination of small and large carnivores, a measure that would spare both expense and suffering. Thus, we would be able to stop persecuting not only black-footed ferrets, badgers, foxes, coyotes, and bobcats, but also wolves, cougars, and bears. These animals would not be considered such a grave threat if our livestock could defend themselves.

Using bison instead of crops or cattle would facilitate the restoration of native prairie grasses and forbs, which stabilize topsoil and prevent erosion and dust storms. Bison are not immune to droughts, but need less water than western cattle (van Vuren 1983; Fuhlendorf, Allred, and Hamilton 2010; Allred, Fuhlendorf, and Hamilton 2011; M. T. Kohl et al. 2013), while being more tolerant of the cold than indicine and African cattle (Christopherson, Hudson, and Richmond 1978; Christopherson, Hudson, and Christophersen 1979). In Western and Plains states, an agricultural system centered on bison and elk ranching would be more resistant to environmental stressors than one based on tillage, and would help prevent another Dust Bowl like that of the 1930s from appearing. With bison as livestock, ranchers would not need to be as involved in the operations of their pastures, and would be able to take a more hands-off approach, allowing a wide range of wild species to flourish nearby, without being threatened by these other animals.

Concerns

Around the turn of the 20th Century, when bison were critically endangered, some ranchers rescued them but enforced hybridization with domestic cattle (Geist 1996; Isenberg 2000; Lott 2002; Zontek 2007), producing animals known as “cattalo.” The resulting female offspring were fertile, but not so the males, a pattern seen in many interspecific hybrids, known as Haldane’s Rule (Haldane 1922). This setback led to the abandonment of the project, although some ranchers still intentionally breed “beefalo,” a hybrid that is 3/8 bison and 5/8 cattle (Drew and Baskin 1989). In both cases, the purpose of this artificial crossing was to obtain livestock with the toughness of bison, but the yield of cattle.

Such historical practices have complicated bison conservation today, when most bison exhibit 3-5% cattle gene introgression, meaning that although they look and behave like pure bison, they carry a small percentage of cattle genes from when their ancestors were hybridized with cattle a century ago. Such bison have no recent history of hybridizing with cattle, but carry some genes from that event in the past (Todd J. Ward et al. 1999; T J Ward et al. 2001; Kiesow, Kasmarik, and Binstock 2011). Cattle introgression has been detected in nuclear and mitochondrial DNA from both commercial and conservation herds, but the phenomenon is more prevalent in the former. For this reason, conservation and commercial herds are kept separate and not allowed to interbreed. Only a few herds remain with no evidence of cattle introgression, including those of the Yellowstone and Wind Cave National Parks (Halbert et al. 2005; Halbert and Derr 2007).

The phenotypic effects of cattle introgression on American bison have been little studied, although American bison with cattle introgression have been shown to be smaller than pure American bison (Derr et al. 2012). However, the effect of this difference on fitness has yet to be demonstrated, and in other respects, bison with cattle introgression appear to be as healthy as pure bison. This is similar to what is seen in other mammals with gene introgression from related species, such as coyotes (*Canis latrans*) with introgression from wolves and dogs (*C. lupus*) (Kays, Curtis, and Kirchman 2009; P. J. Wilson et al. 2012; Wheeldon et al. 2013), and humans (*Homo sapiens*) with introgression from Neanderthals (*H. neanderthalensis*) (Mendez et al. 2012; Mendez et al. 2013; Ding et al. 2014a; Ding et al. 2014b). None of this is to say that introgression should be encouraged, but rather if it has occurred, it is not necessarily detrimental, and may actually be adaptive (Evans et al. 2006; Abi-Rached et al. 2011; Hedrick 2013; Racimo et al. 2015).

American bison were reduced from some 30 million to less than 100 in the 19th Century, causing some reduction in their genetic diversity (Freese et al. 2007; Hedrick 2009; Gates et al. 2010; Hedrick 2010). Today's population of about 500,000 represents a conservation success, but only a partial recovery, as there are still only about 1/60th as many bison as there were just over a century ago. Only a few thousand of these bison in conservation herds are considered genetically pure, and the rest – in conservation and commercial herds alike – have some level of cattle gene introgression. Given the compromised gene pool and relatively small population size of American bison, we cannot afford to ignore the vast majority of bison alive today, especially when gene introgression is not necessarily harmful (Hawks 2007).

Even without cattle gene introgression, some conservationists are concerned that commercial bison ranching may cause bison to become extinct in the wild, as happened with aurochs, or to remain extant but vulnerable or endangered, like the wild conspecifics of some other livestock (sheep, goat, yak, gaur, water buffalo, camel, llama, alpaca, horse, and ass) (Luxmoore 1989). This need not be the case, however. Boar (*Sus scrofa*) and reindeer exist both in the wild and in captivity, and can continue to do so as long as they are not threatened by overhunting or habitat loss.

The last concern is that commercial ranchers will domesticate the bison, altering its behavior and morphology for increased financial gain (“less hump, more rump”) (Lott 2002). Unlike many other bovine species such as cattle (*Bos taurus*), yak (*B. grunniens*), gaur (*B. frontalis*), and water buffalo (*Bubalus bubalis*), the American and European bison (*Bison* spp.) have never been domesticated, and may not have the potential for domestication. It may be possible to selectively breed bison for different characteristics (Sanderson et al. 2008; Gates et al. 2010). However, this need not be the case, for it is feasible and even desirable to continue keeping them as wild livestock, without ever altering or domesticating them. Bison that have been artificially selected for certain traits should be kept separate from wild populations to prevent genetic pollution. However, many bison ranchers want to preserve the wildness of bison, because they value their toughness and want them to be able to forage naturally, defend themselves against carnivores, and calve on their own (Dave Carter, Executive Director of National Bison Association, *personal communication*). Such ranchers can be great allies to conservation biologists and wildlife managers in efforts to restore bison, and may be the great catalyst that refills the plains with bison, elk, and other animals once again.

Wildlife livestock

The idea of using wildlife as a sort of stock is not novel. Fish stocking, particularly of salmon in the Pacific Northwest, offers an ambitious example. Each year, millions of salmon (*Oncorhynchus* spp.) are released into the streams, to be fished recreationally and commercially from April to October (Stouder et al. 1997). Terrestrial wildlife can be used in a similar but subtler way. Wild game ranching has been around since Ancient times in Eurasia, and resumed during the 1960s in parts of Eurasia, Africa, North America, and Australia (Drew, Bai, and Fadeev 1989; Fletcher 1989).

Wild ungulates have been naturally and not artificially selected, so they have certain advantages over domestic livestock, such as resistance to drought and disease, and higher dressing percentages. In addition, several different ungulate species can be kept on the same range. Because they occupy different niches (browsers, grazers, and mixed feeders), they compete little and can utilize resources more efficiently and completely than can large herds of the same species (Hudson and Dezhkin 1989; Watson and Owen-Smith 2000). However, a disadvantage is that wild ungulates are typically more agile and more difficult to enclose or capture. Unless care is taken to keep them calm and accessible, and unless they are speedily dispatched, the quality of their carcass can be affected (John D. Skinner 1989; Carruthers 2008). Nevertheless, wild ungulates provide meat to people who live in areas ill-suited to livestock of Central Eurasian origin, such as cattle, sheep, and goats. Reindeer are a circumpolar species, some of which have remained wild, while others have been used as semi-domesticated livestock in Eurasia since at least the 1600s CE, and perhaps as early as 800 CE (Andersen 2011).

The African nations of Kenya, South Africa, and Zimbabwe have been pursuing private game ranching as an economically viable means of conserving wildlife since the 1960s. Most of this sector consists of recreational hunting (66%), and the trade in meat makes up only 1%. Of this, only a fraction comes from fresh meat, with the majority coming from biltong, or cured meat (Carruthers 2008). A number of species are used in this industry, including ostrich, common and giant eland, greater kudu, springbok, bontebok, blesbok, and Cape buffalo. Since the 1970s, South Africa and Zimbabwe have been ranching the native common eland

(*Taurotragus oryx*) and giant eland (*T. derbianus*) as an alternative to Africa's already drought-tolerant breeds of domestic cattle. Although they do not form large herds like cattle, eland can forage on the native vegetation, without provisioning or protection. In fact, while cattle are grazers, eland are browsers, so the two species partition their environment and can be maintained in the same area without much competition (Watson and Owen-Smith 2000). Like American bison, eland are more agile than domestic cattle, so modified fencing is required to keep them confined in a given pasture. Otherwise, however, maintaining them is not labor-intensive or cost-intensive. Thus, African ranchers have benefited by diversifying their livestock with these native herbivores.

Since the 1980s, Australia has also been involved in sustainable wildlife enterprises to diversify their animal resource base. Like Africa and North America, Australia is characterized by large areas of arid and semi-arid land inhospitable to domestic livestock. Although still not commonly harvested, emus (*Dromaius novaehollandiae*), kangaroos (*Macropus* spp.), and feral dromedary camels (*Camelus dromedarius*) are abundant, and Australians are increasingly turning to them as alternative sources of meat. The meat of emus and kangaroos is both nutritious and palatable, and Aborigines have been hunting them for thousands of years (Adams et al. 1997; Moloney et al. 2011; G. Wilson et al. 2013). Dromedaries were introduced to Australia in 1840, and now number about one million (Spencer and Woolnough 2010). All three of these species are adapted to dry environments, need no supplemental food or water, and are lighter on the land than cattle.

In South America, people have been using the native lamine camelids for thousands of years. About 6,000 years ago, the wild guanaco was domesticated into the llama, and the wild vicuña into the alpaca, with hybridization occurring between the two domestic forms along the way (Stanley, Kadwell, and Wheeler 1994; Kadwell et al. 2001; J. C. Wheeler 2012; Barreta et al. 2013). Both animals are widely used in South America today, and have even been exported elsewhere. Wild guanacos once numbered 30-50 million, but after extensive hunting and some recovery, now number only about 600,000 (Raedeke 1979; Lauenroth 1998; Coates and Ayerza 2004; Marin et al. 2008). However, today live-shearing of guanaco wool allows these animals to be used sustainably, and could allow their numbers to increase (Lichtenstein and Carmanchahi 2012; Carmanchahi et al. 2011; Rey et al. 2012; Carmanchahi et al. 2014). There were once millions of greater rhea and Darwin’s rhea on the South American Pampas, but overhunting and habitat loss have caused them to become near-threatened (Conway 2005). However, like the ostrich and emu, local farmers now raise them for their meat, eggs, hide, feathers, and oil (Sales et al. 1999; Navarro et al. 2001; Uhart and Milano 2002).

