ECOLOGICAL HIERARCHY OF FORAGING IN A LARGE HERBIVORE: THE PLAINS BISON PERSPECTIVE IN TALLGRASS PRAIRIE

by

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B.S., University of Maine-Machias, 2006
M.S., Nicholls State University, 2010

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2015
Abstract

Foraging decisions by native grazers in fire-dependent landscapes reflect fire-grazing interactions. I assessed behavioral responses associated with the attraction of grazers to recently burned areas at multiple spatial scales. (a) I focused on feeding in the area between steps in a foraging bout – the feeding station – where forage quality and vegetation architecture underlie these fine-scale decisions. The ‘forage maturation hypothesis’ (FMH) predicts the distribution of large herbivores based on the temporal dynamics of forage quality and quantity, but does not address herbivore responses to inter-patch variation caused by fire-induced increases of forage quality. The ‘transient maxima hypothesis’ (TMH) also predicts variable forage quality and quantity, but in response to intermittent disturbance from fire. I described the effects of variable spring burn history to bison foraging and their spatio-temporal distribution at Konza Prairie. Forage attributes met predictions of the TMH to explain how forage maturation affects foraging behavior across watersheds with varying burn frequency. At sites burned in the spring after several years without burning, intake rate increased with increasing vegetation biomass at a greater rate during the early growing season than during the transitional mid-summer period. This foraging behavior occurred in response to a non-equilibrial pulse of high quality resource that set the stage in the burned area, and was then retained by repeated grazing over the growing season. Thus, bison responded to forage resource availability in response to transient maxima in infrequently-burned watersheds burned that spring and they used these areas intensely until forage availability was greatly diminished and forage regrowth was not possible. (b) At the patch scale, bison selected areas of low-to-moderate grass cover in which to feed and avoided areas of high forb cover in the growing season. During the dormant season, however, bison selected feeding-sites with uniformly high canopy cover in watersheds that were not burned. (c)
At the landscape-scale, infrequently burned watersheds (compared to watersheds that were not burned) provided the strongest significant predictor of bison space use in all early growing- and transitional-season months. (d) The probability of habitat selection was driven by availability of high foliar, protein and low-to-intermediate herbaceous biomass throughout the growing season. These results explain the hierarchy of foraging by a dominant consumer in an experimental landscape by linking two prominent hypotheses, TMH-FMH, proposed to explain spatial variation in forage quality and quantity at local and landscape scales.
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Acknowledgements

Conducting research, teaching, and living at Kansas State Biology, Konza LTER, and Manhattan, Kansas has been a splendid experience. My first and chief acknowledgement is for Tony Joern. Tony has been an outstanding major advisor. I pursued a dissertation that spanned nutritional, movement, resource, fire, and community ecology. This accomplishment speaks volumes for how wide-ranging Tony’s reach is. To advise my research, he had to learn more about movement and resource ecology than what he already knew; this demonstrates what a flexible and creative thinker Tony is. It also reflects his amazing dedication to his work and his students. Tony very patiently taught me to improve my writing abilities. Also, improving my presenting capabilities for conferences or seminars was greatly enhanced by his efforts. Lastly, Tony has made my time at K-State better outside of work, teaching me how to row on Tuttle and improve my diet. I feel very fortunate to have completed a dissertation in the Joern lab and I am looking forward to continuing to work with him in the future. John Briggs was a grassland guru and great advisor. He reminded of the importance of the work that I was conducting and made it easier to accomplish this work due to his ability to keep Konza running smoothly. He also provided encouragement and insight into research, presenting, and writing. I look forward to working with him in the future.

My lab and committee have been fantastic. Jesus Gomez has been a fun lab mate and is also open to talk comics and movies and life in general. Ellen Welti has been a great asset to the lab and informed me of several programming and data management tricks as well as many fun adventures off campus. Angela Laws was a great teacher of prairie research methods when I started and reminded me of what a very hard worker is. Kelsey Girvin, John Girvin, Grant Samms, and Trenton Stringer are fun and bright technicians in our lab that helped with many
projects. David Hartnett continuously taught me about plant-herbivore interactions throughout my time at K-State and even put up with me ticking as many sub-Saharan African birds as possible, 211 in total, during his two-week course in Botswana and South Africa that I was lucky enough to be a participant of in 2012. Doug Goodin was great to talk to about spatial methods with and he even put up with me attempting to row on Tuttle. John Blair, although not an official member of my committee, has provided critical input on my work especially in the context of how my work connects to past work on Konza. Keith Gido, although not an official member of my committee, taught me ecological, multivariate statistics, was always open to helping with statistical methods, and providing words of wisdom and encouragement. Brett Sandercock, also not an official member of my committee, taught me demographic methods, collaborated with me on a restoration ecology study with riparian birds, and helped me secure my upcoming post-doctoral position. Jesse Nippert, another non-committee member, provided insight into stable isotope analysis as well as the data itself but also further filled my lack of knowledge on plant-climate-herbivore interactions. Also, Jesse and I traded some great albums from time to time.

I am also extremely thankful for the stimulating academic environment of the Division of Biology. I have learned an amazing amount from classes within the department, including “Community Ecology, “Landscape Ecology”, and “Demographic Methods”. The biology seminar series has brought in outstanding speakers and even let me host a prominent resource and movement ecology researcher, Daniel Fortin, in April 2014. Outside of Biology, I have really enjoyed working with Leigh Murray (Statistics Department) on statistical problems. Also outside of Biology, Ted Cable (Horticulture, Forestry and Recreation Resources) provided data for the restoration ecology study on riparian birds and tamarisk and showed me the best birding
spots in Kansas from the “Wetlands” to “Morton County” and even to Chautauqua County on an unsuccessful chase. Ted really helped me get a handle on the beauty of the Great Plains.

I have also been lucky to have a great group of friends in Manhattan, Kansas and a very supportive family. Hannah Tetreault, my beloved wife, is one of the hardest working and open people I know. She has been supportive throughout this degree program and constantly providing support, new ideas, and fun experiences, from New Orleans to Monterey Bay and countless concerts primarily east of Manhattan, Kansas. Zak Ratajczak, Vera Smirnova, Joseph and Jonathon Lautenbach, Drew Ricketts, Emily Weiser, Bart Grudzinski, Bram Verheijen, Kirsten Grond, Kim O’Keefe, Brian Kearns, Eunbi Kwon, Alaina Thomas, Mark Herse, Ben Vanderweide, Dan Carter, Aaron Balough, Emily Williams, and everyone that comes to Bluestem Bistro on Fridays have been great friends. I would also like to thank Hawthorne Beyer for help and guidance with movement modeling. My mother, step-father, father, uncle, and grandmother have supported my goal to be in school and research since I can remember, and especially over the last four years. My mother, as an extremely hard worker and business woman, instilled in me a love for accomplishment. My father is also a driven person and I feel that I have some of that trait in me. My grandmother always encouraged my studies of the natural world. My step-father taught me many aspects of life and without those lessons I’d be a very different person today. My uncle has also taught me similar lessons and I appreciate the “examples”.

Adequate funding made this dissertation possible, and greatly enhanced my time in the Division of Biology. Most of this dissertation was only possible because of the NSF grant acquired by Tony Joern and John Briggs. Without the Konza Prairie LTER, which established a platform for studies of plant-herbivore interactions in tallgrass prairie, I wouldn’t have been to
ask such interesting questions about the fire-grazer interaction. Maintaining the Konza fire and
grazing experiments and all of its long-term data-sets for over 30 years has been the result of
large and dedicated group of people. I am particularly indebted to Lloyd Hulbert for envisioning
the Konza LTER, and Sara Baer, John Blair, John Briggs, Scott Collins, Walter Dodds, David
Gibson, Keith Gido, David Hartnett, Alan Knapp, Anthony Joern, Adam Skibbe, Melinda Smith,
and Gene Towne, all of who have contributed to the Konza research program over the years
and/or insured long-term maintenance of Konza data. Funding for Konza LTER provided by the
Kansas State University-Division of Biology, National Science Foundation, and the Nature
Conservancy. My last school year was funded by the EIDRoP NSF GK-12 program established
at K-State by Carolyn Ferguson. The Institute of Grassland Studies, the Biology Graduate School
Association, and the Kansas State University Graduate School also provided funding to attend
conferences.
Chapter 1 - Introduction, Foraging Behavior, Fire-Grazer Interactions, and Animal Distribution


Because of their size and high biomass, large herbivores exert many direct effects on vegetation through trampling and consumption of vegetation (Owen-Smith 1988). Hence, they sustain patch heterogeneity in systems that would otherwise support continuous woody vegetation (Holdo et al. 2013). For example, bison maintain grasslands, and their wallows increase habitat diversity for a variety of both plants and animals (Gates et al. 2010, McMillan et al. 2011). Large herbivore populations are either collapsing (60% of species; Ripple et al. 2015) or are being continuously confined within fixed boundaries (Painter and Ripple 2012). Therefore, understanding their foraging behavior and space use patterns are critical for both conservation programs and to maintain the services they provide to ecosystems.

