Rangeland Ecology & Management 70 (2017) 405–410

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Original Research

Are Bison Intermediate Feeders? Unveiling Summer Diet Selection at the Northern Fringe of Historical Distribution

Joshua L. Leonard [a,*], Lora B. Perkins [b], Duane J. Lammers [c], Jonathan A. Jenks [d]

[a] Graduate Research Assistant, Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007-1696, USA
[b] Assistant Professor, Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007-1696, USA
[c] General Manager, Olson's Conservation Bison Ranches LTD, Pine River, MB, R0L 1M0, Canada
[d] Distinguished Professor, Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007-1696, USA

ARTICLE INFO

Article history:
Received 28 July 2016
Received in revised form 8 December 2016
Accepted 11 January 2017

Key Words:
bison
diet selection
DNA barcoding
grass-roughage-intermediate feeders
Manitoba
next-generation sequencing

ABSTRACT

Bison *(Bison bison)* were historically distributed throughout North America with the northern edge of the distribution occurring in north-central Manitoba and surrounding provinces. Despite bison occupying the boreal zone of North America, little is known of their forage selection patterns of herbaceous plant material when occupying pastures within a densely forested aspen ecosystem. In 2015 we initiated a study to examine forage selection patterns for bison among and within summer months (June–August). We hypothesized that vegetative composition of bison diets would be consistent with availability, would shift with forage availability, and would predominately consist of grass and sedge species. We opportunistically collected adult female bison fecal samples ($N = 99$) and identified forage composition using the DNA barcoding method. We estimated availability of forage to the lowest taxonomical level possible using a modified Daubenmire frame. Overall, bison diets were composed of 44.3% grass, 37.7% forb, 16.3% browse, and < 2% sedge and rush. Forage availability comprised 51.2% grass, 28.3% forb, 11.0% sedge, and 7.6% rush. All analyses indicated that use and availability for grass, forb, sedge, and rush differed ($P \leq 0.05$) throughout the summer. Grass and forbs were important dietary components for bison, comprising > 80% of bison diets. However, bison selected for these two dietary components independently as the summer progressed. Our results indicate that these bison consume a large portion (~54.0%) of low-cellulose, high cell-soluble forages to meet their dietary needs. This suggests that bison may be or become intermediate foragers and are more like elk *(Cervus elapus)* than domestic cattle or sheep when inhabiting forested systems at the northern edge of their historical distribution. Herd managers and biologists should be cognizant of the importance of eudicots for bison and adopt a management plan that promotes a spatially heterogenous vegetative schematic.

Introduction

Historically, bison *(Bison bison)* inhabited most of North America, ranging as far north as Alaska and the Northwest Territories, to Mexico in the south, and spanning coast to coast, from New Jersey to California (Truett, 1996; Lammers et al., 2013). Bison currently occupy most of these same regions in North America (for the most part, with herds ≤ 300 individuals restricted to small, fenced areas), but information on bison forage selection in the Boreal Plains Ecozone is lacking. On the basis of forage selection and ruminant physiology, Hofmann (1989) describes three overlapping morphophysiological ruminant feeding types: concentrate selectors; intermediate-opportunistic mixed feeders (hereafter, intermediate feeder); and grass-roughage feeders. Concentrate selectors, like moose *(Alces alces)* or white-tailed deer *(Odocoileus virginianus)*, have evolved to digest nutritious, high-soluble plant material, such as forbs and browse (e.g., any part of a woody plant; Hofmann, 1989). Intermediate feeders, like elk *(Cervus elapus)*, opportunistically forage between both extremes, consuming a mixed diet while displaying short-term or seasonal dietary shifts in response to forage quality (Hofmann, 1989). Plains bison (*Bison bison bison;* portrayed by domestic cattle in Hofmann's, 1989 Fig. 2.) are typically classified as grass-roughage feeders, almost exclusively foraging on graminoids (Peden et al., 1974; Larter and Gates, 1991), such as grasses (Poaceae) and sedges (Cyperaceae). However, recent research in mixed-grass prairies of the Midwest contradicts this classification, with bison diets comprising high concentrations of eudicots, primarily forbs (Bergmann et al., 2015; Craine et al., 2015).

Diet selection of herbivores is typically determined through comparison of vegetative composition of use and forage cover-abundance (hereafter, availability; Larter and Gates, 1991). Selection of a food item can be assumed if use is greater than forage availability (Johnson, 1980). In contrast, avoidance of a food item can be assumed if use is

* Correspondence and present address: Joshua L. Leonard, Dept of Ecosystem Science and Management, University of Wyoming, Laramie, WY 82071-2001, USA.
E-mail address: joshualloydleonard@gmail.com (J.L. Leonard).

http://dx.doi.org/10.1016/j.rama.2017.01.005
1550-7424/

less than availability (Klein, 1970; Johnson, 1980). Typically, herbivore diets are quantified using the microhistological analysis method, first described by Baumgartner and Martin (1939) and later verified in numerous studies (e.g., Denham, 1965; Sparks and Malechek, 1968). Microhistological analysis is popular and has been used to quantify ungulate diets worldwide (Jenks et al., 1996; Schuette et al., 1998; Gibbs et al., 2004; Beck and Peek, 2005; Forsyth and Davis, 2011). DNA barcoding is a relatively new technique currently in use for analysis of herbivore diets (Valentini et al., 2009) and is gaining popularity (Czernik et al., 2013; Bergmann et al., 2015; Craine et al., 2015; Kartzinel et al., 2015). The technique has proven more accurate for quantifying composition of complex plant mixtures; 75% of the plant DNA extracted from fecal samples was identifiable to the genus level versus 20% using microhistological analysis (Soininen et al., 2009).