What’s more, game ranches in the USA, UK, Ukraine, and Russia have taken up ranching some of these exotic animals as well. In addition to Eurasian livestock, they now have access to ostrich, emu, rhea, llama, alpaca, and common eland. These animals make up smaller markets outside of their native countries, but demand has grown. Since the 1960s, exotic game ranches in Texas and elsewhere in the United States have supported numerous species of deer, antelope, sheep and goats, bovines, and other ungulates for the purposes of conservation, hunting, and meat production (Mungall 2007). This practice takes place legally on private land, and may even be morally justified. However, the impetus for restoring native megafauna or their proxies (J. Donlan et al. 2005; C. J. Donlan et al. 2006) should be at least as strong if not stronger.

Ironically, although American farmers do use the native turkey, the bison garners only a small market share in the United States, even though they perform well in their native habitat. If there is a place in American ranching for domestic animals such as chickens and cattle, and exotic animals such as emu and alpaca, then surely there must also be a place for wild, native animals like bison and elk. American ranchers and the systems they manage stand to benefit from native animals, just as those in Eurasia, Africa, and Australia have done with their own.

Implementing policy

Comprehensive prairie conservation with sustainable, diversified ranching could be put into effect in the Great Plains through a series of steps. First, exclusive rights for ranching domestic cattle on the shortgrass steppe could be gradually removed, as would subsidies for industrial crops and feedlots. In their place, tax breaks would be initially offered for people to restore native prairie grasses, forbs, and woody vegetation, and to ranch native bison and elk. Again, these activities would not be required, only incentivized. In a few years' time, once populations had become established, such incentives could be removed, leaving funds only for relief and grants, and making the Great Plains economically viable once more. Because wildlife in the core-buffer areas would proliferate, such operations would have the opportunity to absorb animals migrating on their property as part of their commercial herds. Diseases like brucellosis, bovine tuberculosis, malignant catarrhal fever, Johne's disease, and others would of course be monitored, prevented, and controlled as needed. With such a system in place, the Great Plains would become self-sufficient and sustainable in only a few years.

Conclusion: argument from American identity

Bison are intricately tied to American identity. For many people the shaggy beasts are merely a nostalgic, collective memory, but they need not be. Just as Americans have chosen to deliberately and decisively protect other aspects of American heritage, be it natural grandeur (Yosemite National Park) or cultural history (ranching culture), the Great Plains can be preserved as an aspect of American identity as well.

One main issue is tolerance. The authors' community of Boulder, Colorado, known for being environmentally astute, recently rejected a plan to reintroduce a small herd of bison into its city limits (Meltzer 2012). Ted Turner offered twenty young bison to the town as a gift, partly for its location in the American West, and partly because the mascots of the University of Colorado, Boulder are Ralphie, a real bison, and Chip, an anthropomorphic one. The town rejected the plan for various reasons: concerns with cost, unsatisfactory location, public disapproval of fencing, and restrictions the bison would place on Open Space. Despite the identification with and celebration of the animal as a symbol, the city was not willing to make concessions or sacrifices to share their space with these animals. Arguments for tolerance may be more palpable if Boulderites and other Americans, particularly of the Great Plains region, consider bison a part of their identity. Bison are the American bovine. They are the emblematic animal of America's heartland. They are distinct to the continent and the region, and offer Americans the chance to identify with their natural home in a number of ways.

Meanwhile, countries in Eurasia are ahead of the United States in their Pleistocene rewilding programs (Fraser 2009; Monbiot 2013). Scimitar-horned oryx (*Oryx dammah*) have been successfully reintroduced to Saudi Arabia, and thanks to the Rewilding Europe program, primitive Konik horses (similar to the extinct tarpan subspecies) and primitive Heck cattle (similar to the extinct aurochs subspecies) have been reintroduced to the Netherlands, as have horses and cattle, in additional to wisent or European bison (*Bison bonasus*) been reintroduced to Latvia (Marris 2009; Navarro and Pereira 2012; Gross 2013; Seddon et al. 2014). Primitive horses have also been reintroduced to the Danube Delta, and so have wisent and brown bears (*Ursus arctos*) been reintroduced to the Carpathian Mountains. Chamois (*Rupicapra rupicapra*) and griffon vultures (*Gyps fulvus*) have also been reintroduced to Croatia, and horses, Iberian ibex (*Capra pyrenaica*), and Iberian lynx (*Lynx pardinus*) have been reintroduced to the Iberian Peninsula. In addition, Sergey and Nikita Zimov operate the renowned Pleistocene Park in Siberia, where they have reintroduced moose (*Alces alces*), elk, reindeer, musk oxen (*Ovibos moschatus*), wisent, and horses (Zimov 2005).

Gary Snyder and Gary Paul Nabhan, among many others, have called for an environmentalism stemming from a connection to place. By “living in place” and being aware of both the local environment and its restrictions, one can better harmonize with and embrace one’s surrounding native species and climate (Snyder 2008; Gary Paul Nabhan 2012). This movement, bioregionalism, inspires one to live better in coordination with the natural environment, rather than to sidestep or conquer it with technology. Snyder encourages Americans to become “native” Americans, to live as Americans rather than as Europeans in America. One way to be bioregional is to change one’s eating habits, and to eat what grows well near you: salmon in the Northwest, lobster in the Northeast, elk in the Mountain West, moose in the North, deer in the East, and bison in the Great Plains.

Environmentalists increasingly focus on food. Organic and local food movements are motivated by concerns for the health of both our environment and ourselves. Renewing America’s Food Traditions [RAFT] and other organizations promote local food cultures so that they are not lost, and so that people can live lighter on the land. This approach is as much about saving tradition and cultural identity as about protecting the environment. A great herd of bison would offer a fundamental food source for a huge bioregion of this continent: a “Buffalo Nation”

(Zontek 2007). Such a project, and coordination of its stakeholders, would protect not just the bison and their ecosystem, but also forty-seven traditional foods currently threatened or endangered, including Lakota squash, Lola Queen peach, and the Texas wild pecan (Nabhan and Rood 2004). This emphasis on food is simultaneously pragmatic and principled, because including sustenance in our conception of nature ties us to our environment, both biologically and ideologically.

Final statement

There is an urgent need to reform land use practices in the Great Plains. Not only are prairie habitats and their flora and fauna endangered, but current means of procuring precious food are unsustainable and have long been part of boom-and-bust cycles, environmental degradation, poverty, and emigration. Finding suitable areas for restoring prairie and using diversified livestock, such as bison and elk, will prove invaluable as sources of food, employment, education, recreation, and spirituality. Large, continuous, and interconnected expanses of suitable habitat are needed for fostering conservation, sustainable agriculture, and interchange between the two. It is great news that the Northern Great Plains is currently involved in large-scale prairie restoration, but the Southern Great Plains should not be overlooked in this regard. Allocating resources toward the procurement and protection of a Great Plains habitat network for private and public gain should be a priority of this and future administrations.

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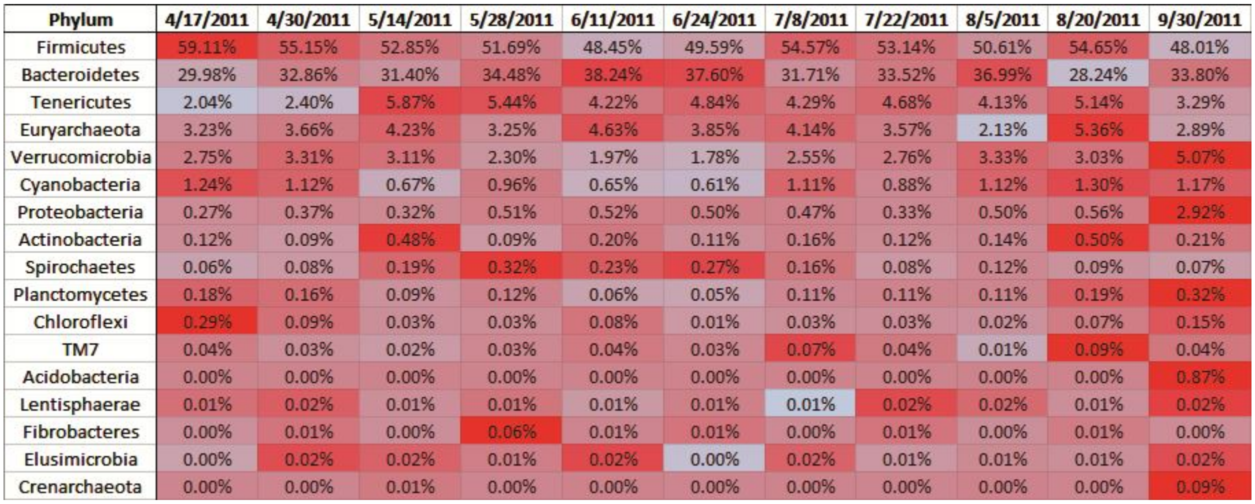
TABLES

Table 1.1. Heat map showing relative abundance of microbial phyla over time, based on sequences recovered from the feces of free-ranging bison. Numbers indicate mean relative abundance. Colors indicate z-score, with red representing positive z-scores, blue representing negative z-scores, and brightness of color representing absolute value of z-scores.