In this study, I focused on shifts in foraging activities of a large mammalian grazer in response to vegetation quality and quantity to ask how foliar nitrogen (protein) availability determines use of a grassland across an ecological hierarchy of spatial scales in foraging (feeding station to patch to landscape (Senft et al. 1987). In grasslands, fire is a major driver that affects each scale of the foraging hierarchy. Konza Prairie Biological Station (KPBS) is designed and
managed as a replicated watershed-level experiment where different watersheds are burned at varying frequencies. This mosaic of watersheds with different burn histories becomes the habitat mosaic available for grazing by plains bison (Bison bison bison; Knapp et al. 1999). The replicated fire treatments at KPBS allowed me to measure how bison foraging and space use patterns shift in response to plant abundance and nutritional content across a variety of spatial and temporal scales. In this study, I examined effects of fire-induced variation in forage resources on foraging and space use at multiple scales, from fine-scale foraging kinetics and patch selection to the broad-scale distribution of bison in nutritionally heterogeneous grassland.

**Theoretical Basis of Grazer Foraging**

Foraging behaviors of consumers rarely occur at random (Schaefer and Messier 1995). The mechanisms responsible for these non-random behaviors have been studied using optimal foraging theory (OFT) as a platform for hypothesis generation (Holling 1959; 1965, MacArthur and Pianka 1966, Belovsky 1978, McNamara and Houston 1985, Spalinger and Hobbs 1992). OFT, which proposes that consumers forage in a manner that maximizes their net energy intake per unit time (Schoener 1971, Charnov 1976), uses mathematical models to predict an energy-maximizing diet given various constraints (Stephens and Krebs 1986, Bergman et al. 2001, Langevelde et al. 2008). In this dissertation, I will use tenets of optimal foraging theory to infer how bison use forage resources (Chapter 2 and 3) that guide their spatiotemporal distribution at KPBS (Chapter 4 and 5).

The classical model describing food intake by predators hunting specific prey is Holling’s Type II functional response: as prey density increases, predator intake also rises as a decelerating function and approaches to an upper asymptote (Gross et al 1993). The deceleration in predator intake rate results from a trade-off between searching for prey items and handling them after and
during capture. Therefore, the more prey a predator handles, the less time is spent searching for food. The asymptote in this model is set by the reciprocal of the handling time for each captured prey item, while the rate at which the curve rises to the asymptote results from the animal’s searching efficiency (Holling 1959; 1965). Grazing herbivores also exhibit a similar functional response as vegetation availability increases, but the underlying assumptions of the model describing grazing intake rates differ from consumers such as carnivores. Focusing on herbivore grazers, Spalinger and Hobbs (1992) modified Holling’s Type II functional response to include an herbivore’s ability to search while still handling food. They demonstrated that post-capture handling time is not likely causing the deceleration in herbivore intake rate because most herbivores can continue searching for new bites as they crop and chew (handle) others, whereas most predators must consume their prey before starting a new search. Most studies of grazing on cultivated swards show bite mass and bite rate exhibit an inverse relationship with increasing forage abundance, which drives grazer forage intake rates (Spalinger and Hobbs 1992, Laca et al 1994). Specifically, Gross et al. (1993) found an asymptotic response to bite size and an inverse relationship between cropping rate and bite size in feeding trials of several mammalian herbivores. Because larger bites require an herbivore to invest more effort in mastication before swallowing, and because chewing movements cannot occur simultaneously as cropping movements, they hypothesized that cropping rate declines with increasing bite size. Empirically, the Gross et al. (1993) model accounted for 77% of the variability in herbivore intake rate and strongly supported the hypothesis that competition between cropping and chewing (processing) is responsible for the Type II functional response observed in herbivores. These results provide the theoretical foundation for predicting how variation in plant morphology and vegetation structure can influence fine-scale foraging strategies and inevitably influence coarse-scale
distribution of large mammalian herbivores. How do disturbances such as fire that initiate variation in forage quality and quantity affect grazer foraging behavior?

**Animal Distribution and Space Use**

Patterns of animal distribution and space use arise from a complex interaction between environmental conditions and behavioral responses. Understanding processes that drive animal movement, and the evolutionary consequences of movement, are fundamental research areas in ecology (Nathan et al. 2008). Foraging behavior governs animal movement and is a central component of population and community ecology because foraging decisions can ripple across the food web, and ultimately alter the structure and function of entire communities and ecosystems (MacArthur and Pianka 1966). One goal when studying animal space use is to develop an understanding of the behavioral strategies underlying how animals use heterogeneously distributed resources and habitat in time and space, and how animals manage risk and competing demands that influence fitness (Rosenzweig 1991, Morris 2003). Such insight about drivers of animal space use is integral for elucidating the evolutionary forces shaping resource-consumer systems (Fussmann et al. 2007).

Many animals respond to environmental heterogeneity by being selective in their choice of habitats to fulfill basic nutritional requirements. Habitat selection is the process whereby individuals preferentially use a nonrandom set of available habitats (Morris 2003). Biotic or abiotic components of an environment and an animal’s ability to utilize resources impose constraints on movement and the realization of an optimal diet. These processes result from habitat-specific variation in fitness and have important implications for population dynamics (Fretwell and Lucas 1970, Holt 1985, Pulliam 1988).
Non-equilibrial Forage Dynamics

The Transient Maxima Hypothesis (TMH; Seasteadt and Knapp 1993, Blair 1997) describes the development of a shifting mosaic of vegetation quantity and quality in response to a fire-mediated release from resource limitations in tallgrass prairie with great potential to influence grazer–fire interactions. In tallgrass prairie, primary productivity is often co-limited by light, energy, and soil nutrients, with the relative importance of individual resources dependent on time since last fire (Fig. 1, Blair 1997). The pulse in forage quality and quantity in grassland that has not burned in at least four years, four-and twenty-year burn watersheds at KPBS, provides a platform to test predictions of why bison are attracted to recently-burned forage of high quality due to intermediate fire frequency and how their concomitant space use in the landscape is governed.

Figure 1-1. Diagram of ‘pulsed’ release of soil nutrients from light-limitation (above) induced by fire and response in ANPP and forage quality in infrequently-burned, frequently-burned, and unburned watersheds (below). (A) Diagram of the transient maxima in resource availability: the increased levels of soil Nitrogen content (solid black line) which is made available to plants after fire releases the light-limited canopy (dashed black line) from previous years’ dead plant tissue. Soil Nitrogen declines after the release...
Due to use by aboveground plant processes and canopy light-limitation again occurs as fire is suppressed. (B) Variation in grassland aboveground resource availability based on burn frequency: the pulsed response in resource availability of infrequently-burned grassland in year of burn (solid black line), the static response of frequently-burned grassland burned that year, which is not light-limited and therefore supports lower soil N content, and no response in grassland that is not-burned which is dominated by light limitation and offers little green tissue. Modified after Seastedt and Knapp (1993), Blair (1997).