Plains and wood bison *(B. bison athabascae)* diets have been analyzed across North America using microhistological analysis and observational forage bouts (Peden et al., 1974; Peden, 1976; Reynolds et al., 1978; Larter and Gates, 1991; Plumb and Dodd, 1993; Knapp et al., 1999). To our knowledge, only two studies have analyzed bison diets from feces using DNA barcoding (Bergmann et al., 2015; Craine et al., 2015); however, neither study analyzed forage availability to assess diet selection. Therefore, the objectives of our study were to determine forage selection patterns of herbaceous (nonwoody stem) plant material for bison in pastures among and within summer months (June–August) in central Manitoba. We hypothesized that vegetative composition of bison diets would be equal to availability and that bison diets would vary as the availability of forage shifted between pastures. Additionally, we hypothesized that bison would select for grass and sedge species as would be expected for a grass-roughage feeder (Hofmann, 1989).

Methods

Study Area

Our study was conducted June–August 2015 within the East, East-Center, South Sclater, and North Sclater pastures on the Pine River Ranch (lat 51°47′N, long 100°30′W), which is part of Olson's Conservation Bison Ranches located within the Rural Municipality of Mountain (south), Manitoba, Canada. The privately operated ranch encompasses 12 500 ha of 9 cross-fenced pastures (range: 291 − 3 316 ha) and manages approximately 350 mature (≥ 3 yr old) female bison, which are rotationally grazed during the early spring and summer through each pasture once, annually.

The Pine River Ranch is situated in the Interlake Plain Ecoregion (IPE) of the Boreal Plains Ecozone (Smith et al., 1998; Thorpe, 2014). Topography of the region is predominantly ridge and swale with an average elevation of 260 m above mean sea level (Thorpe, 2014). The IPE mean annual temperature was 1.4°C, and the area received about 50 cm of precipitation (Smith et al., 1998; Land Resource Unit, 2000; Thorpe, 2014). The growing season was approximately 174 d with 1 644 growing degree-days annually (Thorpe, 2014).

Land cover of the four pastures sampled consisted of tree cover (71.0%), grasslands (fields; 19.1%), and wetlands (9.9%). Overstory tree cover was dominated by upland species including trembling aspen *(Populus tremuloides)*, balsam poplar *(P. balsamifera)*, and willows (*Salix* spp.). Fields were primarily dominated by sedge (*Carex* spp.), meadowgrass (*Poa* spp.), and reed (*Phalaris* and *Calamagrotis* spp.; Smith et al., 1998). Soil classification for the Rural Municipality of Mountain was characterized as predominately eutric brunisol, dark gray chernozem, gray luvisol, organic, regosol, and gleysol soils (Ellis, 1938; Soil Classification Working Group, 1998; Land Resource Unit, 2000).

Forage Availability

Before sampling, we identified fields within pastures (roughly 19% of the landscape) by searching them on a utility terrain vehicle or using satellite imagery; polygons for pastures were later digitized using ArcGIS 10.3 (ESRI, Redlands, CA). We generated random sample points in ArcGIS within fields available to bison to estimate herbaceous forage availability using a modified Daubenmire (1959) frame. At each sample point ($N = 198$; East [85], East-Center [65], South Sclater [16], and North Sclater [32]), we placed a 25-cm^2 frame, 1 m from plot center, in each cardinal direction. We identified grass, forb, sedge, and rush to the lowest taxonomical level (usually species) and estimated aerial cover. We estimated cover score (0 − 20) for each species within 5% intervals ranging from 0 − 100% cover within each frame. Unknowns were classified as either "unknown grass," "unknown sedge," "unknown forb," and "unknown rush." Forests in our study were not sampled as research has shown that bison spend 80% of their time inside or within 25 m of meadows (Fortin et al., 2003), and we were only interested in calculating herbaceous forage selection. Additionally, personal observations while on the ranch further support this as we only encountered the bison in fields or on the forest edge (Leonard, 2016).

Fecal Collection

We collected fresh adult female bison fecal samples ($N = 99$) June − August 2015. Fecal samples were collected at random in East (26 samples; 3 316 ha; June), East-Center (26 samples; 1 190 ha; July), North Sclater (26 samples; 2 747 ha; August), and South Sclater (21 samples; 1 911 ha; August) pastures. These samples were collected opportunistically to ensure freshness and stored in test tubes with dry silica beads. Fecal samples were collected ≤ 2 min after defecation. All fecal samples for each month were collected within fields and in the same 7-d period that fields were sampled to estimate vegetation composition. Because mean retention time for bison is ≤ 80 h (Schaefer et al., 1978), we did not collect fecal samples ≤ 4 d of animals being moved to new pastures to allow for previously consumed plant material to completely digest. We mixed a 4:1 ratio of dry silica beads to feces, respectively, to ensure complete desiccation (Murphy et al., 2002). Samples were stored at room temperature (~21–24°C) until DNA extraction.