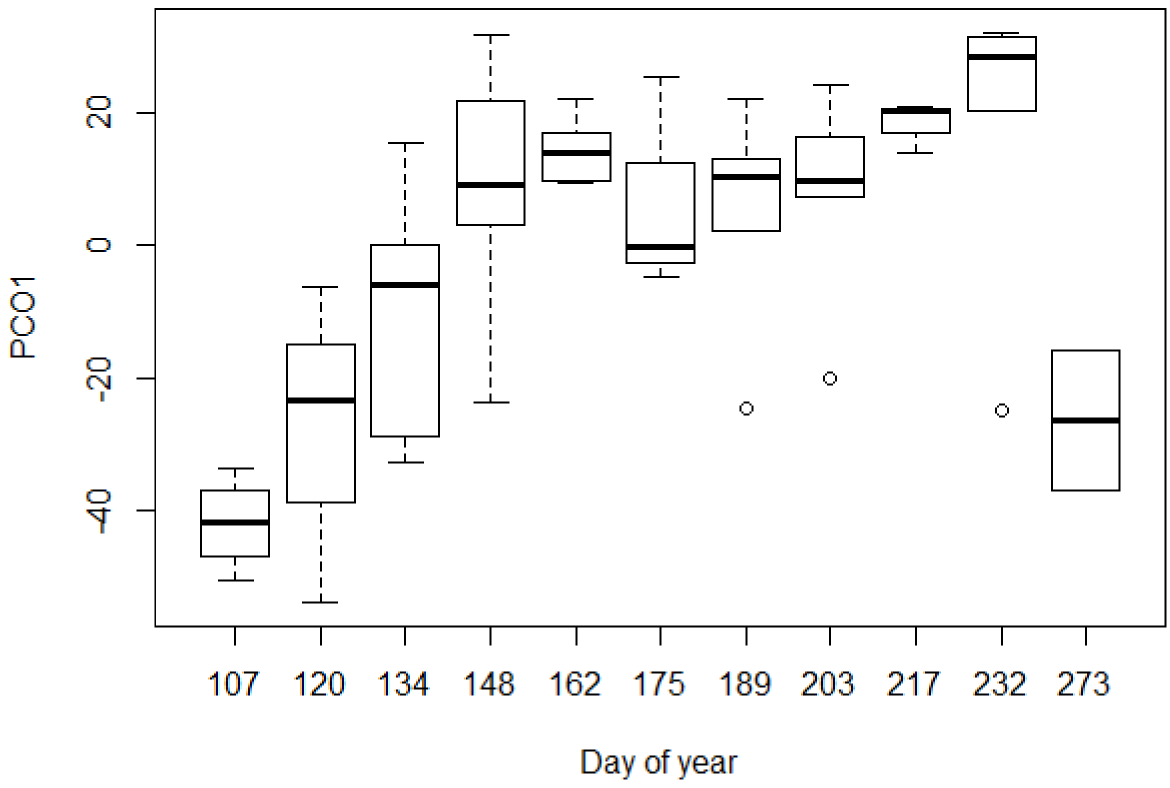


Phylum	4/17/2011	4/30/2011	5/14/2011	5/28/2011	6/11/2011	6/24/2011	7/8/2011	7/22/2011	8/5/2011	8/20/2011	9/30/2011
Firmicutes	59.11%	55.15%	52.85%	51.69%	48.45%	49.59%	54.57%	53.14%	50.61%	54.65%	48.01%
Bacteroidetes	29.98%	32.86%	31.40%	34.48%	38.24%	37.60%	31.71%	33.52%	36.99%	28.24%	33.80%
Tenericutes	2.04%	2.40%	5.87%	5.44%	4.22%	4.84%	4.29%	4.68%	4.13%	5.14%	3.29%
Euryarchaeota	3.23%	3.66%	4.23%	3.25%	4.63%	3.85%	4.14%	3.57%	2.13%	5.36%	2.89%
Verrucomicrobia	2.75%	3.31%	3.11%	2.30%	1.97%	1.78%	2.55%	2.76%	3.33%	3.03%	5.07%
Cyanobacteria	1.24%	1.12%	0.67%	0.96%	0.65%	0.61%	1.11%	0.88%	1.12%	1.30%	1.17%
Proteobacteria	0.27%	0.37%	0.32%	0.51%	0.52%	0.50%	0.47%	0.33%	0.50%	0.56%	2.92%
Actinobacteria	0.12%	0.09%	0.48%	0.09%	0.20%	0.11%	0.16%	0.12%	0.14%	0.50%	0.21%
Spirochaetes	0.06%	0.08%	0.19%	0.32%	0.23%	0.27%	0.16%	0.08%	0.12%	0.09%	0.07%
Planctomycetes	0.18%	0.16%	0.09%	0.12%	0.06%	0.05%	0.11%	0.11%	0.11%	0.19%	0.32%
Chloroflexi	0.29%	0.09%	0.03%	0.03%	0.08%	0.01%	0.03%	0.03%	0.02%	0.07%	0.15%
TM7	0.04%	0.03%	0.02%	0.03%	0.04%	0.03%	0.07%	0.04%	0.01%	0.09%	0.04%
Acidobacteria	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.87%
Lentisphaerae	0.01%	0.02%	0.01%	0.01%	0.01%	0.01%	0.01%	0.02%	0.02%	0.01%	0.02%
Fibrobacteres	0.00%	0.01%	0.00%	0.06%	0.01%	0.01%	0.00%	0.01%	0.00%	0.01%	0.00%
Elusimicrobia	0.00%	0.02%	0.02%	0.01%	0.02%	0.00%	0.02%	0.01%	0.01%	0.01%	0.02%
Crenarchaeota	0.00%	0.00%	0.01%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.09%

FIGURES

Figure 1.1. Changes in the composition of (A) diet and (B) gut microbiota over time, as indicated by *trn*L chloroplast genes and 16S ribosomal RNA genes, respectively. Plot depicts primary axis of principal coordinate analysis (PCoA) for relative abundance data. In PCoA, the first axis accounts for the greatest amount of variation in the dataset. The effect of time in each dataset was tested using PERMANOVA ($P < 0.001$ in both cases).

A)



B)

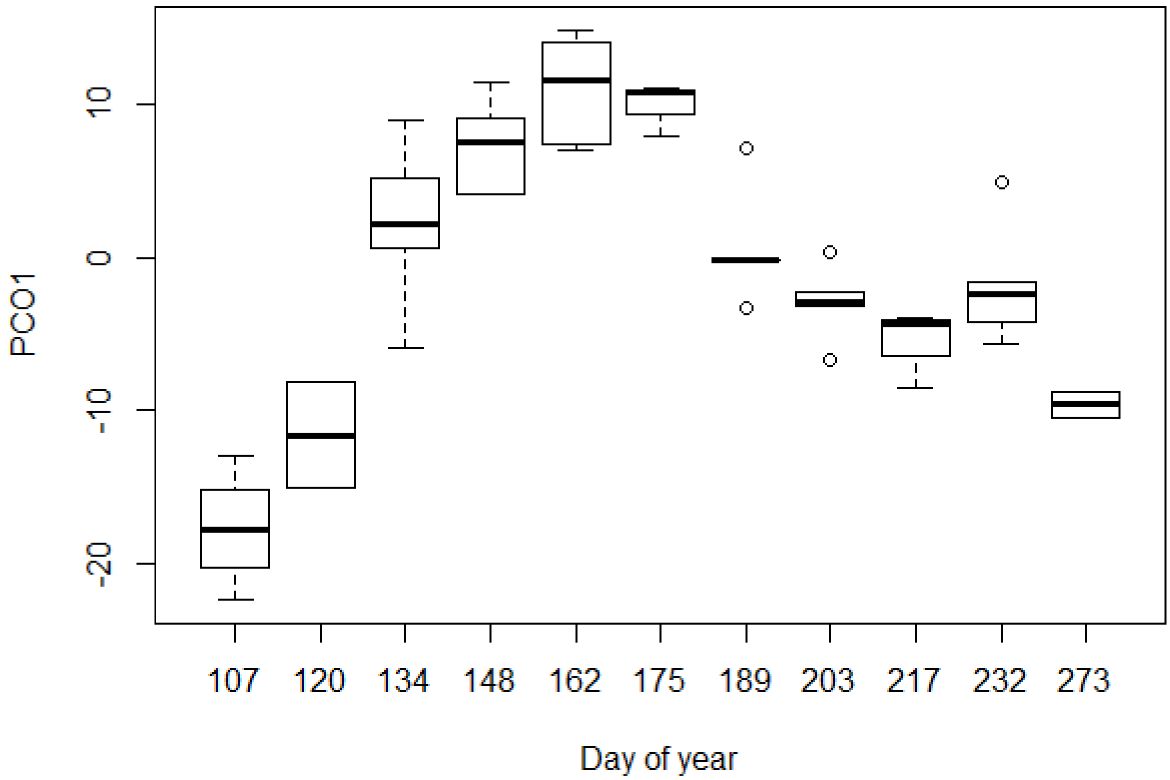

PCO1
10
0
-10
-20
107
120
134
148
162
175
189
203
217
232
273
Day of year

Figure 1.2. Changes in plant diet as indicated by shifts in the relative abundance of *trn*L chloroplast gene sequences. Plant species were grouped by growth habit (forb, graminoid, and woody). The effect of time in each dataset was tested using repeated measures ANOVA with Bonferroni correction. All three functional groups exhibited significant temporal change in proportion of the diet ($P < 0.05$).