The Forage Maturation Hypothesis

The forage maturation hypothesis (FMH; Fryxell 1991) is derived from OFT principles to explain patch utilization and spatial and temporal distributions of foraging behavior (Wilmshurst et al. 1999, Durant et al. 2004). The FMH proposes that aggregation by large herbivores is adaptive because collective foraging maintains grassland in a state of intermediate forage quantity and quality with increased production of young forage tissue (McNaughton 1979). Such areas are called ‘grazing lawns’ (McNaughton 1984), and offer bison the opportunity to regularly eat immature plants in areas of low-to-intermediate quantity that are nutritionally superior to mature, high-biomass vegetation. Because protein content and digestibility of forage has an inverse relationship with maturation stage (Miller et al. 1965, Van Soest 1996), a positive feedback between grazing and forage palatability is seen on grazing lawns (Archibald et al. 2005, Verweij et al. 2006, Kerby et al. 2007). Additionally, the daily forage intake rate of an herbivore is constrained by forage ingestion and digestion (handling time) according to the FMH (Fig. 2a; Fryxell 1991). The rate of forage ingestion is determined by daily foraging time, cropping rate, and bite size (Ungar 1996), and is usually found to be an asymptotic function of forage quantity (Gross et al. 1993, Spalinger and Hobbs 1992, Bergman et al. 2000). The rate of forage digestion mainly depends on forage quality, which is defined as the digestibility of food particles determined by the amount and size of digestible and indigestible particles (Poppi et al. 1981,
Illius and Gordon 1991). The negative relationship between forage quantity and forage quality in natural grasslands results in a digestion rate of forage, which is commonly found to be a negative function of forage quantity. Therefore, the potential daily intake rate is limited by the constraints of forage ingestion and digestion (Drescher et al. 2006). In patches of intermediate forage mass, the intersection of the forage ingestion and digestion constraints is where the maximum net intake rate is found (Fig. 2b; Fryxell 1991).

![Figure 1-2. Schematic showing general mechanisms of the forage maturation hypothesis (FMH). (a) Foraging constraints of daily cropping (solid line) and digestion (fine-dotted line) that result in a foraging optima (arrows), where optimal energy/nutrient assimilation occurs, at low-to-intermediate biomass. (b) The arrow indicates maximization of energy/nutrient intake by foraging in patches of low-to-intermediate forage quantity over a coarser time period. Modified after Fryxell 1991, Drescher et al. 2006.](image)

Variation in Forage Resources Driven by Prescribed Burning

have assessed floristic heterogeneity in landscapes resulting from fire-grazing interactions
(Hartnett et al. 1996, Fuhlendorf and Engle 2001, Collins and Calabrese 2012), although the
spatio-temporal patterns of grazing in response to recent burning has only been assessed at broad
spatial and temporal scale investigations in burned or unburned grassland (Vinton et al. 1993,
the impact of burn-type (dormant and growing season) of grassland sites on seasonal bison
grazing activity and herd composition, while Vinton et al. (1993) examined bison grazing
patterns in relation to burning regime and graminoid-type (C3 vs. C4) at the watershed-scale.
Furthermore, neither study focused on fine-scale foraging behavior by bison such as forage
intake rate relative to recent burning or addressed how behavior may vary when grazing in
grassland burned at different frequencies over the extent of a growing season. The foraging
kinetics responsible for this marked response to burning remains unexplored and the
experimental setting at KPBS has been ideal for such an investigation. Heterogeneity of resource
abundance in seasonal burns during their first and subsequent growing seasons likely influences
bison foraging strategies both temporally and spatially. I found that the impetus behind these
responses to fire-induced nutrient enhancement in forage by large herbivores may be found by
investigating activities at the micropatch (feeding station [Chapter 2]) and patch (feeding area
[Chapter 3]) scales. I hypothesized that adjustments in fine-scale feeding rates to control energy
and nutrient intake and to potentially maximize time in non-feeding activities may be an outcome
of a grazer’s strong response to recently burned areas. Such adjustments may be modulated by
the grassland’s time since last burn, which impacts forage quality and quantity (Seastedt and
Knapp 1993, Blair 1997). Consequently, a response in fine-scale foraging behavior to grassland
offering differing levels of resource availability due to burn frequency may dictate landscape-level space use.

**Grazer Distribution in a Nutritionally Heterogeneous Landscape**

Understanding the grazer-plant interaction as affected by fire in a tallgrass prairie ecosystem is central for understanding mesic grassland ecosystems. Along with climate, fire and especially the fire-grazer interaction are key drivers of grassland ecosystem function and structure (Archibald et al. 2005, Anderson et al. 2007, Fuhlendorf et al. 2009, Allred et al. 2011, Allred et al. 2014). Effects of the fire-grazer interaction include altered vegetation quality and primary productivity (Anderson et al. 2007), increased plant, arthropod, and vertebrate species richness (Collins et al. 1998, Joern 2005, Fuhlendorf et al. 2012), and increased woody encroachment in response to long burn intervals where grasslands could become increasingly woody and ultimately no longer grasslands in its absence (Ratajczak et al. 2014). In this context, it is important to understand how fire affects landscape-level distributions of ungulate grazers in time and space as they track and use food resources of the highest available quality (Archibald and Bond 2004, Archibald et al. 2005, Anderson et al. 2007, Prins and van Langevelde 2008). This becomes a bigger challenge for ruminants foraging in heterogeneous landscapes as food often can be of substandard quality and the best quality food is distributed spatially in a patchy configuration that varies over time as a shifting mosaic. In turn, the spatial and temporal heterogeneity of forage quality dictates the spatial distribution and movement kinetics of large herbivores at the landscape level, although predation risk or physical features of the environment can also affect habitat use (Fryxell 1991, Fryxell et al. 2005, Anderson et al. 2010, Ford et al. 2014). Moreover, large herbivores can themselves alter the spatial heterogeneity of forage resources through their significant levels of forage consumption and effects on subsequent fuel
loads, because of their relative large individual and population sizes. Accurate spatial memory allows large ungulates to anticipate the heterogeneous distribution of food resources that coupled with their high mobility increases the likelihood they will select sites with high forage quality (Prins and van Langevelde 2008, Merkle et al. 2014, Merkle et al. 2015). Although the study of foraging and distribution of grazers, in time and space, requires an understanding of herbivore-plant interactions at multiple scales (Johnson 1980, Senft et al. 1987, Levin 1992), other aspects of the landscape may also contribute to ungulate distributions, including topography, availability of soil mineral nutrients (Tracy and McNaughton 1995), distance to water or shade, risk of predation, and physical factors (e.g., temperature, soil water) (Anderson et al. 2010, Allred et al. 2013).

The final portion of this dissertation, Chapter 5, incorporates a recent development in the field of movement ecology: the development of quantitative tools to identify landscape features that constrain movement by taking into account the relative utility of both the habitat where the animal currently resides and that of where it is moving (Potts et al. 2014, Beyer et al. 2014). Extrinsic biases to bison movement were evaluated using a comparison between observed and random steps through the heterogeneous landscape. The statistical approach used here is based on conditional logistic regression analysis, and was inspired by resource selection studies based on a case-control design (e.g. Compton et al. 2002, Boyce et al. 2003). In contrast, I used an approach that compares landscape ‘segments’ instead of individual GPS-locations (Arthur et al. 1996, Boyce et al. 2003) or areas (Johnson et al. 2002). Consequentially, I explicitly considered landscape characteristics that bison would have been likely to encounter along their path (a step selection function design; Fortin et al. 2005). This procedure is novel, however, because estimating the movement and habitat preference models simultaneously facilitates unbiased
parameter estimation (Beyer et al. 2014), and it is applied to a system with an intact fire-grazer interaction, which is a first, to my knowledge.

