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

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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

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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).

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