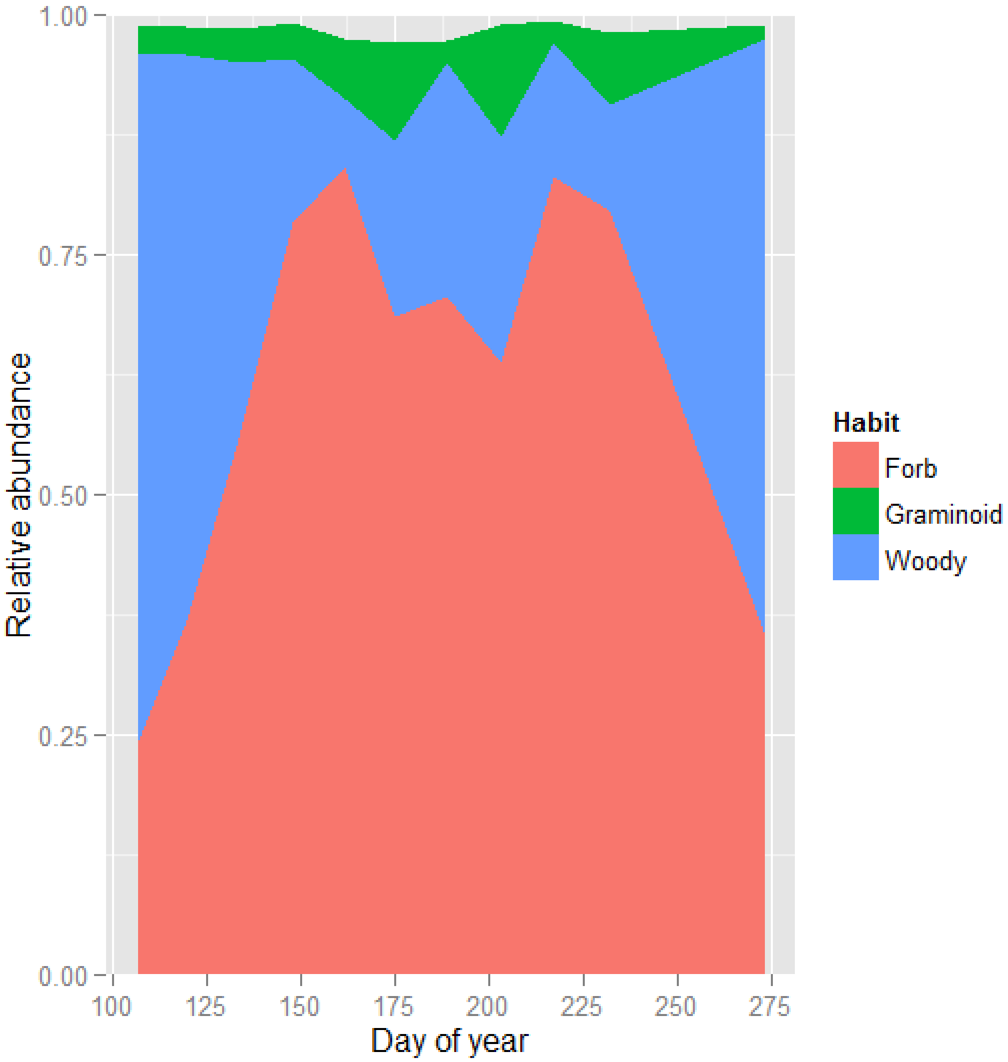


Figure 1.3. Plant relative abundance as indicated by sequencing of *trn*L chloroplast genes. Plants were identified to species by matching database sequences at the 100% level. See Results for the identity of species in clusters. The effect of time in each dataset was tested using repeated measures ANOVA with Bonferroni correction. Three taxa (*Lespedeza violacea*, *Ceanothus herbaceus*, and the *Oligoneuron* forb cluster) exhibited significant temporal change in proportion of the diet (P < 0.01).

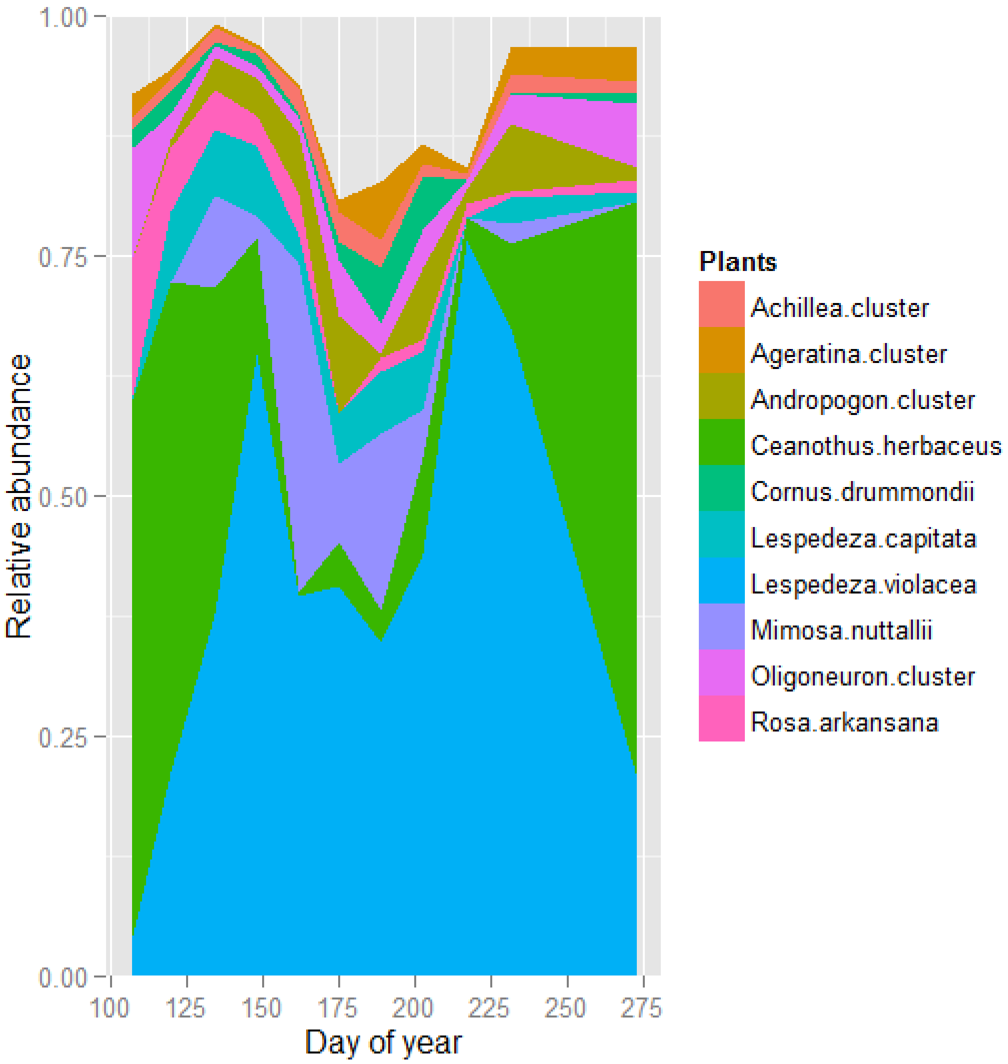


Figure 1.4. Relative abundance of microbial phyla as indicated by sequencing of 16S ribosomal RNA genes. The effect of time on each microbial phylum was tested using repeated measures ANOVA with Bonferroni correction. The phylum *Tenericutes* exhibited a significant shift in relative abundance over the growing season ($P < 0.001$).