**Research Objectives**

In this dissertation, I focused my research efforts on identifying foraging behaviors at two spatial scales, the feeding station and patch, in efforts to understand the ruminant foraging decisions that drive their landscape-level distribution. Foraging decisions made at these two basal levels of the foraging hierarchy by large herbivores dictate where foraging efforts will occur in a landscape (Senft et al. 1987). Using empirical information collected on the spatiotemporal distribution of nitrogen (protein), herbaceous biomass, and adult female bison distribution, I elucidated aspects of nutritional and movement ecology that drives the grazer component of the intact fire-grazer interaction at KPBS. Detailed measurements of foraging behavior and space use by bison were studied to: (1) determine whether bison adjust foraging behaviors in response to forage and nutrient availability in grassland burned at varying frequencies, (2) evaluate how bison select feeding sites at different stages of maturation in burned and unburned watersheds, while concomitantly assessing fine- and coarse-temporal scale foraging tactics over the growing season, (3) assess the effect of watershed-level varying burn frequencies on female bison space use, and (4) evaluate how dynamic and static environmental variables drive movement and habitat selection of female bison in a nutritionally heterogeneous grassland with an intact fire-grazer interaction during the growing season. Combined, results from these four approaches demonstrate that bison:

- (Chapter 2) can show increased feeding rates in the early growing season only in infrequently-burned watersheds burned that year and shift forage kinetics to optimize nutrient intake in times of low forage quality,
• (Chapter 3) select feeding sites of high protein content and low forage stature as long as plant regrowth is possible then shift foraging behavior and diet in order to attain forage resources in times of uniformly low forage quality at the cost of spending more of the daytime feeding,

• (Chapter 4) disproportionately utilize infrequently-burned watersheds throughout the growing season (May to September) then shift to using watersheds that did not burn that previous spring while simultaneously avoiding annually-burned watersheds during the dormant season (December to February),

• (Chapter 5) respond to the underlying dynamic forage resources and static landscape characteristics of the shifting mosaic of vegetation quantity and quality at KPBS by selecting areas of high foliar protein and low herbaceous biomass content, while mostly avoiding low elevations, steep slopes, and non-south facing areas.

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Chapter 2 - Bison foraging responds to fire frequency in nutritionally heterogeneous grassland

This chapter is formatted for the journal “ECOLOGY”
The citation for this chapter is: Edward J. Raynor, Anthony Joern, and John M. Briggs 2015. Bison foraging responds to fire frequency in nutritionally heterogeneous grassland.

Abstract

Foraging decisions by native grazers in fire-dependent landscapes modulate the fire-grazing interaction. Uncovering the behavioral mechanisms associated with the attraction of grazers to recently burned areas requires understanding at multiple spatial scales in the ecological foraging hierarchy. This study focused on feeding in the area between steps in a foraging bout, the feeding station, as forage chemistry and vegetation architecture play central roles in these fine-scale, feeding-station decisions. The forage maturation hypothesis (FMH) uses the temporal dynamics of forage quality and quantity in grasslands to explain the distribution of large herbivores, but does not address herbivore responses to inter-patch variation caused by fire-induced nutrient increases of forage quality. Using an experimental setting with contrasting fire treatments we describe the effects of variable burn history on foraging kinetics by bison at Konza Prairie Biological Station (KPBS). We assessed the potential to link the FMH in a complementary fashion to the transient maxima hypothesis (TMH) to explain temporal variation in bison responses to grassland forage quality and quantity in response to burning at different temporal frequencies. Forage attributes met predictions of the TMH that allowed us to investigate how forage maturation affects feeding station foraging behavior across watersheds.
with varying burn frequency. At sites burned in the spring after several years without burning,
both bite mass and intake rate increased with increasing biomass at a greater rate during the
growing season than during the transitional mid-summer seasonal period. In these infrequently
burned watersheds, early growing season bite mass (0.6 ± 0.05), bite rate (38±1.5), and intake
rate (21±2.3) was reduced by ~15, 13, and 29% during the mid-summer transitional period. A
behavioral response in foraging kinetics at the feeding station occurred where a non-equilibrial
pulse of high quality resource was made available and then retained by repeated grazing over the
growing season. Our results provide the first experimental evidence for demonstrating the fine-
scale behavioral response of a large grazer to fire-induced changes in forage attributes, while
linking two prominent hypotheses proposed to explain spatial variation in forage quality and
quantity at local and landscape scales.

Keywords: fire ecology, forage maturation hypothesis, grassland, grazing, nutritional
ecology, tallgrass prairie, transient maxima hypothesis

INTRODUCTION

In grasslands, spatial and temporal variation in forage quality and quantity results from multiple
interacting abiotic factors such as precipitation, topography, and soil nutrients, which in turn
affect the foraging behavior of grazing ungulate herbivores (Owen-Smith 2002, Prins and
Langevelde 2008). Equally important, such heterogeneity in forage quantity and quality in a
landscape also reflects recursive fire-grazer interactions (Milchunas et al. 1988, Fuhlendorf and
“ecological magnet” for many grazer species (Archibald et al. 2005), resulting in heavy selection
and sustained use of regrowth in post-burned areas (Coppedge and Shaw 1998, Sensenig et al.
2010, Eby et al. 2014). In turn, recent grazing negatively reduces fuel and the likelihood a patch
will burn in the near future. While the spatial distributions and movement patterns of large herbivores in response to recent fires are increasingly understood at coarse-scale landscape levels (Vinton et al. 1993, Schuler et al. 2006, Allred et al. 2011a, b, Augustine and Derner 2014), much remains to be learned about how fire-grazing interactions affect foraging at fine-scales, i.e. the feeding station level. A feeding station is defined as the forage available to an herbivore without moving its front feet during a foraging bout (Bailey et al. 1996). The feeding station is the spatial unit of finest ecological resolution in the ecological hierarchy where foraging decisions are made that can affect coarser-scale distributional decisions (Morris 1987, Senft et al. 1987).

Fryxell (1991) modeled the forage maturation hypothesis (FMH) (McNaughton 1986, Hobbs & Swift 1988) as a trade-off between forage quality and quantity to evaluate grazer behavior at multiple scales, providing a framework to understand patch use and the spatial and temporal distributions of grazing herbivores (Wilmshurst et al. 1999, Hebblewhite et al. 2008, Dancose et al. 2011, Bischof et al. 2012). In this model, optimal intake rates by foragers occur at low to intermediate levels of forage biomass. FMH posits that aggregations of large herbivores reflect optimal combinations of forage quality and quantity to maximize intake rate (Fryxell 1991). In turn, collective consumption pressure at intermediate to high grazer densities may maintain vegetation in a state of low to intermediate forage quantity but high quality through regrowth of young forage tissue (McNaughton 1979, Fryxell 1991); i.e., seasonal maturation to high biomass is repressed by repeated foraging pressure.

Fire is a major ecosystem driver in many grasslands, where it leads to spatially heterogeneous distributions of forage quality, appearing as a shifting mosaic within and among years depending on the time since a patch last burned. Fire significantly increases leaf nutrient
concentrations in post-fire growth (Blair 1997, van de Vijver et al. 1999) while removing older, non-palatable tissues (Pfeiffer and Hartnett 1995). Complementary to direct grazer-vegetation interactions and the FMH, the Transient Maxima Hypothesis (TMH) (Seastedt and Knapp 1993, Blair 1997) describes the development of a shifting mosaic of vegetation quantity and quality in response to fire-mediated release from resource limitations in tallgrass prairie with great potential to influence grazer-fire interactions. In tallgrass prairie, primary productivity is often co-limited by light, energy and soil nutrients, with the relative importance of individual resources dependent on time since last fire (Blair 1997). Annually burned grassland receives sufficient light and temperatures are non-limiting, but soil nitrogen becomes limiting. For unburned grassland when litter accumulates, light / temperature is limiting, and available soil-N increases with time as it is not fully used by plants.

A post-fire “pulsed” increase in ANPP occurs in vegetation that is released from an extended period of fire suppression. An abrupt release of light limitation coupled to the availability of increased accumulation of available soil nitrogen leads to a short-lived, non-equilibrium pulse in ANPP. This non-equilibrium period is referred to as a “transient maxima” – when availability of both potentially limiting factors is sufficient to support increased ANPP (Seastedt and Knapp 1993). In tests of the TMH in tallgrass prairie, Blair (1997) found increased ANPP and higher concentrations of shoot tissue nitrogen (N) in years with burning when vegetation was exposed to intermediate fire frequencies (e.g. every several years) compared to annual burning or long periods of fire suppression (Fig. 1a; Blair 1997). Enhanced ANPP and plant tissue-N content following an infrequent fire derive from the ability of vegetation to exploit higher soil inorganic and mineralizable-N accumulated in the absence of fire, under new high-light conditions. Moreover, net N-mineralization rates and foliar-N content both decline with
successive annual spring burning, ultimately reducing nutritional quality available to grazers; unburned sites provide less palatable forage because of the significant proportion of mature, low quality leaf tissue in standing vegetation (Vinton et al. 1993, Pfeiffer and Hartnett 1995, Knapp et al. 1999). Consequently, a shifting mosaic of areas of varying fire frequency can modulate the spatial and temporal distribution of large herbivores through combined effects on forage quality and quantity (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2009) similar to the FMH. Differences in nutrient value and palatability of forage available in areas burned frequently, infrequently, and not burned should alter foraging behavior at the feeding station level where diet selection occurs (Senft et al. 1987).