DNA Extraction

Desiccated fecal samples were submitted to Jonah Ventures (Boulder, CO) for DNA analysis. Genomic DNA from samples were extracted using the MoBio PowerSoil htp-96 well Isolation Kit (MoBio, Carlsbad, CA) according to the manufacturer's protocol. A portion of the chloroplast trnL intron was polymerase chain reaction (PCR) amplified from each genomic DNA sample using the c and h trnL primers (Taberlet et al., 2007). Both primers also contained a 5′ adaptor sequence to allow for subsequent indexing and Illumina sequencing. Each 40 μL PCR reaction was mixed according to the Promega PCR Master Mix specifications (Promega catalog # M5133, Madison, WI), which included 0.4 uM of each primer and 3.2 μl of gDNA. DNA was PCR amplified using the following conditions: initial denaturation at 94°C for 1 min, followed by 36 cycles of 1 min at 94°C, 30 sec at 55°C, 30 sec at 72°C, and a final elongation at 72°C for 1 min. Amplicons were then cleaned using the UltraClean-htp 96 well PCR Clean-up kit (Mo Bio) according to the manufacturer's specifications and stored at 4°C. A second round of PCR was performed to give each sample a unique 12-nucleotide index sequence. The indexing PCR included Promega Master mix, 0.5 uM of each primer, and 4 μl of template DNA (cleaned amplicon from the first PCR reaction) and consisted of an initial denaturation of 95°C for 3 min followed by 8 cycles of 95°C for 30 sec, 55°C for 30 sec, and 72°C for 30 sec. After the trnL-specific and indexing PCR reactions, 5 μl of PCR products of each sample were visualized on a 2% agarose gel. Final indexed amplicons from each sample were cleaned and normalized using SequalPrep Normalization Plates (Life Technologies, Carlsbad, CA) before being pooled for sequencing on an Illumina MiSeq (San Diego, CA) in the Colorado University Boulder BioFrontiers Sequencing Center using the v2 300-cycle kit (cat# MS-102-2002).

DNA Sequencing

TrnL amplicons were processed via the UPARSE pipeline (Edgar, 2013) and assigned taxonomy via the UTAX protocol (http://www.drive5.com/usearch/manual/utax_user_train.html) available in usearch (v8.1.1861; Edgar, 2013). Sequences were demultiplexed using a python script (available at: https://github.com/leffj/helper-code-for-uparse/blob/master/prep_fastq_for_uparse_paired.py). Paired end reads were then merged using the *-fastq_mergepairs* option of usearch (Edgar, 2010). Because merged reads often extended beyond the amplicon region of the sequencing construct (staggered merges; http://drive5.com/usearch/manual/cmd_fastq_mergepairs.html), usearch automatically trims overhangs, essentially removing the majority of primer and adapter regions. Further filtering of any primers and adapter regions that may remain were removed using cutadapt (Martin, 2011). Sequences were quality trimmed to have a maximum expected number of errors per read of less than 0.5.

To assign taxonomy to each operational taxonomic unit (OTU), an "in-house" UTAX trnL reference database was constructed by downloading annotated GenBank (Benson et al., 2005) records that contained the trnL gene. The amplicon region bounded by the trnL c & h primers (Taberlet et al., 2007) was extracted from the GenBank records using the UTAX protocol. All extracted amplicon regions were dereplicated to 100% sequence identity, and any identical sequence across lineages was collapsed to the lowest-common-ancestor. Closed-reference OTUs were generated by searching against the trnL reference database at 99% sequence similarity. To ensure increased specificity of trnL OTU assignment against the reference database, the *-maxaccepts* and *-maxrejects* usearch options were increased 64 and 256, respectively.

Dietary Statistical Analysis

We used ANOVA (JMP 12; SAS Institute, 2013) with repeated measures to calculate compositional differences (i.e.; percent use of a food item to percent available of the same food item) of taxonomical groups: grass, forb, sedge, and rush, for assessing bison use and availability throughout the summer. We had two type variables, bison use and availability; three time intervals (June, July, and August); and four pastures (East, East-Center, North Sclater, and South Sclater). Among-month analyses of variances (ANOVAs) investigated the difference of type, month, and interaction of type and month. Because time and pasture are identical covariates for between-month analysis, pastures were only included during the within-month analysis, while North and South Sclater were combined for between-month analyses. We sampled two separate pastures during August (North and South Sclater) to evaluate within-month variation of diet selection. The within-month ANOVA investigated the difference of type (use vs. available), pasture (North and South Sclater), and interaction of type and pasture to determine similarity and differences between the two pastures during the same month. All statistical assumptions were met.

We calculated selection indices for taxonomical groups for each month to understand how bison foraging shifted throughout the summer. Additionally, we calculated selection indices for both pastures sampled in August. Selection indices were based on the percentage of plant composition in diets compared with the percent composition of vegetation available (Krueger, 1972; Rosiere et al., 1975; Ramírez et al., 1993). Typically, an index of 1.0 indicates that percentage of forage in diets was equal to availability; however, we subtracted 1 from all indices so that 0 would indicate equal diets and availability:

$$\text{Selection Index} = \frac{\%\text{plant composition in diet}}{\%\text{plant composition available}} - 1$$

Thus, indices > 0 indicated selection by bison, while indices < 0 indicated avoidance (Beck, 1975; Beck and Peek, 2005). Finally, we calculated one-sample *t*-tests to determine if the selection or avoidance indices were statistically different from zero and a comparison of means *t*-test to determine if means were statistically different for within-month indices.