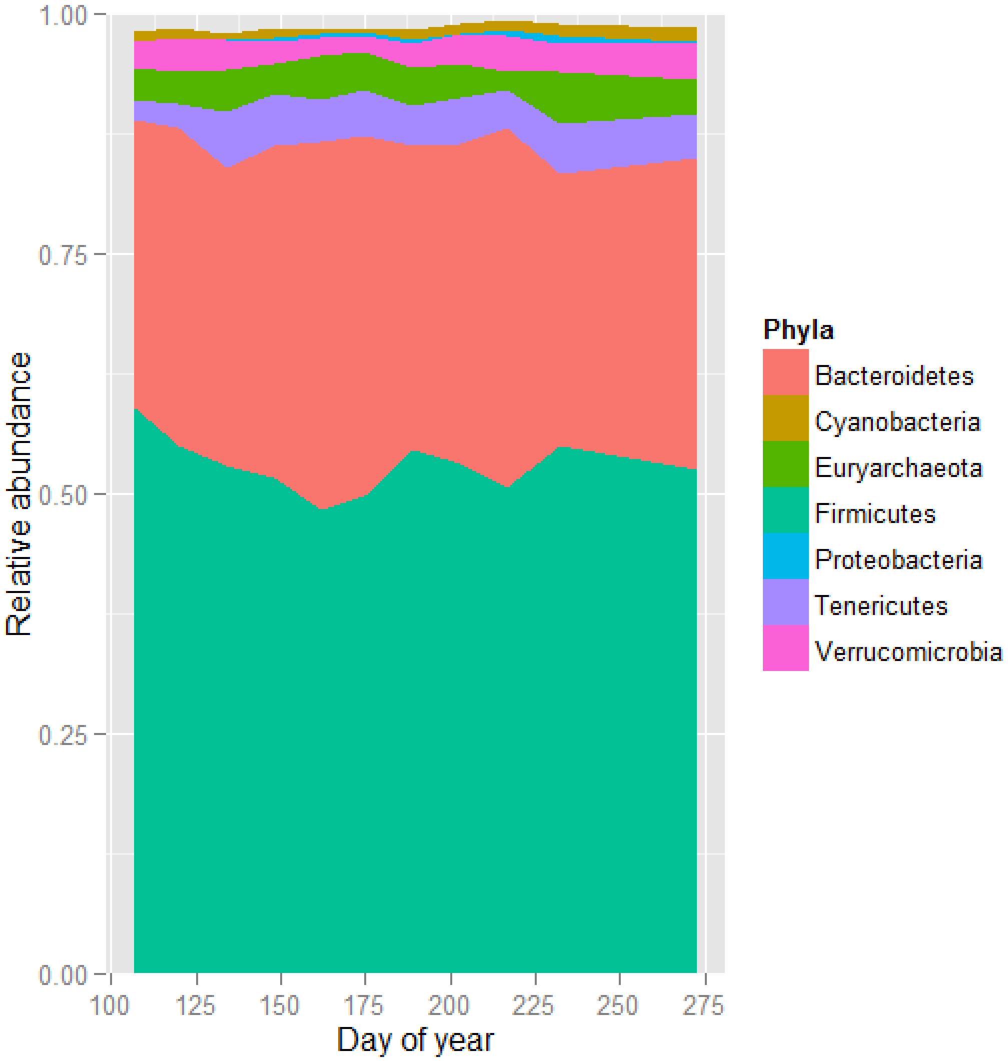
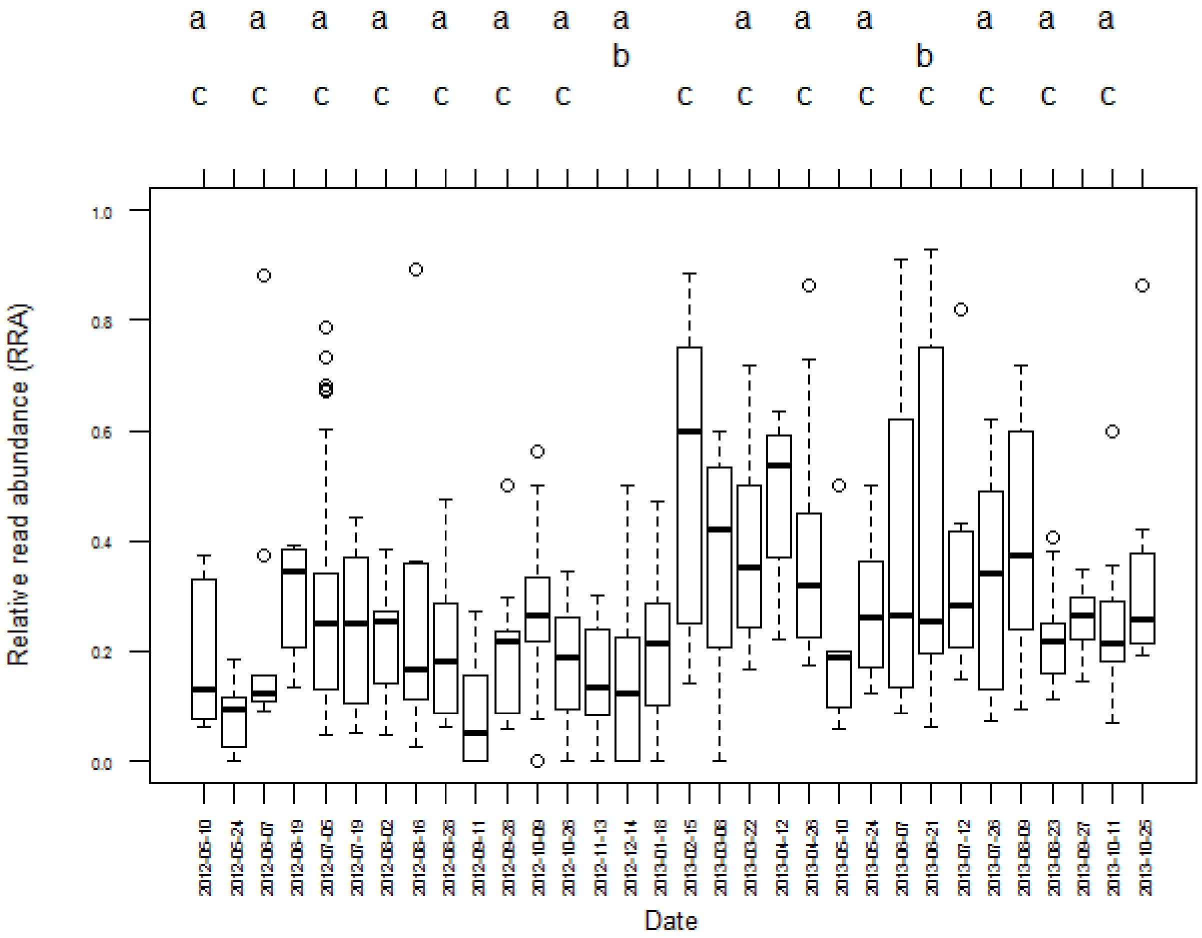
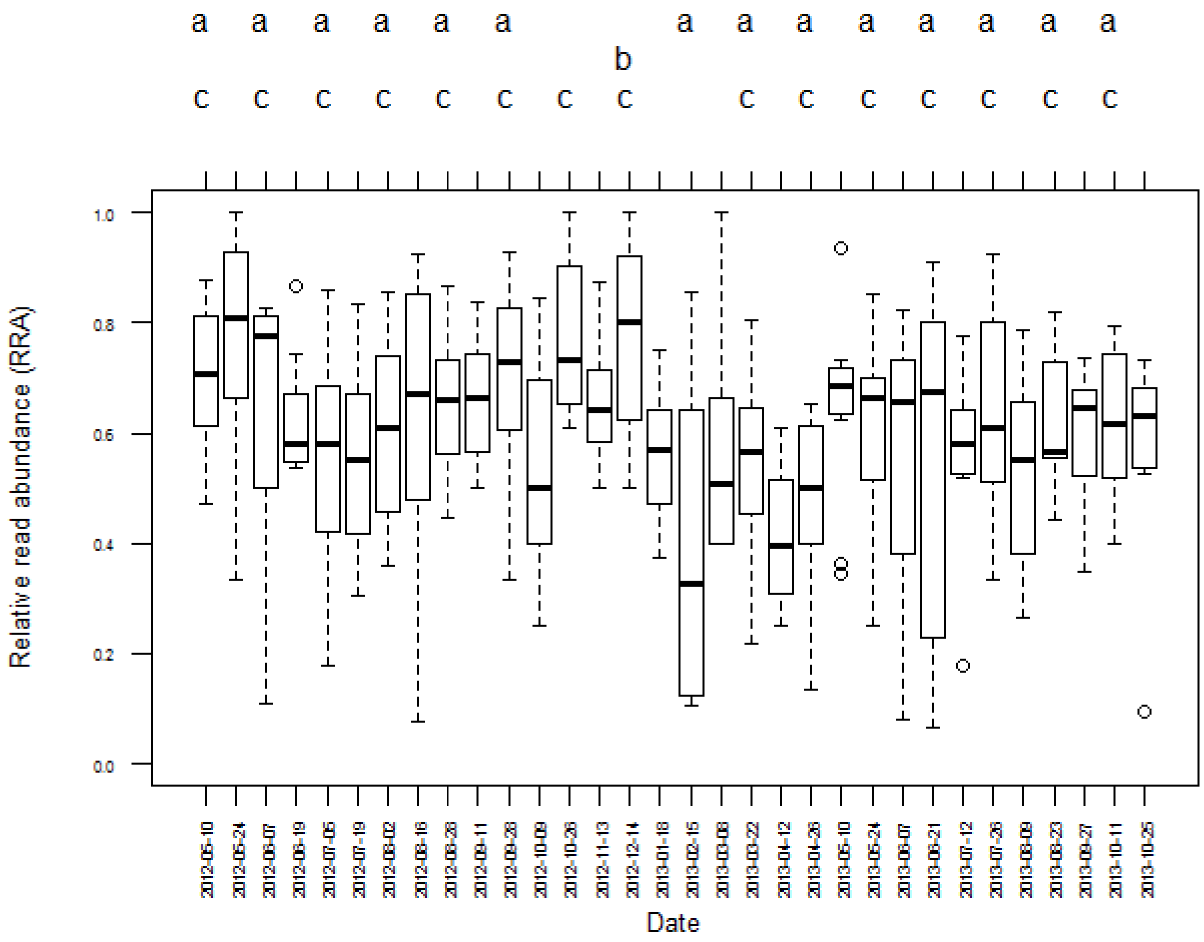


Figure 2.1. Results of repeated measures ANOVA with Tukey HSD on diet data from bison at Rocky Mountain Arsenal National Wildlife Refuge (RMA) during the period of May 10, 2012 to October 25, 2013. Dates with same letters above graph exhibited responses that were not significantly different from one another, while those with different letters had responses that were significantly different. Statistics for linear regression are reported with each of the following response groups. A) Forbs (*P* < 0.001, $R^2 < 0.05$), B) graminoids (*P* < 0.05, $R^2 < 0.05$), C) browse (*P* < 0.01, $R^2 < 0.05$), and D) Shannon diversity index (*P* > 0.05, $R^2 < 0.05$).

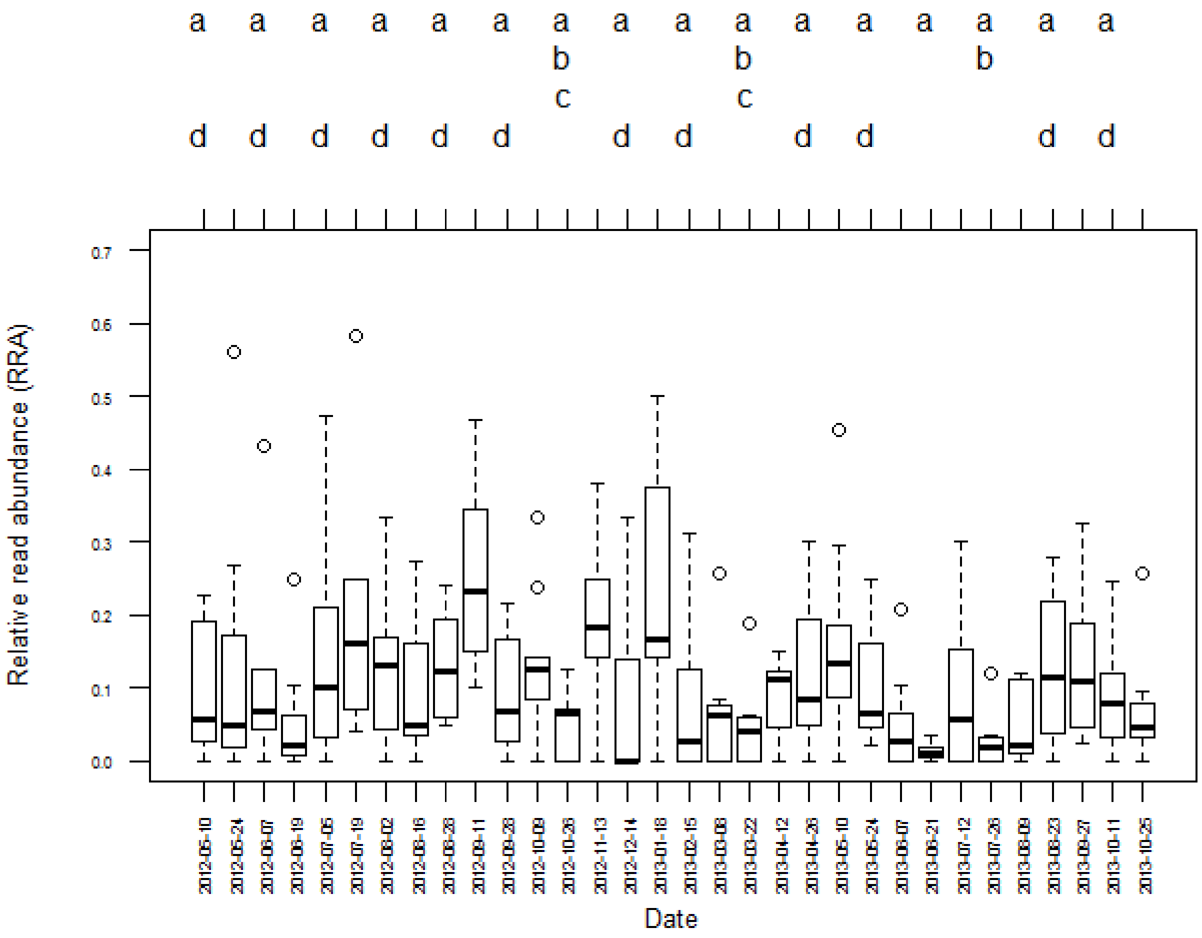
A)