The overall significance of the fire-grazing interaction can be determined by examining how fire influences grazing behavior, the key to understanding the link between fire and grazing (Fuhlendorf and Engle 2004, Allred et al. 2011a). Although it is well known that large grazers are attracted to recently burned grassland, the mechanisms drive forage nutrient availability and resulting fine-scale foraging behavior after a fire remain unexplored. For example, the initial post-fire surge in forage nutrient availability in infrequently burned grassland (TMH) may interact with subsequent concentrated grazing pressure (FMH) to maintain grassland in an ideal state of forage quality and quantity, where large herbivores realize short-term benefits in nutrient acquisition (Fig 1b). The shifting mosaic from both fire-induced and concomitant grazing enhanced forage quality is well known (Schuler et al. 2006, Allred et al. 2011b, Eby et al. 2014).

Here, we hypothesize that mechanisms underlying FMH and TMH interact as two complementary diet optimization drivers that guide bison distributions during short-term periods. Because protein (i.e. N content) is often a limiting factor for ungulate performance (Van Soest
1996), foraging responses to variable fire frequency and associated plant responses will provide insight into how frequent and infrequent fires impact bison behavior.

To date, few if any studies have directly quantified and compared fine-scale foraging behavior by ungulates at the feeding-station scale in grasslands managed under variable burning regimes. Most studies are conducted in unburned grasslands (but see Shrader et al. 2006), and studies evaluating ungulate preference for burned areas have not investigated detailed foraging kinetics (Vinton et al. 1993, Sensenig et al. 2010, Allred et al. 2011a-b). Moreover, no investigations have linked the TMH as a mechanism to complement the FMH in explaining large herbivore foraging behavior. Coarse-scale distributional patterns of grazers indicate that an elevated response of forage quality to fire after a period of reduced light availability initially attracts ungulates to the recently-burned area (Eby et al. 2014). Furthermore, total compensation of grass and forbs occurs in recently-burned, bison-grazed watersheds at Konza Prairie (Knapp et al. 2012). We hypothesize that repeated grazing maintains periodically burned areas in a state of low-to-intermediate biomass until forage senescence occurs. With senescence, bison no longer select recently burned areas and their spatial distributions become random and directed towards forage-laden, unburned watersheds during the dormant season; this was observed at Konza Prairie (Vinton et al. 1993). Loss of high-quality forage can be expected to change ungulate foraging behavior and to lower within-season site fidelity (Wittmer et al. 2006).

An inverse relationship between leaf development stage and protein content and forage digestibility (Waite et al. 1963, Miller et al. 1965), predicts a positive feedback between grazing activity and forage palatability (Archibald et al. 2005, Verweij et al. 2006, Kerby et al. 2007) – a tenet of FMH. Forage quantity influences grazer foraging behavior at the feeding station scale
(Ruyle et al 1987, Drescher et al. 2006), outcomes that are sure to be influenced by fire-induced alterations in forage quality are in need of study.

Here, we examine the foraging behavior of the plains bison (*Bison bison*) in tallgrass prairie at Konza Prairie Biological Station (KPBS) as individuals freely selected forage among multiple watersheds that differ in fire and grazing history. We first evaluated how vegetation quantity and nutritional quality varied throughout the growing and dormant seasons across watersheds burned at different frequencies, and then quantified how vegetation attributes under different burn histories influenced bite mass, bite rate and instantaneous intake rate of focal individuals. We predicted: (a) intake rate would increase with biomass on feeding stations of high quality and bite rate should eventually decline at high biomass; (b) intake rate would increase at a greater rate in infrequently burned watersheds in years of burning, where protein availability is greatest, (c) concomitant with a behavioral response in foraging kinetics to a fire-induced transient maxima in infrequently-burned grassland would be maintained in a low-to-intermediate state of forage quantity in infrequently-burned grassland; (d) a behavioral response in foraging kinetics to fire-induced nutrient enhancement of frequently-burned watersheds would be minimal; and (e) foraging kinetics in frequently-burned watersheds would be similar to that observed in not-burned watersheds because ANPP has been reported to be similar between the two fire regimes in bison-grazed watersheds at KPBS (Knapp et al. 2012). We interpret and discuss our results relative to feeding stations in a fire-dependent landscape using the framework linking TMH and FMH as described above.
METHODS

Study Area

Konza Prairie Biological Station (KPBS) is 3487 ha of native, C₄-dominated grassland in the Flint Hills of northeastern Kansas (39°05'N and 96°35'W), located approximately 13 km south of Manhattan, KS. The site is representative of Flint Hills tallgrass prairie with a variable continental climate with warm, wet springs, hot summers and dry, cold winters. The 32 year mean annual precipitation (1982 to 2013) is 832.9 ± 61.1 mm with ~75% falling during April to September. KPBS experienced below average precipitation in 2012 (568.9 mm, a deviation of -46% from the annual average precipitation), while 2011 (814 mm, -2% from the annual average annual precipitation) and 2013 (783.4 mm, -6% from the annual average precipitation) were near average precipitation. Vegetation is mostly native tallgrass prairie (>90%) dominated by C₄ perennial grasses (*Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, and *Schizachyrium scoparium*) where interstitial forbs constitute >75% of species richness (~575 species) (Towne 2002). Bison have access to a contiguous 1,012 ha fenced enclosure comprising 10 hydrologically-delineated watersheds with different fire treatments. Two replicate watersheds each have been burned in the spring since 1988 at one of three fire frequencies (1, 2, and 20 years), while four watersheds have been burned once every four years. Hereafter, we refer to watersheds with fire frequencies of 1-2 years and that did burn in the spring (late March-early April) prior to focal animal observations (late April to December) as frequently-burned watersheds (n= 3 in both years). Watersheds with fire frequencies of 4 or 20 years and that burned in the spring prior to focal animal observation are referred to as “infrequently-burned” watersheds (n=2 in 2012, 1 in 2013). Watersheds that were not burned (n=5 in 2012, 6 in 2013) in the spring prior to our observations are referred to as “not-burned” sites in this study,
regardless of the historical burn frequency. Bison stocking rate is currently maintained at ~260 adults (plus ~100 spring-born calves) annually or ~14.5g bison / m² resulting in a target density that removes ~25 of the ANPP.

**Focal Sampling**

To quantify fine-scale behavior, foraging bouts (n=208) of individual adult bison (excluding yearlings and calves) were recorded (1.4 ± 0.05 observations per individual) with a digital video camera using focal animal protocol (Altmann 1974) for at least 5 minutes (range: 5 to 10 min). Observations were done from May to December in 2012 and 2013 in replicated frequently, infrequently burned, and not-burned watersheds. Video footage of focal animals was scored with behavioral analysis software (Observer XT v11.0) for bite number, displacement of the front feet, head raising and lowering, and when an animal lays down. Video was recorded from the cab of a truck parked on-site at a distance of 10-100 m for at least 10 minutes prior to recording to allow bison to acclimate to its presence and thus minimize disturbance to feeding from the presence of the observer.