Results

Overall, bison diets were composed (mean ± SEM) of 44.3 ± 3.5% grass, 37.7 ± 2.6% forb, 16.3 ± 2.3% browse, 1.1 ± 2.4% sedge, and 0.6 ± 1.3% rush, while forage availability was 51.2 ± 1.9% grass, 28.3 ± 1.5% forb, 11.0 ± 1.3% sedge, and 7.6 ± 0.7% rush (Table 1). Bison use and availability differed ($P \le 0.05$) for each taxonomical group between months throughout the summer. Grass and forbs comprised > 80% of bison diets (see Table 1). However, bison selected grass during June (0.19; $t_{24} = 2.22$; $P \le 0.05$) but avoided grass during July (−0.45; $t_{24} = -8.41$; $P \le 0.05$) and August (−0.18; $t_{45} = -3.23$; $P \le 0.05$), whereas bison selected forbs during July (0.92; $t_{24} = 6.50$; $P \le 0.05$) and August (0.74; $t_{45} = 5.53$; $P \le 0.05$) but did not select or avoid them in June (−0.06; $t_{45} = -0.72$; $P = 0.48$; see Fig. 1). Throughout the summer, bison avoided rush (−0.89; $t_{97} = -32.96$; $P \le 0.05$) and sedge (−0.93; $t_{97} = -59.02$; $P \le 0.05$; see Table 2), while selection of grass and forbs shifted throughout the summer.

August bison diets were composed of 46.0 ± 3.2% grass, 34.0 ± 2.0% forb, 17.4 ± 2.3% browse, 1.9 ± 2.2 sedge, and 0.6 ± 0.7% rush, while forage availability was composed of 56.1 ± 3.2% grass, 19.6 ± 2.0% forb, 18.2 ± 2.2% sedge, and 4.6 ± 0.7% rush (Table 3). Moreover, bison use and availability differed ($P \le 0.05$) for all taxonomical groups within the month of August. Selection indices were similar for forbs, sedge, and rush for both North and South Sclater pastures ($P > 0.05$). However, bison selection of grass differed ($t_{44.52} = -5.46$; $P < 0.05$) in August; bison forage use was equal to availability for grass in North Sclater (0.08; $t_{24} = -6.96$; $P = 0.41$), but they avoided grass in South Sclater (−0.45; $t_{19} = -6.96$; $P \le 0.05$).

Discussion

Change in dietary composition throughout the summer was not surprising as North American bison are temperate ruminants that take advantage of available vegetation throughout the summer (Schuler et al., 2006; Fortin and Fortin, 2009). However, bison diets did not shift according to availability as predicted. Grass became more abundant as summer progressed, but use declined, whereas use of forbs increased as availability decreased (see Fig. 1). This may be explained by plant phenology (Bergmann et al., 2015;) herbivores tend to forage on new growth that is higher in moisture and protein content while lower in fiber and secondary metabolites, which yields forages with higher

Table 1
Forage availability and bison diet use percentages (mean ± standard error) for June—August, 2015 on Olson's Conservation Bison Ranch's, Pine River Ranch, Manitoba, Canada.

	June		July		August	
Taxonomical Group	Available	Use	Available	Use	Available	Use
Grass	47.12 ± 1.46	56.12 ± 4.01	52.99 ± 1.99	29.24 ± 2.72	56.11 ± 3.17	45.99 ± 3.09
Forb	35.70 ± 1.48	33.48 ± 2.19	25.17 ± 1.13	48.35 ± 3.39	19.61 ± 1.13	34.05 ± 2.54
Sedge	5.99 ± 1.02	0.12 ± 0.22	12.35 ± 1.92	0.70 ± 0.16	18.23 ± 2.99	1.90 ± 0.57
Rush	9.97 ± 1.02	0.81 ± 2.44	6.97 ± 0.93	0.37 ± 0.13	4.59 ± 0.96	0.67 ± 0.20
Browse	–	9.47 ± 3.61	–	21.35 ± 3.63	–	17.39 ± 3.19

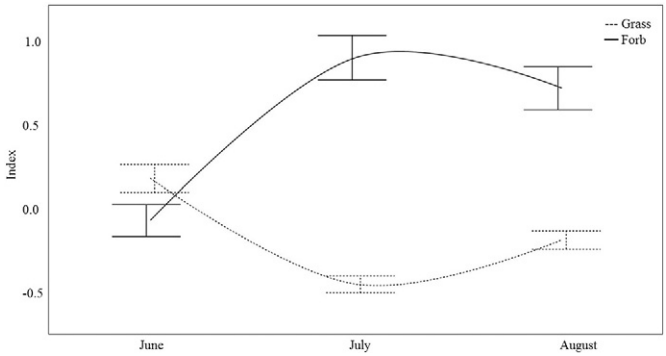

Figure 1. Grass and forb selection indices for summer bison diets on Olson's Conservation Bison Ranch's, Pine River Ranch, Manitoba, Canada. Positive indices indicate selection, and negative indices indicate avoidance. Each error bar is constructed using 1 standard error from the mean.

digestibility and palatability (Craine, 2009). Moreover, as the cell walls of grass develop, phenolic acids, cellulose, and lignin are deposited, lowering digestibility and palatability over time (Jung and Allen, 1995). However, grass-roughage feeders like bison and cattle have evolved to exploit forage with low digestibility, thus suggesting bison may not actually be a predominately grass-roughage feeder. Alternatively, bison may be exhibiting a functional response to the decreased forb availability as summer progresses (Spalinger and Hobbs, 1992). For example, if forbs provide a unique nutrient (e.g., vitamin, mineral, protein) in small quantities, then we would not expect to observe selection for that food item until it becomes less abundant on the landscape. Nevertheless, bison diet selection of herbaceous plants is likely influenced by an interaction between forage availability, palatability, and timing of when plants are most nutritious as bison are energy maximizers (Van Vuren and Bray, 1983; Van Vuren, 2001; Ranglack and du Toit, 2015) and select for high-protein plant species (Coppock et al., 1983; Larter and Gates, 1991; Fortin et al., 2003). Thus, it would be advantageous to calculate diet selection of free-roaming bison in a landscape similar to central Manitoba to determine what may be driving bison forage selection.