B)


a a a a a a a a a a a a a a
b
c c c c c c c c c c c c c c c
Relative read abundance (RRA)
1.0
0.8
0.6
0.4
0.2
0.0
2012-05-10
2012-05-24
2012-06-07
2012-06-19
2012-07-05
2012-07-19
2012-08-02
2012-08-16
2012-08-28
2012-09-11
2012-09-28
2012-10-09
2012-10-26
2012-11-13
2012-12-14
2013-01-18
2013-02-15
2013-03-08
2013-03-22
2013-04-12
2013-04-26
2013-05-10
2013-05-24
2013-06-07
2013-06-21
2013-07-12
2013-07-26
2013-08-09
2013-08-23
2013-09-27
2013-10-11
2013-10-25
Date

C)


a a a a a a a a a a a a a a a a
b b b
c c
d d d d d d d d d d d d
Relative read abundance (RRA)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
2012-05-10
2012-05-24
2012-06-07
2012-06-19
2012-07-05
2012-07-19
2012-08-02
2012-08-16
2012-08-28
2012-09-11
2012-09-28
2012-10-09
2012-10-26
2012-11-13
2012-12-14
2013-01-18
2013-02-15
2013-03-08
2013-03-22
2013-04-12
2013-04-26
2013-05-10
2013-05-24
2013-06-07
2013-06-21
2013-07-12
2013-07-26
2013-08-09
2013-08-23
2013-09-27
2013-10-11
2013-10-25
Date

D)

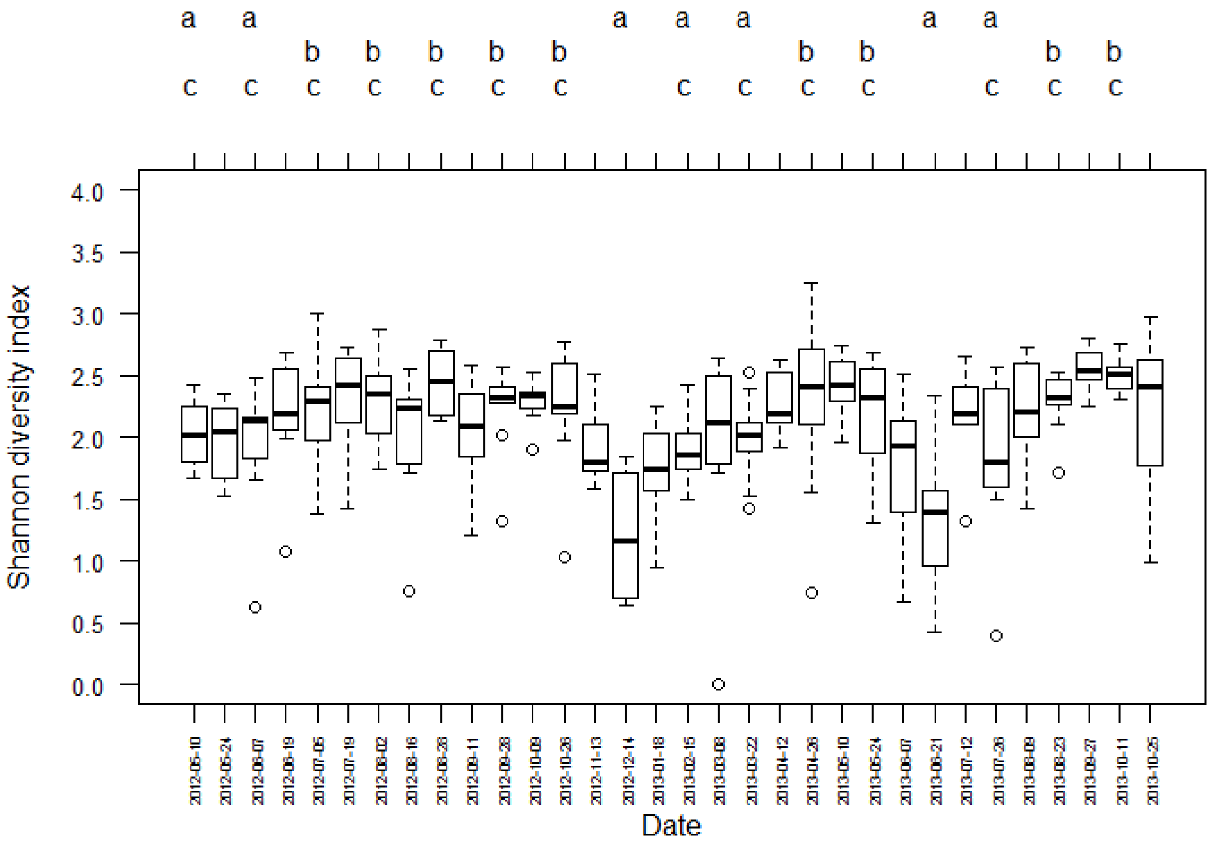

a a a a a a a
b b b b b b b b b
c c c c c c c c c c c c c c
Shannon diversity index
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
2012-05-10
2012-05-24
2012-06-07
2012-06-19
2012-07-05
2012-07-19
2012-08-02
2012-08-16
2012-08-28
2012-09-11
2012-09-28
2012-10-09
2012-10-26
2012-11-13
2012-12-14
2013-01-18
2013-02-15
2013-03-08
2013-03-22
2013-04-12
2013-04-26
2013-05-10
2013-05-24
2013-06-07
2013-06-21
2013-07-12
2013-07-26
2013-08-09
2013-08-23
2013-09-27
2013-10-11
2013-10-25
Date

Figure 2.2. Heat map representation of bison diet during the months of May-August at three sites: A) KZA (2011), B) RMA (2012 and 2013), and C) APR (2013). Plants were grouped by growth habit (forb, graminoid, and browse). Those few plants that could not be identified to the species level were not assigned to a growth habit.

A)

Habit	May.2011	June.2011	July.2011	August.2011
Graminoid	31.7% ± 12.2%	31.7% ± 13.0%	60.3% ± 18.0%	52.2% ± 11.3%
Forb	14.1% ± 5.6%	42.7% ± 23.7%	25.8% ± 16.1%	28.9% ± 11.0%
Woody	53.5% ± 15.6%	25.6% ± 15.7%	14.0% ± 8.0%	18.6% ± 7.2%
Other	0.7% ± 0.9%	0.0% ± 0.0%	0.0% ± 0.0%	0.2% ± 0.6%

B)

Habit	May.2012	June.2012	July.2012	August.2012	May.2013	June.2013	July.2013	August.2013
Graminoid	73.4% ± 17.9%	63.9% ± 19.2%	54.7% ± 19.5%	63.1% ± 19.6%	63.1% ± 17.6%	54.4% ± 29.4%	59.8% ± 18.7%	57.4% ± 15.9%
Forb	13.6% ± 11.4%	26.4% ± 19.8%	29.4% ± 20.5%	23.7% ± 17.7%	21.7% ± 13.4%	41.5% ± 31.7%	33.7% ± 20.3%	31.2% ± 19.0%
Woody	11.4% ± 14.7%	8.0% ± 11.1%	14.5% ± 13.2%	11.7% ± 9.0%	13.6% ± 10.9%	3.1% ± 4.8%	5.9% ± 8.6%	8.8% ± 8.8%
Other	1.6% ± 2.5%	1.6% ± 1.9%	1.4% ± 2.3%	1.5% ± 2.6%	1.6% ± 2.5%	1.0% ± 1.9%	0.6% ± 1.3%	2.6% ± 4.2%

C)

Habit	May.2013	June.2013	July.2013	August.2013
Graminoid	17.2% ± 20.4%	3.8% ± 2.6%	16.0% ± 10.3%	8.3% ± 4.8%
Forb	53.7% ± 18.4%	23.0% ± 14.8%	46.6% ± 14.5%	73.8% ± 23.8%
Woody	28.8% ± 20.8%	73.0% ± 16.1%	35.5% ± 9.2%	17.4% ± 19.8%
Other	0.3% ± 0.7%	0.2% ± 0.3%	2.0% ± 4.4%	0.4% ± 0.6%

Figure 2.3. Results of principal coordinate analysis (PCoA) on plant species in the diet of bison, showing comparison of the months of May-August at three sites: KZA (2011), RMA (2012 and 2013), and APR (2013).