**Vegetation Surveys at Feeding Stations**

Following each observation of bison feeding, forage attributes were measured using three quadrats at arbitrary locations parallel to the foraging area monitored during the 5 min foraging bout. Quadrats consisted of 1m² sampling frames split into five 0.2 m² sub-plots placed within a 10 m radius circle centered on the feeding location (Schaefer and Messier 1995). In every sub-plot, plant cover and percentage of green material was estimated visually using 10% classes in four vegetation groups: grasses and sedges, forbs (all herbaceous dicots), litter (previous year’s dead grass), and bare ground. Mean grass height was calculated by measuring three representative plants to the nearest cm at twenty points along a 30-m transect running parallel to
the grazed path. Total dry plant biomass (B, in grams per square meter) was estimated by clipping standing biomass to 1 cm height from a 0.1-m$^2$ sampling frame placed parallel to the foraging path. Three 0.1-m$^2$ swaths were clipped and adjusted to 1 m$^2$. Total biomass was then multiplied by proportions of graminoids, forbs, and litter determined from visual percent cover estimates to estimate biomass of the three vegetation elements. To estimate forage quality at feeding stations, three swaths of vegetation within 2 m parallel to the foraging path were clipped to 1 cm height from a 0.1 m$^2$ sampling frame (< 24 hr since grazed).

Samples were dried for 48 h at 60° C to a constant mass, and sorted into graminoids, forbs, and litter. Because graminoids comprise 98% of the year round diet of bison in tallgrass prairie (Coppedge et al. 1998), graminoids were separated from clipped vegetation samples and analyzed for nutrient content. For each foraging observation sample, two of the three clipped graminoid samples were randomly selected for nutrient analysis. Graminoid nutritional properties, including lignin, NDF (neutral detergent fiber), N (crude protein), P, and in vitro digestibility after 30 hours were determined using NIRS (Near Infrared Spectroscopy) analysis. Crude protein was estimated as %×N in plant tissue * 6.25, while NDF is inversely related to forage quality as it indicates the relative amount of cellulose and lignin in plant tissue, both of which reduce forage digestibility. A total of 470 samples of feeding station biomass, 2-3 samples per foraging observation, were dried, ground to a 1mm particle size and analyzed by Dairyland Laboratories Inc. (Arcadia, WI) on a Foss model 5000 NIR instrument. Appendix A describes methodology for permanent vegetation sampling stations established to determine temporal variation in vegetation in each watershed in the bison enclosure.

Estimation of bite size
Within a 1-m radius circle of each feeding station for each animal observation period, we located three to four small square quadrats of 9.5 x 9.5 cm per sampled feeding station, corresponding to approximate width and snout length of a bison’s mouth (Janis and Ehrhardt 1988), and clipped grass to the average grazing depth adjacent to the feeding station. We estimated bite mass by first measuring with a ruler the grazing depth of the ten nearest grazed plants from the center of the foraging path, and calculated the mean grazing depth (St-Louis and Côté 2012). Bite samples were oven dried for 48 h at 60°C, and weighed using a 0.001 g precision balance. Bite quality was evaluated as a function of bite sample digestibility and NDF content (Drescher et al. 2006). The 10 bite subsamples for each foraging observation were combined for nutrient analysis, so that bite quality represents the nutrient quality of 10 combined subsamples.

**Ingestion Time**

Bite rate was measured by scoring foraging bout video using Noldus Observer XT V.11 software programmed to record the number of bites taken per feeding step and the number of bites per second. Each observation spanned at least five minutes (range: 5 to 10 min) from an average distance of 20 m in a truck. A feeding step was defined as a single step with one of the front legs where the bison took at least one bite. Observations of bite rate did not include non-feeding steps. Bite rate was calculated by dividing the total number of bites by the time taken in feeding steps.

Instantaneous forage intake rate was calculated as the product of bite rate and bite size. Because intake rate of dry matter at feeding stations by ungulates is limited by ingestion time (Spalinger and Hobbs 1992), we used functional responses estimated during foraging bouts to determine the ingestion time of forage. We determined dry matter forage intake rate (I; g/min) by multiplying the bite rate (BR; bites/min) derived from analysis of foraging videos by bite mass.
Forage intake rate was then related to forage biomass \((B)\) using the Michaelis-Menten form of the type II functional response:
\[
\frac{MB}{\beta + B}
\]
where \(M\) is the maximum feeding rate \((g/min)\) and \(\beta\) is the half-saturation constant \((g/m^2)\). Appendix B summarizes the methodology for estimation of recent grazing activity.

Data Analysis

A mixed linear model was used to determine variation in total grass biomass and crude protein content of grass shoots for burn treatments, seasonal periods, and years. Fire treatment, seasonal period, and year were main effects with month within seasonal period included as the random effect. Observations were delineated to three seasonal periods: growing (April 15-June 30), mid-to-late summer transition (July 1-October 7), and dormant (October 8–December 31).

Sattherwaite’s approximation was used to calculate effective degrees of freedom of a linear combination of independent sample variances.

A general linear model was used to analyze the variation in mean bite mass, bite rate, and intake rate with burn treatment, seasonal period, and station grass biomass. Functional response relationships for bite mass, bite rate, and short-term intake rate were derived using the ungrazed forage characteristics adjacent to the foraging path. Prior to performing ANCOVA to compare slopes and intercepts of the seasonal trends in foraging behavior relative to grass biomass, we contrasted the slopes of the categorical variables of interest relative to forage biomass to test interactions among slopes using SAS system 9.2 (SAS Institute Inc. 2010).

RESULTS

Temporal Trends in Grass Availability
Mean standing stock of live and dead grass biomass (g m$^{-2}$) averaged across topographic positions was greater in not-burned, watersheds in comparison to frequently- and infrequently-burned watersheds burned the previous spring (Fig. 2a). However, grass biomass after the spring burn in 2013 for infrequently-burned, grazed watersheds reached similar levels to frequently- and not-burned watersheds by the end of the growing season, unlike the consistently low levels of grass biomass for infrequently-burned sites in 2012. Analyses of total grass biomass revealed significant main effects of seasonal period ($F_{2,7.5}= 7.5, P=0.02$) and burn treatment ($F_{2,22.7}=8.11, P=0.002$) in addition to a significant year-by-season interaction ($F_{2,25}=4.3, P=0.02$; Appendix A, Table A1). The transitional period had greater total grass biomass than the dormant period except in 2012; the transitional period and dormant period had similar levels of grass biomass.

Frequently-burned and infrequently-burned watersheds had significantly less total grass biomass than not-burned watersheds during the study (Fig. A1), which is in accord with the prediction that initial attraction to high quality forage instigated repeated grazing (Fig. B4). In 2012, grass biomass sampled during the peak of production in an annually burned, ungrazed site (watershed 1D), was 19% (320.3 g m$^{-2}$) below the annual mean of 399.7 g m$^{-2}$ estimated from 1989 to 2013 (mean grass biomass averaged over topographical positions, Konza-LTER dataset PAB01). In 2011 this watershed had above average ANPP with 540.6 g m$^{-2}$ (+37%). In 2013, grass biomass was 38% above the recorded average with 551.2 g m$^{-2}$).

Crude protein content of live forage at feeding stations declined as the season progressed in 2012 (curvilinear regression, $F_{1,100}=26.2 \ R^2=0.35, P<0.0001$) and 2013 (curvilinear regression, $F_{1,93}=229.3, R^2=0.8, P<0.0001$), although a substantial increase in protein content was evident in late summer 2012 (Fig. 2c,d). Lignin content increased with increasing day of the year in 2012 (curvilinear regression, $F_{1,100}=21.5, R^2=0.30, P<0.0001$) and 2013 (curvilinear regression,
Crude protein content of forage peaked during the early growing season of both years and protein content of forage from infrequently-burned watersheds was generally higher throughout the study. Analyses of variation in crude protein content of grass shoots by burn treatment revealed a marginally significant difference in addition to a marginally significant year-by-seasonal period interaction. Infrequently-burned watersheds had higher crude protein content of grass shoots than not-burned watersheds throughout the study (Bonferroni’s least squared differences [lsd], \(P=0.01\)), while frequently-burned watersheds had marginally lower crude protein content of grass shoots than infrequently-burned watersheds (lsd, \(P=0.1\); Fig. A2). The year-by-seasonal period interaction revealed crude protein content of grass shoots was lower in the 2012 dormant season than in the 2013 dormant season (lsd, \(P=0.009\)).