Historically, bison have been considered strict grazers (Peden, 1976; Reynolds et al., 1978; Plumb and Dodd, 1993; Coppedge and Shaw, 1998; Knapp et al., 1999) and are currently classified as grass-roughage feeders (Hofmann, 1989), similar to that of cattle and sheep. However, our results, along with others (Bergmann et al., 2015; Craine et al., 2015), have indicated that eudicots, such as forbs and browse, comprised a large proportion of bison diets (see Tables 1 and 3). Forbs and browse were a large proportion of bison diets (> 50%), and forbs were selected for when grasses were abundant, suggesting that bison may be intermediate feeders (Hofmann, 1989). A common example of an intermediate feeder is an elk. Elk in both the forested ecosystem of the Pacific Northwest and the mixed conifer-prairie ecosystem of the Midwest predominately consume grass and forb classes during the summer months (Leslie et al., 1984; Gibbs et al., 2004). Summer dietary shifts of elk were similar to that of bison in our study. Grasses dominated bison and elk diets in June, and both ruminants shifted to a higher forb concentrated diet during July and August, again suggesting a change in the forage characterization (grass roughage to intermediate forager) of bison.

Browse comprised 16.3% of all bison summer diets, which is unusually high considering bison do not typically use woody vegetation, unlike cattle (see Tables 1 and 3; Plumb and Dodd, 1993). However, this consumption may be incidental, as research indicates that aspen stands in central Canada have been expanding in the past 100 years (Strong, 1977; Looman, 1979; Archibold and Wilson, 1980; Hildebrand and Scott, 1987), occupying grassland prairies and thus increasing the probability that bison and other large ungulates with large bite sizes (Hudson and Frank, 1987) incidentally consume young growth of encroaching woody vegetation. Additionally, high-protein plants, such as eudicots, may be over-represented in the trnL libraries relative to biomass density as protein concentration among plants is likely associated with differences in chloroplast density (Bergmann et al., 2015). Therefore, future research is necessary to determine if proportions of trnL sequences in fecal samples are similar to those consumed. Moreover, information is lacking on whether DNA degradation of consumed forages from different taxonomical groups is equal or disproportionate. This, along with the lack of management to limit forest encroachment into fields on this ranch and the surrounding area may explain the high browse consumption. Nevertheless, our results suggest that future sampling of forest vegetation may be advantageous to determine if browse is an essential food item for bison or if it is being incidentally consumed in this densely forested landscape.

Although suggestions have been made that bison diets may be changing because of climate change (Craine et al., 2015), we believe that it may be due to the spatial limitations enforced on bison. It is plausible to believe that bison diets may be more like those of their nomadic ancestors if given the ability to migrate across North America. Most ruminants occupying the Afrotropic and Holarctic ecozones shift their diets seasonally (Hjeljord et al., 1990; Watson and Owen-Smith, 2002; Tshabalala et al., 2010) and those that do not change diets respond via migration (Wilmshurst et al., 2000; Sawyer and Kauffman, 2011). Large ruminants, including bison, are sometimes migratory (Berger, 2004). Migration is a strategy in which animals maximize fitness during seasonal and spatial resource variation (Boyce, 1979; Swingland and Greenwood, 1983). Moreover, migration allows individuals to maximize intake rates of high-quality forage by following spatiotemporal patterns (i.e., pheonological gradients; Fryxell et al., 2004; Hebblewhite et al., 2008). However, now spatially limited, bison may have adapted by shifting their diets seasonally and consuming more browse and other low-cellulose, high cell-soluble forages to meet their dietary needs. This suggests that domestication of bison may have resulted in foraging behaviors more similar to elk and other intermediate feeders than that of cattle or sheep, especially at the northern edge of the historical distribution of the species.

Our results display bison that are shifting their diet selection of herbaceous food items at large intervals (among months vs. within months), which suggests that bison likely are being influenced seasonally by spatiotemporal and nutritional plant variation across the landscape. Unfortunately, our sampling was restricted to the summer as bison were supplementally fed throughout remaining seasons (Fall–Spring). Sampling year-round would contribute significantly to

Table 2
Bison diet selection index (mean ± standard error) for functional groups during the summer on Olson's Conservation Bison Ranch's, Pine River Ranch, Manitoba, Canada.

Taxonomical Group	Month		
	June	July	August
Browse	6.76 ± 2.97	7.45 ± 1.44	10.98 ± 2.20
Forb	−0.06 ± 0.10	0.92 ± 0.13	0.74 ± 0.13
Grass	0.19 ± 0.09	−0.45 ± 0.05	−0.18 ± 0.06
Rush	−0.92 ± 0.06	−0.95 ± 0.02	−0.85 ± 0.04
Sedge	−0.98 ± 0.01	−0.94 ± 0.01	−0.90 ± 0.03

Table 3
Forage availability and bison diet use percentages (mean ± standard error) in South and North Sclater pastures for August 2015 on Olson's Conservation Bison Ranch's, Pine River Ranch, Manitoba, Canada.