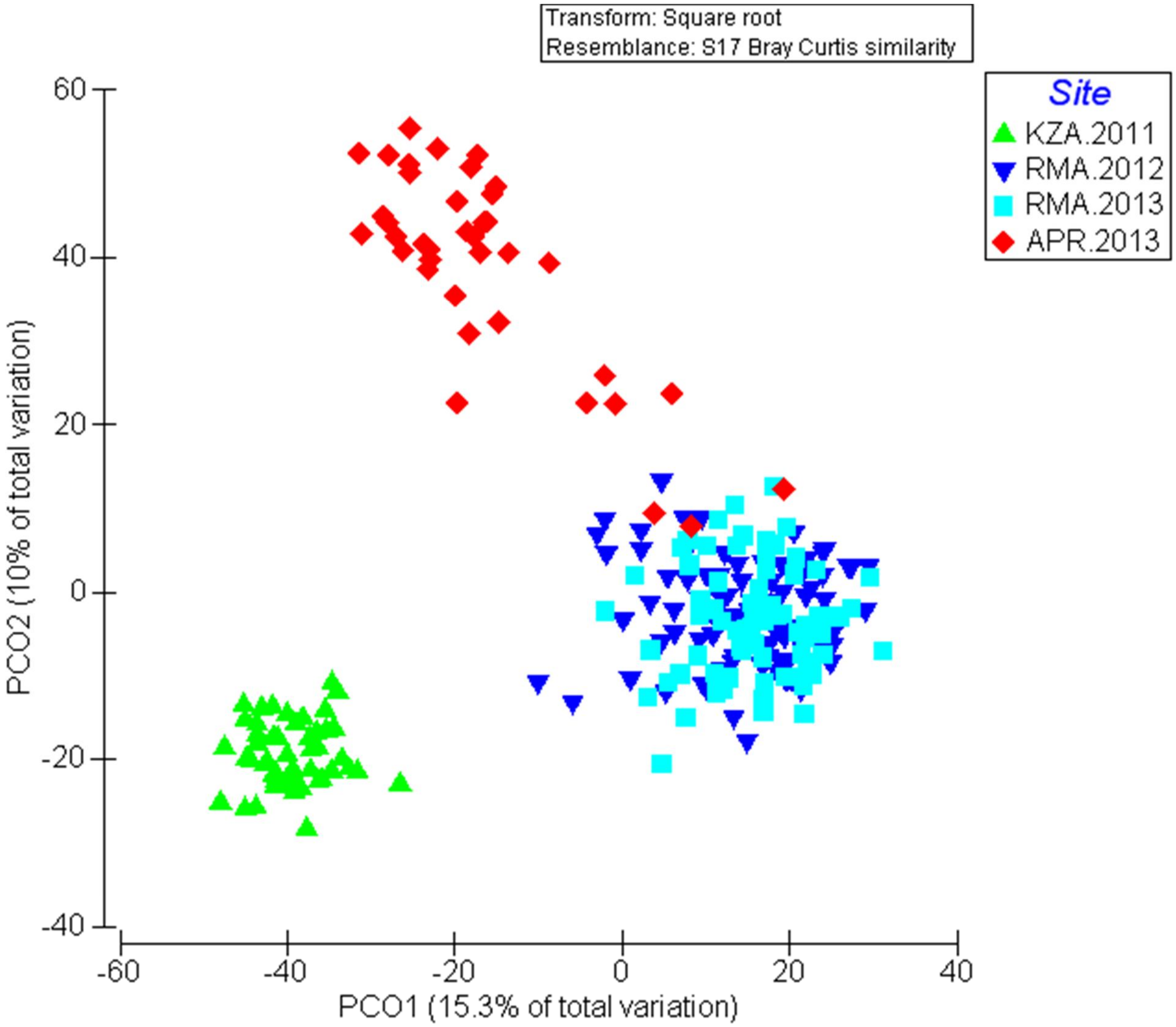
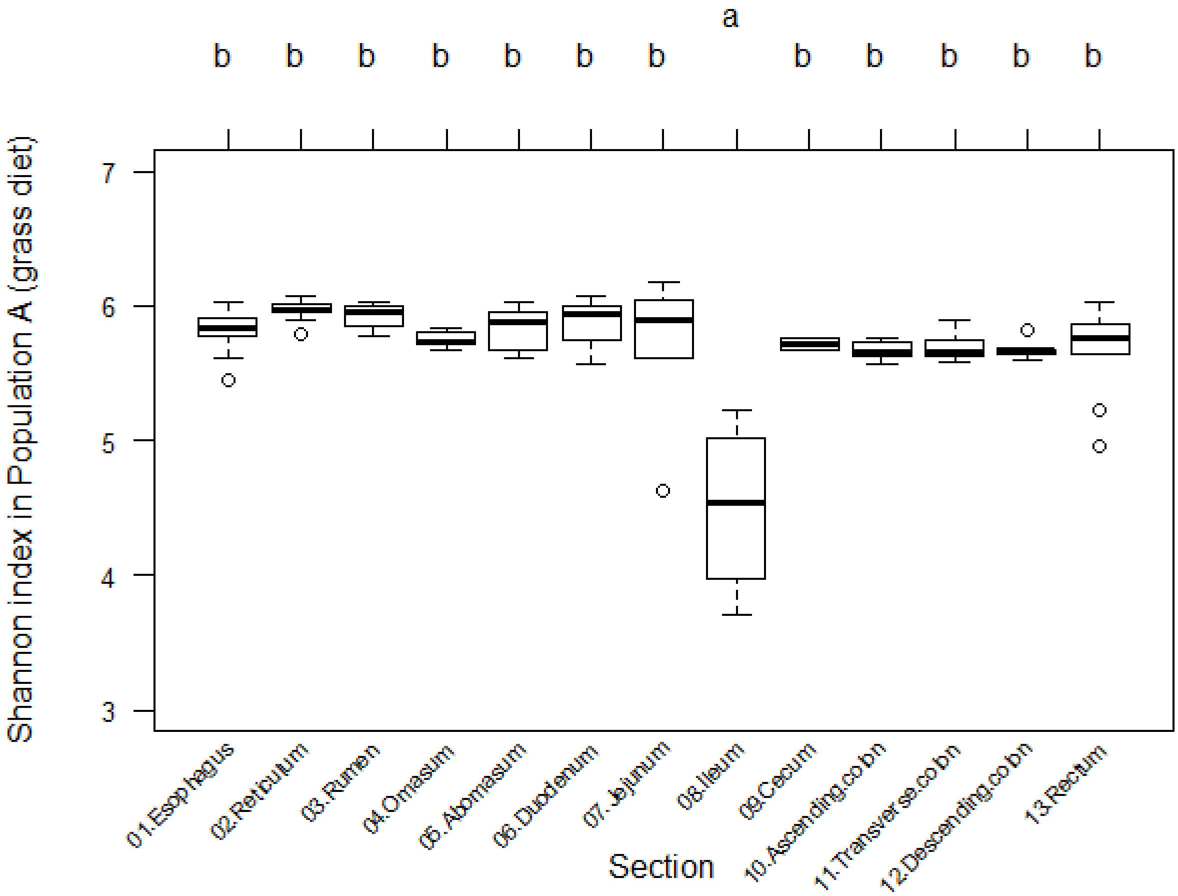


Figure 3.1. Microbial diversity along the length of the bison digestive tract. Letters above the chart indicate results of Tukey’s HSD test; sections marked with different letters were significantly different from one another. **A)** Diversity of the gut microbiota in forage-finished bison, as measured by the Shannon index. **B)** Diversity of the gut microbiota in grain-finished bison, as measured by the Shannon index.

A)



B)

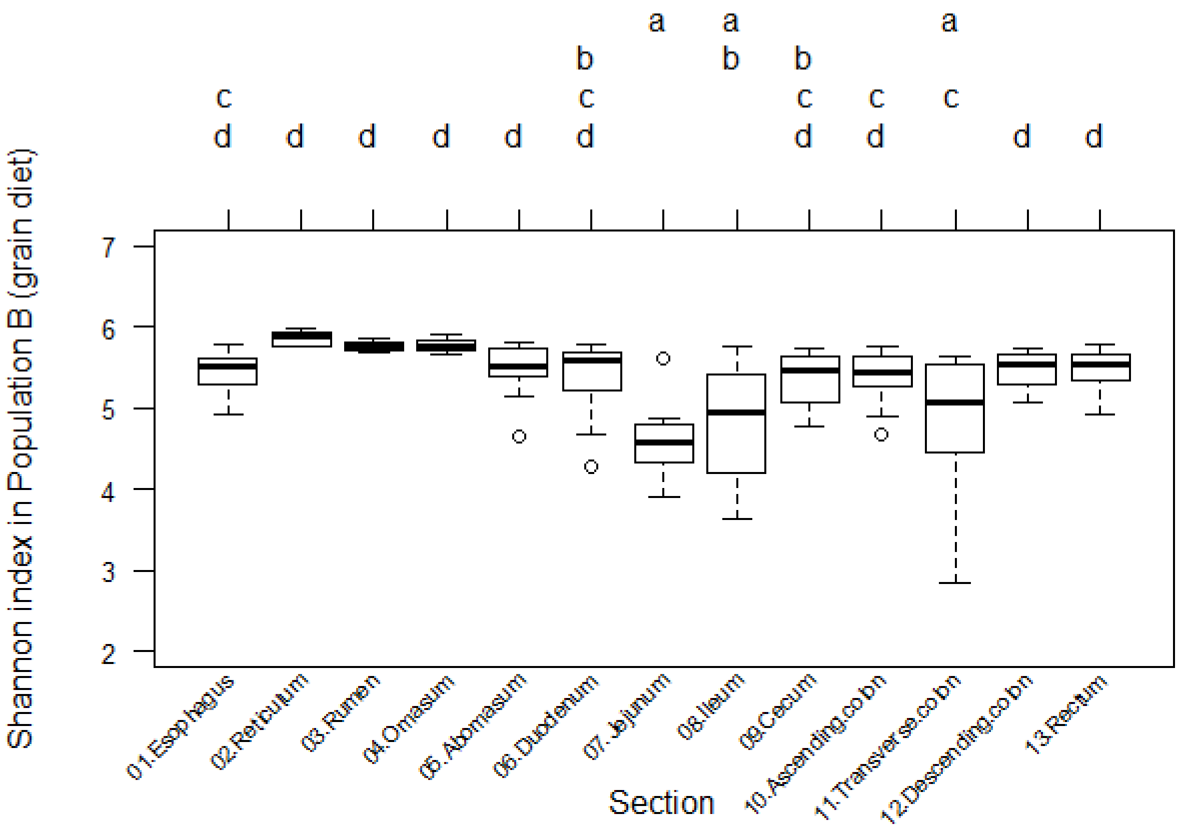

c d
d
d
d
d
b c d
a
a b
b c d
c d
a c
d
d
7
6
5
4
3
2
Shannon index in Population B (grain diet)
01.Esophagus
02.Reticulum
03.Rumen
04.Omasum
05.Abomasum
06.Duodenum
07.Jejunum
08.Ileum
09.Cecum
10.Ascending.colon
11.Transverse.colon
12.Descending.colon
13.Rectum
Section

Figure 3.2. Principal coordinates analysis (PCoA) of microbial operational taxonomic units (OTUs) for entire digestive tract in both populations (forage- and grain-fed) of captive bison. ES = Esophagus, RE = Reticulum, RU = Rumen, OM = Omasum, AB = Abomasum, DU = Duodenum, JE = Jejunum, IL = Ileum, CE = Cecum, AC = Ascending colon, TC = Transverse colon, DC = Descending colon, and RC = Rectum.