**Functional Responses to Feeding Station Biomass**

Bite mass increased linearly with increasing grass biomass across all treatments (\(F_{2,206}=32.39, P<0.0001, R^2=0.14\)). The mean bite mass relative to grass biomass level did not differ significantly among burn treatments (\(F_{4,198}=1.32, P=0.27\)) or among seasons in watersheds that did not burn in the spring prior to observation (slope, \(F_{2,76}=1.94, P=0.15\); intercept, \(F_{1,76}=5.09, P=0.03\), Fig. 3c). In infrequently-burned watersheds, there was a marginally significant interaction between season and grass biomass in the bite mass ANCOVA (slope, \(F_{1,50}=3.37, P=0.07\), intercept, \(F_{1,50}=0.1, P=0.75\), Fig. 3b). Thus, we tested whether the slope of the relationship of bite mass with grass biomass differed between seasons. Bite mass differed significantly between growing and transitional seasons independent of differences in grass biomass with growing season bite mass increasing with grass biomass at a greater rate than the transitional season in infrequently-burned watersheds. Only five observations in infrequently-
burned watersheds for the dormant season were available and were not included in analyses. In frequently-burned watersheds, the relationship of bite mass to grass biomass did not differ significantly among seasons (slope, $F_{2,67}=1.12$, $P=0.33$, intercept, $F_{2,67}=1.25$, $P=0.29$, Fig. 3a). The upper envelope to the scatter of points suggests that maximum bite mass for each watershed type could be obtained from a feeding station biomass of 40 g m$^{-2}$. Overall, the mean bite mass was similar among watersheds types: frequently-burned ($\bar{x} \pm SE=0.58 \pm 0.1$ g), infrequently-burned ($\bar{x}=0.53 \pm 0.1$ g), and not-burned ($\bar{x}=0.64 \pm 0.1$ g; Fig. 4a).

Bite rate declined significantly with increasing grass biomass at the feeding station, averaged across all three burn treatments ($F_{2,206}=19.11$, $P<0.0001$, $R^2=0.08$). Bite rate did not differ significantly among burn treatments ($F_{4,198}=0.30$, $P=0.88$). A seasonal difference in bite rate was measured at feeding stations with similar grass biomass within treatment combinations as seen for frequently-burned watersheds (Fig 3d). Bite rate was greater in the dormant season than the growing season, but not different from the transitional season (slope, $F_{1,67}=0.83$, $P=0.44$, intercept, $F_{2,67}=2.64$, $P=0.08$, Fig 3d). Because we found a marginally significant interaction between season and grass biomass for bite rate (ANCOVA, $F_{1,53}=2.95$, $P=0.09$, intercept, $F_{1,50}=0.74$, $P=0.39$, Fig. 3e) in infrequently-burned watersheds, we tested whether the slope of bite rate with increasing grass biomass differed between seasons. Bite rate differed significantly between growing and transitional seasons independent of grass biomass differences with transitional season bite rate decreasing at a greater rate than the growing period in infrequently-burned sites. This meets our prediction of an inverse relationship between bite mass and bite rate at high quality feeding stations as biomass increases. In watersheds not burned the spring prior to observation, bite rate was similar among seasons although the slopes were marginally different with the dormant season having a positive slope while the growing and transitional season bite...
rate decreased with increasing grass biomass (slope, $F_{2,71}=1.44, P=0.08$; intercept, $F_{1,71}=1.44, P=0.24$). Maximum bite rates ~55 bites min$^{-1}$ were observed in each watershed type on grass biomass up to 40 g m$^{-2}$. Mean bite rate in frequently-burned ($\bar{x}=34\pm 2.3$ bites min$^{-1}$), infrequently-burned ($\bar{x}=37\pm 2.4$ bites min$^{-1}$), and not burned grassland ($\bar{x}=35\pm 2.1$ bites min$^{-1}$) were similar (Fig. 4b).

Intake rate increased linearly with biomass availability at the feeding station across all three burn treatments ($F_{2,206}=8.15, R^2=0.04, P=0.005$). A maximum limit to the intake rate was reached at feeding stations of ~50 g m$^{-2}$ (40 g min$^{-1}$ in frequently-burned watersheds; 35 g min$^{-1}$ in infrequently-burned; and 50 g min$^{-1}$ in watersheds not burned in the spring prior to observation). Intake rate relative to total grass biomass at feeding stations did not differ significantly among watershed types ($F_{4,206}=1.04, P=0.36$) or among seasons for frequently-burned (slope, $F_{1,67}=2.05, P=0.14$; intercept, $F_{2,67}=2.37, P=0.10$) and not-burned watersheds (slope, $F_{2,71}=0.73, P=0.49$; intercept, $F_{1,71}=0.63, P=0.54$, Fig. 3g,i). This indicates a minimal response in forage kinetics at feeding stations in frequently-burned watersheds and in not-burned watersheds, which exhibit similar patterns of productivity. In infrequently-burned watersheds, a significant interaction between season and grass biomass influenced intake rate (ANCOVA, slope, $F_{1,50}=6.83, P=0.01$; intercept, $F_{1,50}=0.69, P=0.41$, Fig. 3h). Thus, we tested whether the slope of the relationship between intake rate and grass biomass differed between seasons. At infrequently-burned sites, intake rate differed significantly between growing and transitional seasons independent of grass biomass with intake rate during the growing season increasing at a greater rate relative to biomass than during the transitional season. This result met our prediction that a behavioral response in foraging kinetics would occur where a pulse of available nutrients was utilized following infrequent fire. Seasonal intake rate relative to feeding station grass
biomass levels remained similar ($F_{4, 198} = 0.64, P = 0.64$). Overall, the mean intake rate was similar among grassland types: frequently-burned ($\bar{x} \pm 95\% \text{ CI} = 19.1 \pm 2.5 \text{ g min}^{-1}$), infrequently-burned ($\bar{x} = 19.0 \pm 3.2 \text{ g min}^{-1}$), and not-burned watersheds ($\bar{x} = 21.7 \pm 2.6 \text{ g min}^{-1}$; Fig. 4c). Results of feeding measures across seasons by burn treatment with increasing live grass mass, feeding measures across seasons irrespective of burn treatments, and patterns in grazing activity are summarized in Appendix B.

**DISCUSSION**

Spatial heterogeneity in forage quality and quantity in tallgrass prairie is driven by fire-grazer interactions, leading to a shifting mosaic of not only vegetation characteristics, but also the distribution and foraging behavior of grazers (Fuhlendorf et al. 2009; Allred et al. 2011a). A new appreciation for the complementary nature of the FMH and the TMH emerges from our study and sets the stage for mediating food-processing rates at feeding stations and grazer aggregation responses to these patches at watershed levels. While the TMH was previously applied with the goal of understanding how primary productivity responds to disturbance when controlled by contrasting limiting factors at equilibrium states, we extend the importance of this mechanism to the next trophic level. Moreover, the impact of grazing on vegetation quantity and quality can mediate forage intake by grazers through the FMH to maintain seasonally attractive and profitable patches. Recent burning of infrequently-burned areas leads to especially attractive patches for grazers (from the TMH) that then remain so because of subsequent grazing in accordance with the FMH.

*Fine-scale foraging behavior and fire frequency*

Fine-scale feeding behaviors ultimately contribute to coarse-scale foraging decisions and landscape distribution by large herbivores (Senft et al. 1987). We assessed how fine-scale
feeding behaviors by bison in recently-burned watersheds responded to fire frequency in tallgrass prairie. Observational and experimental data indicate that variation in fire frequency plays a significant role for understanding seasonal changes in large herbivore foraging behavior. Moreover, the time since last burn in watersheds with different burn histories is a critical link between fire and grazing and is an important driver behind variation in feeding measures at this fine scale. Our results indicate that bison feeding responses to forage availability and quality at the feeding station are influenced by fire-induced transient maxima dynamics.