	South Sclater		North Sclater	
Taxonomical Group	Available	Use	Available	Use
Grass	66.27 ± 3.31	34.54 ± 3.64	53.03 ± 4.21	55.24 ± 3.94
Forb	23.42 ± 1.50	44.86 ± 3.53	17.71 ± 1.41	25.31 ± 2.58
Sedge	8.21 ± 3.89	1.69 ± 0.60	23.25 ± 3.77	2.07 ± 0.91
Rush	0.90 ± 6.10	0.84 ± 0.43	6.44 ± 1.30	0.54 ± 0.12
Browse	—	18.06 ± 3.88	—	16.84 ± 4.91

understanding how bison diets shift on a seasonal time scale as research has shown when foraging in a similar habitat, bison almost exclusively forage on sedge during the winter (Larter and Gates, 1991). If free-roaming bison in the boreal plains eco-zone exhibit the same behavior, then management for a more heterogeneous vegetation schematic should be favored to meet dietary requirements for bison year-round.

Implications

We recognize that bison reintroductions across North America are becoming more popular (ADF&G, 2015; Banff National Park, 2015; Steenweg et al., 2016), thus increasing the need for better understanding diet selection across North America. To date, managers and biologist have used management plans and estimated stocking rates for bison that focus primarily on providing sufficient forage availability of monocots (e.g., grasses, sedges, rushes). However, the high eudicot presence in our study and recently supported articles (Bergmann et al., 2015; Craine et al., 2015), provide insight to managers on the importance of these food items for bison in spatially restricted systems. Because most bison are restricted spatially in some sense, managers and biologists should adopt management plans that promote a spatially heterogenous vegetative schematic to maximize bison growth and development. Additionally, managers who rotationally graze pastures annually should do so in a way that best suits bison dietary selection depending on the time of year and their location. For example, given our results, bison in a northern climate should be grazed in pastures with higher concentrations of eudicots during late summer and early fall and moved to pastures with higher concentrations of monocots during the winter and early spring months.

Acknowledgments

Research was funded in part by Olson's Conservation Bison Ranches LTD and South Dakota State University's Department of Natural Resource Management. We thank R. Metcalfe for field and logistical support. Thanks also to J. M. Craine and A. J. Beckley, Jonah Ventures, Boulder, Colorado, for analysis of bison fecal samples. N. Martorelli provided statistical assistance. Thanks to W. M. Inselman, W. M. Giuliano, and two anonymous reviewers for insightful comments that improved our manuscript significantly.

References

Alaska Department of Fish and Game, 2015. Wood bison free in Alaska. Available at: http://www.adfg.alaska.gov/index.cfm?adfg=pressreleases.pr04032015_bison Accessed 11 July 2015.

Archibold, O.W., Wilson, M.R., 1980. The natural vegetation of Saskatchewan prior to agricultural settlement. Canadian Journal of Botany 58, 2031–2042.

Banff National Park, 2015. Reintroduction plan: plains bison in Banff National Park. Parks Canada. Available at: http://www.pc.gc.ca/eng/pn-np/ab/banff/plan/gestion-management/~/media/pn-np/ab/banff/plan/gestion-management/banff-bison/plan-bison-EN.ashx Accessed 11 July 2015.

Baumgartner, L.L., Martin, A.C., 1939. Plant histology as an aid in squirrel food habitat studies. Journal of Wildlife Management 3, 26–268.

Beck, R.F., 1975. Steer diets in southeastern Colorado. Journal of Range Management 4, 48–51.

Beck, J.L., Peek, J.M., 2005. Diet composition, forage selection, and potential for forage competition among elk, deer, and livestock on aspen–sagebrush summer range. Rangeland Ecology & Management 58, 135–147.

Benson, D.A., Karsch-Mizrachi, I., Lipman, D.J., Ostell, J., Wheeler, D.J., 2005. Nucleic Acids Research. GenBank 33, D34–D38.

Berger, J., 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology 18, 320–331.

Bergmann, G.T., Craine, J.M., Robeson II, M.S., Fierer, N., 2015. Seasonal shifts in diet and gut microbiota of the American bison (*Bison bison*). PloS One 10 (11), e0142409.

Boyce, M.S., 1979. Seasonality and patterns of natural selection for life histories. The American Naturalist 114, 569–583.

Coppedge, B.R., Shaw, J.H., 1998. Bison grazing patterns on seasonally burned tallgrass prairie. Journal of Range Management 258–264.

Coppock, D.L., Ellis, J., Detling, J., Dyer, M., 1983. Plant-herbivore interactions in a North American mixed-grass prairie. II. Responses of bison to modification of vegetation by prairie dogs. Oecologia 56, 10–15.

Craine, J.M., 2009. Resource strategies of wild plants. Princeton University Press, Princeton, NJ, USA.

Craine, J.M., Towne, E.G., Miller, M., Fierer, N., 2015. Climatic warming and the future of bison as grazers. Scientific Reports 12, 6.