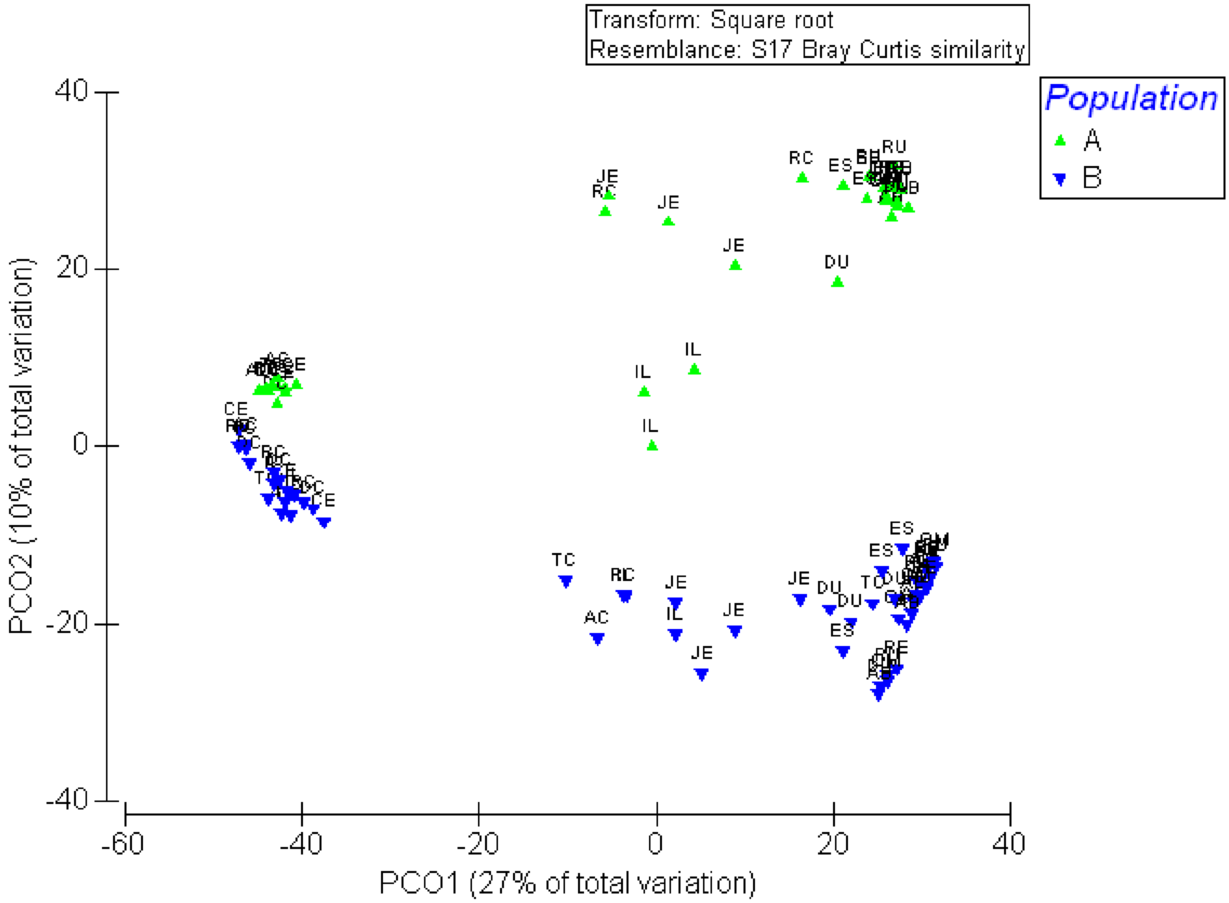
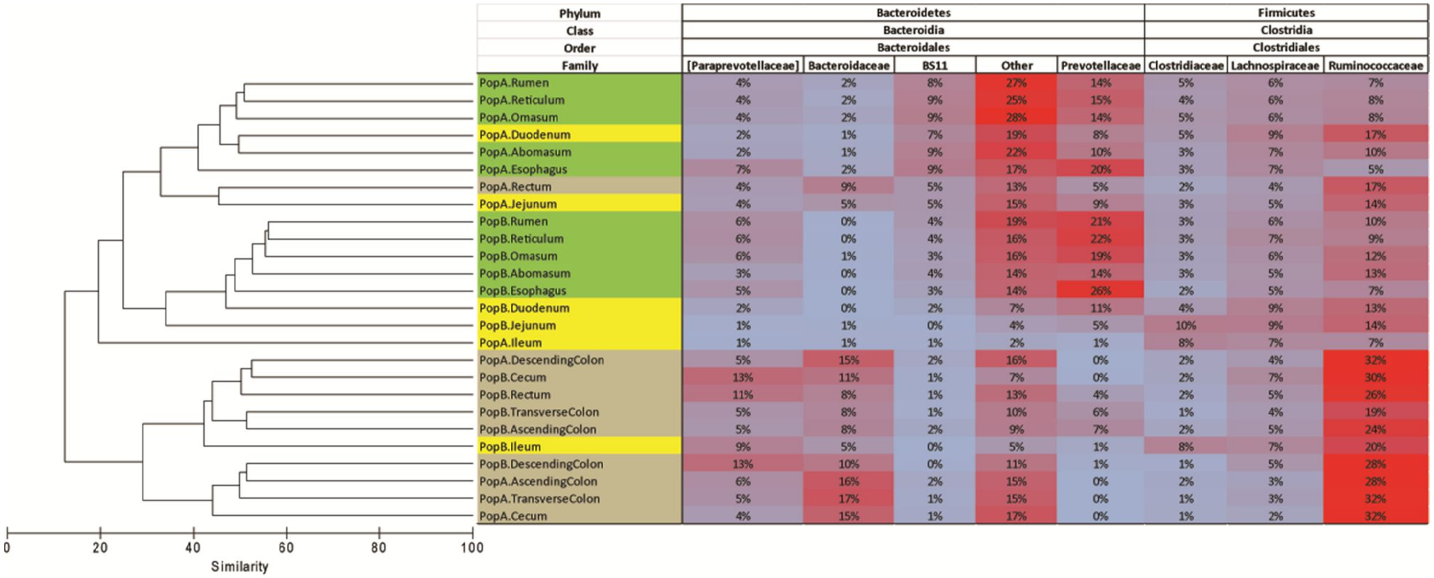


Figure 3.3. Heat map showing bacterial families with a mean relative abundance of at least 3% across all samples, paired with hierarchical cluster analysis of Bray-Curtis similarity among digestive tract sections in forage-finished (Population A) and grain-finished (Population B) bison. These families represent 27-77% of the microbial community in each gut section.



Phylum	Bacteroidetes					Firmicutes		
Class	Bacteroidia					Clostridia		
Order	Bacteroidales					Clostridiales		
Family	[Paraprevotellaceae]	Bacteroidaceae	BS11	Other	Prevotellaceae	Clostridiaceae	Lachnospiraceae	Ruminococcaceae
PopA.Rumen	4%	2%	8%	27%	14%	5%	6%	7%
PopA.Reticulum	4%	2%	9%	25%	15%	4%	6%	8%
PopA.Omasum	4%	2%	9%	28%	14%	5%	6%	8%
PopA.Duodenum	2%	1%	7%	19%	8%	5%	9%	17%
PopA.Abomasum	2%	1%	9%	22%	10%	3%	7%	10%
PopA.Esophagus	7%	2%	9%	17%	20%	3%	7%	5%
PopA.Rectum	4%	9%	5%	13%	5%	2%	4%	17%
PopA.Jejunum	4%	5%	5%	15%	9%	3%	5%	14%
PopB.Rumen	6%	0%	4%	19%	21%	3%	6%	10%
PopB.Reticulum	6%	0%	4%	16%	22%	3%	7%	9%
PopB.Omasum	6%	1%	3%	16%	19%	3%	6%	12%
PopB.Abomasum	3%	0%	4%	14%	14%	3%	5%	13%
PopB.Esophagus	5%	0%	3%	14%	26%	2%	5%	7%
PopB.Duodenum	2%	0%	2%	7%	11%	4%	9%	13%
PopB.Jejunum	1%	1%	0%	4%	5%	10%	9%	14%
PopA.Ileum	1%	1%	1%	2%	1%	8%	7%	7%
PopA.DescendingColon	5%	15%	2%	16%	0%	2%	4%	32%
PopB.Cecum	13%	11%	1%	7%	0%	2%	7%	30%
PopB.Rectum	11%	8%	1%	13%	4%	2%	5%	26%
PopB.TransverseColon	5%	8%	1%	10%	6%	1%	4%	19%
PopB.AscendingColon	5%	8%	2%	9%	7%	2%	5%	24%
PopB.Ileum	9%	5%	0%	5%	1%	8%	7%	20%
PopB.DescendingColon	13%	10%	0%	11%	1%	1%	5%	28%
PopA.AscendingColon	6%	16%	2%	15%	0%	2%	3%	28%
PopA.TransverseColon	5%	17%	1%	15%	0%	1%	3%	32%
PopA.Cecum	4%	15%	1%	17%	0%	1%	2%	32%