Czernik, M., Taberlet, P., Swislocka, M., Czajkowska, M., Duda, N., Ratkiewicz, M., 2013. Fast and efficient DNA-based method for winter diet analysis from stools of three cervids: moose, red deer, and roe deer. Acta Theriology 58, 379–386.

Daubenmire, R., 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33, 46–64.

Denham, A.H., 1965. In vitro fermentation studies on native sandhill range forage as related to cattle selection. [M.S. thesis]. Colorado State University, Fort Collins, CO, USA.

Edgar, R.C., 2010. Search and clustering orders of magnitude faster than BLAST. Bioinformatics 26, 2460–2461.

Edgar, R.C., 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. Nature Methods 10, 996–998.

Ellis, J.H., 1938. The soils of Manitoba. Manitoba Economic Survey Board, Winnipeg, Manitoba, Canada.

Forsyth, D.M., Davis, N.E., 2011. Diets of non-native deer in Australia estimated by macroscopic versus microhistological rumen analysis. Journal of Wildlife Management 75, 1488–1497.

Fortin, D., Fortin, M.E., 2009. Group-size-dependent association between food profitability, predation risk and distribution of free-ranging bison. Animal Behavior 78, 887–892.

Fortin, D., Fryxell, J.M., Lloyd, O.B., Dan, F., 2003. Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. Oecologia 134, 219–227.

Fryxell, J.M., Wilmshurst, J.F., Sinclair, A.R., 2004. Predictive models of movement by Serengeti grazers. Ecology 85, 2429–2435.

Gibbs, M.C., Jenks, J.A., Deperno, C.S., Sowell, B.F., Jenkins, K.J., 2004. Cervid forage utilization in noncommercially thinned ponderosa pine forests. Rangeland Ecology & Management 57, 435–441.

Hebblewhite, M., Merrill, E., McDermid, G., 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78, 141–166.

Hildebrand, D.V., Scott, G.A.J., 1987. Relationships between moisture deficiency and amount of tree cover on the pre-agricultural Canadian prairies. Prairie Forum 12, 203–216.

Hjeljord, O., Hövik, N., Pedersen, H.B., 1990. Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. Holarctic Ecology 13, 281–292.

Hofmann, R.R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78, 443–457.

Hudson, R.J., Frank, S., 1987. Foraging ecology of bison in aspen boreal habitats. Journal of Range Management 40, 71–75.

Jenks, J.A., Leslie, D., Lochmiller, R.L., Melchiors, M.A., McCollum, F., 1996. Competition in sympatric white-tailed deer and cattle populations in southern pine forests of Oklahoma and Arkansas, USA. Acta Theriology 41, 287–306.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource selection. Ecology 61, 65–71.

Jung, H., Allen, M., 1995. Characteristics of plant cell walls affecting intake and digestibility of forages by ruminants. Journal of Animal Science 73, 2774–2790.

Kartzinel, T.R., Chen, P.A., Coverdale, T.C., Erickson, D.L., Kress, W.J., Kuzmina, M.L., Rubenstein, D.I., Wang, W., Pringle, R.M., 2015. DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. Proceedings of the National Academy of Science 112, 8019–8024.

Klein, D.R., 1970. Food selection by North American deer and their response to overutilization of selected plant species. In: Watson, A. (Ed.), Animal populations in relation to their food resources. Blackwell Scientific Publications Ltd., Oxford, England, pp. 25–46.

Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C., Towne, E.G., 1999. The keystone role of bison in North American tallgrass prairie. BioScience 49, 39–50.

Krueger, W.C., 1972. Evaluating animal forage selection. Journal of Range Management 25, 471–475.

Lammers, D., Ogorzalek, K., Olson, T., Flocchini, J., Forrest, S., Anderson, B., Grajal, A., Jorgensen, D., Kremer, C., LeFaive, T., Majerus, J., Montanye, D., O'Brien, D., Sarver, S., Stone, J., 2013. Bison conservation management: guidelines for herd managers. World Wildlife Fund, Washington, DC, USA.

Land Resource Unit, 2000. Soils and terrain: an introduction to the land resource. Brandon Research Centre, Research Branch, Agriculture and Agri-Food Canada Information Bulletin 99—44, Brandon, Manitoba, Canada.

Larter, N.C., Gates, C.C., 1991. Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. Canadian Journal of Zoology 69, 2677–2685.

Leonard, J.L., 2016. Evaluation of bison *(Bison bison)* ecology at the Olson's Bison Conservation Ranches, Pine River Ranch, Manitoba, Canada. [thesis]. South Dakota State University, Brookings, SD, USA.

Leslie Jr., D.M., Starkey, E.E., Vavra, M., 1984. Elk and deer diets in old-growth forests in western Washington. Journal of Wildlife Management 48, 762–775.

Looman, J., 1979. The vegetation of the Canadian prairie provinces: an overview. Phytocoenologia 5, 347–366.

Martin, M., 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet Journal 17, 10–12.

Murphy, M.A., Waits, L.P., Kendall, K.C., Wasser, S.K., Higbee, J.A., Bogden, R., 2002. An evaluation of long-term preservation methods for brown bear *(Ursus arctos)* faecal DNA samples. Conservation Genetics 3, 435–440.

Peden, D.G., 1976. Botanical composition of bison diets on shortgrass plains. American Midland Naturalist 225–229.
Peden, D.G., Van Dyne, G.M., Rice, R.W., Hansen, R.M., 1974. The trophic ecology of *Bison bison* L. on shortgrass plains. Journal of Applied Ecology 11, 489–497.
Plumb, G.E., Dodd, J.L., 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. Ecological Applications 3, 631–643.
Ramírez, R., Sauceda, J., Narro, J., Aranda, J., 1993. Selection indices for forage species grazed by Spanish goats on a semiarid shrubland in Mexico. Journal of Applied Animal Research 3, 55–66.
Ranglack, D.H., du Toit, J.T., 2015. Habitat selection by free-ranging bison in a mixed grazing system on public land. Rangeland Ecology & Management 68, 349–353.
Reynolds, H.W., Hansen, R.M., Peden, D.G., 1978. Diets of the Slave River lowland bison herd, Northwest Territories, Canada. Journal of Wildlife Management 42, 581–590.
Rosiere, R., Beck, R.F., Wallace, J., 1975. Cattle diets on semidesert grassland: botanical composition. Journal of Range Management 89–93.
SAS Institute, 2013. PROC user's manual, version 9.4. SAS Institute. Cary, NC, USA.
Sawyer, H., Kauffman, M.J., 2011. Stopover ecology of a migratory ungulate. Journal of Animal Ecology 80, 1078–1087.
Schaefer, A., Young, B., Chimwano, A., 1978. Ration digestion and retention times of digesta in domestic cattle *(Bos taurus)*, American bison *(Bison bison)*, and Tibetan yak *(Bos grunniens)*. Canadian Journal of Zoology 56, 2355–2358.
Schuette, J.R., Leslie, D.M., Lochmiller, R.L., Jenks, J.A., 1998. Diets of hartebeest and roan antelope in Burkina Faso: support of the long-faced hypothesis. Journal of Mammalogy 79, 426–436.
Schuler, K.L., Leslie, D.M., Shaw, J.H., Maichak, E.J., 2006. Temporal-spatial distribution of American bison *(Bison bison)* in tallgrass prairie fire mosaic. Journal of Mammalogy 87, 539–544.
Smith, R.E., Veldhuis, H., Mills, G.F., Eilers, R.G., Fraser, W.R., Lelyk, G.W., 1998. Terrestrial ecozones, ecoregions, and ecodistricts, an ecological stratification of Manitoba's landscapes. Technical Bulletin 98-9E. Land Resource Unit, Brandon Research Centre, Research Branch, Agriculture and Agri-Food Canada, Winnipeg, Manitoba, Canada.
Soil Classification Working Group, 1998. The Canadian system of soil classification. third ed. National Resource Council of Canada Publication 1646, Ottawa, Ontario, Canada.
Soininen, E.M., Valentini, A., Coissac, E., Miquel, C., Gielly, L., Brochmann, C., Brysting, A.K., Sonstebo, J.H., Ims, R.A., Yoccoz, N.G., Taberlet, P., 2009. Analysing diet of small herbivores: the efficiency of DNA barcoding coupled with high-throughput pyrosequencing for deciphering the composition of complex plant mixtures. Frontiers in Zoology 6, 16.
Spalinger, D.E., Hobbs, N.T., 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. American Naturalist 140, 325–348.
Sparks, D.R., Malechek, J.C., 1968. Estimating percentage dry weight in diets using a microscopic technique. Journal of Range Management 1, 264–265.
Steenweg, R., Hebblewhite, M., Gummer, D., Low, B., Hunt, B., 2016. Assessing potential habitat and carrying capacity for reintroduction of plains bison *(Bison bison)* in Banff National Park. PloS One 11, e0150065.
Strong, W.L., 1977. Pre- and post-settlement palynology of southern Alberta. Review of Palaeobotany and Palynology 23, 373–387.
Swingland, I.R., Greenwood, P.J., 1983. Ecology of animal movement. Oxford University Press, London, UK.
Taberlet, P., Coissac, E., Pompanon, F., Gielly, L., Miquel, C., Valentini, A., Vermat, T., Corthier, G., Brochmann, C., Willerslev, E., 2007. Power and limitations of the chloroplast trnL (UAA) intron for plant DNA barcoding. Nucleic Acids Research 35, e14.
Thorpe, J., 2014. Rangeland classification for Agri-Manitoba. Saskatchewan Research Council Publication 12870-1E14, Saskatoon, Saskatchewan, Canada.
Truett, J., 1996. Bison and elk in the American Southwest: in search of the pristine. Environmental Management 20, 195–206.
Tshabalala, T., Dube, S., Lent, P.C., 2010. Seasonal variation in forages utilized by the African buffalo *(Syncerus caffer)* in the succulent thicket of South Africa. African Journal of Ecology 48, 438–445.
Valentini, A., Pompanon, F., Taberlet, P., 2009. DNA metabarcoding for ecologists. Trends in Ecology and Evolution 24, 110–117.
Van Vuren, D., 2001. Spatial relations of American bison *Bison bison* and domestic cattle in a montane environment. Animal Biodiversity and Conservation 24, 117–124.
Van Vuren, D., Bray, M.P., 1983. Diets of bison and cattle on a seeded range in southern Utah. Journal of Range Management 36, 499–500.
Watson, L.H., Owen-Smith, N., 2002. Phenological influences on the utilization of woody plants by eland in semi-arid shrubland. African Journal of Ecology 40, 65–75.
Wilmshurst, J.F., Fryxell, J.M., Bergman, C.M., 2000. The allometry of patch selection in ruminants. Proceedings of the Royal Society B: Biological Sciences 267, 345–349.