During the early growing season, ungulates restore fat and body weight lost during the winter dormant season, a period during which grazers often compensate behaviorally for nutrient-poor foods by ingesting more food (Illius 2002). A greater rate of increase in bite mass and instantaneous intake rate during the growing season than in the transitional season in infrequently-burned watersheds indicates that bison adjusted their consumption rate to maximize their use of forage when it was in a state of greatest nutritional value in this fire treatment. Furthermore, bite rate declined more rapidly during the transitional season in the infrequently-burned treatment, indicating that handling time increased with plant maturity consistent with FMH predictions. Ingestion constraints may be less limiting with increasing forage biomass when food has high protein content and concomitant palatability, thus allowing large grazers to attain sufficient protein for maintenance requirements (Van Soest 1994, McArt et al. 2009). This observation may explain why nutritional enhancement of grasslands through periodic burning does not reduce stocking rate, deferment, or rest in cattle when compared to annually-burned grassland (Limb et al. 2011). As maximizers of short-term gain (Bergman et al. 2001, Fortin et al. 2002), bison may be foraging in infrequently-burned areas in spring to gain weight most rapidly because summer dietary N intake greatly affects body mass (Hjeljord and Histol 1999,
McArt et al. 2009), or allocate more time for raising young, regulating thermal balance or maintaining social status. If true, the time saved by selecting a diet that maximizes short-term intake should also improve fitness (Fortin et al. 2002).

Response to transient maxima resource availability

The TMH complements the FMH by providing a useful mechanistic framework for understanding grazing herbivores in nutritionally heterogeneous, mesic grasslands; the pulse in forage quantity and quality made available by periodic burning corresponds to patterns of large herbivore use during the early growing season (Archibald and Bond 2004). Periodic fire is essential for the development and maintenance of tallgrass prairie ecosystems and has strong effects on productivity (Briggs and Knapp 1995, Blair 1997) and nutrient cycling rates (Seastedt and Ramundo 1990, Ojima et al. 1994). Throughout the study period, standing crop of grass biomass was generally lower in infrequently-burned watersheds that burned in the spring of that year (late March), followed by intermediate levels of grass biomass in frequently-burned watersheds also burned in the spring of that year, with the highest grass biomass observed in watersheds not burned the previous spring (Fig. 2a). This observation is consistent with the FMH that posits grasslands are maintained by aggregations of large herbivores in a state of low to intermediate quantity (Fryxell 1991, Hebblewhite et al. 2008). Furthermore, bison in tallgrass prairie are sometimes known to use recent burns even after they are virtually devoid of vegetation (Mitchell et al. 1996, Schuler et al. 2006). Foraging at locations offering low to intermediate levels of vegetation, where foragers tradeoff food digestibility and availability corresponds to expectations where herbivores maximize energy and nutrient intake rate (Fryxell 1991, Bergman et al. 2001). Fine-scale foraging behavior by the KPBS bison herd can be viewed as a tradeoff between forage quality and quantity where fire attracts aggregations of large
herbivores, especially to periodically-burned watersheds, and subsequent prevention of forage maturation by grazing in burned watersheds guides the spatio-temporal distribution of grazers as long as regrowth is possible. Although the generality of these results to other grasslands remains to be tested we anticipate this interaction between non-equilibrial forage resources and ungulate foraging behavior is a key driver for ungulate distributions in fire-prone systems generally. 

*Bison nutrient acquisition in the tallgrass prairie*

Ungulates increase forage intake following periods of low food availability to regain body condition in both arctic and alpine systems and to compensate for a decline in food quality during the dry season (Van der Wal et al. 2000, Hamel and Côté 2008). In arid systems, equids reduce intake rate during the dormant season when plant greenness is lowest (St-Louis and Côté 2012) although the behavioral mechanism behind reduced intake rate is poorly understood and has not been addressed in temperate systems with an intact fire-grazer interaction. In the Serengeti, Thomson’s gazelles (*Gazella thomsoni thomsoni*) compensate for unfavorable temporal variation in resource availability (e.g. due to depletion of quality resources) at small spatial scales (Fryxell et al. 2005). In bison, we found that bite quality during the growing season was positively associated with plant nutrients and bite mass was negatively associated with plant structural properties. Late summer bite quality and bite mass were positively associated with plant digestibility and plant structural properties, respectively. The inverse relationship between bite mass and plant structural properties observed in the growing season differed from feeding station behavior during late summer when both average short-term forage intake and nutrient intake rate were minimal. This suggests bison were compensating for low foliar nutrient availability by increasing bite mass which concomitantly reduced mean intake rate in the dormant season. This pattern was most pronounced during 2013 when forage quality did not
increase in late summer with increased precipitation as was observed in 2012 when precipitation was markedly reduced.

Foliar protein concentration in grasses often increases in years of reduced precipitation (Milchunas et al. 1995, Joern and Mole 2005). Bite mass and intake rate increased during the late summer of 2013 while protein content of available green forage continued to decline. We surmise bison were compensating for low protein availability by consuming more forage consistent with other studies (Laca et al. 1994); rather than mobilizing fat reserves to meet shortfalls in nutrient needs (Shrader et al. 2006). Our interpretation of this behavioral adjustment is that bison were compensating for lower forage quality in late summer by consuming more food to keep the rumen microbial system primed with adequate protein content for microbes to maximize gains during critical times of the year (Faverdin 1999). This shift in foraging behavior at the end of the growing season may be a mechanism to modulate weight reduction, which occurs at KPBS in years without late summer rains and without the concomitant flush of protein availability (Craine et al. 2009). Results presented here demonstrate an extension of the TMH to an additional trophic level, consumers, and how it complements the FMH but we also demonstrate foraging and nutrient acquisition tactics of a large, native grazer at the finest scale of foraging in a landscape with an intact fire-grazer interaction which, to our knowledge, has not been investigated.

Synthesis

The interplay between fire-induced nutritional enhancement of forage and temporal variation in feeding behavior suggests that fine-scale foraging is an integral component of understanding the role of fire on bison distribution and foraging activity in this nutritional landscape. The observed increase in bite mass and instantaneous intake rate of individual bison during the growing season
in periodically burned grassland indicates the "pulse" of N availability and ANPP driven by fire in previously light-limited, unburned grassland modulated ungulate foraging behavior. Thus, the importance of fire in controlling grazer behavior at the feeding station scale was temporally contingent upon fire frequency, the elapsed time since the last burn, and the timing of plant productivity pulses. Whether such behavioral responses occur in grasslands where burning occurs at other times of the year remain unclear.

The dynamics of feeding station use in this study sheds light on how grazing herbivores respond to nutritionally heterogeneous forage resources across seasons and between years of contrasting forage quality and availability. Although resource depletion is known to change the dormant season habitat selection of temperate ungulates due to the trade-off between forage quality and quantity (van Beest et al. 2010), our data clarify how temperate ungulates shift foraging behaviors in response to forage depletion at the feeding station scale.

Our investigation of fine-scale foraging behavior in mesic grasslands when fire results in markedly different nutritional value also provides baseline information for forecasting animal foraging behavior in other fire-prone ecosystems. While grassland fires are influential in generating large herbivore distributions in and of themselves (Sensenig et al. 2010, Allred et al. 2011a,b), we conclude that the fine-scale behavioral mechanism associated with foraging at the feeding station is also responsible for herbivore affinity to recently-burned grassland. Our data suggest that fire-induced heterogeneity in vegetation quality may be an important landscape scale process that helps promote nutrient attainment in a historically important native grazer and illustrates the utility of linking optimal foraging theory with insights from consumer resource and fire ecology.
ACKNOWLEDGEMENTS

We thank H. Tetreault, J. Girvin, K. Girvin, G. Samms, and T. Stringer for assistance during the project. J. Blair, K. Gido, J. Gomez and E. Welti provided useful discussion and comments on the manuscript. We also thank R. Ruess, A. Shrader, and an anonymous reviewer for extremely helpful comments on a previous version of this manuscript. The Konza Prairie is owned by the Nature Conservancy and managed by Kansas State University Division of Biology.

We are grateful for support from NSF/DEB 1020485 (to AJ), the NSF Konza LTER, NSF GK-12 program, and the Division of Biology, KSU. This paper is a contribution of the Kansas Agricultural Experiment Station (manuscript number 15-204-J).

LITERATURE CITED


Figure 2-1. (A) Graphical illustration of the transient maxima hypothesis, which predicts transient “pulses” of plant N availability (solid line) that are greater than the average N availability in tallgrass prairie that is annually-burned (fine-dotted line) sites as a result of increased light availability and gradually declining N availability as plants senesce. Note that the figure illustrates patterns of change over a post-spring burn period in a year. (B) Schematic showing general mechanisms of the forage maturation hypothesis (FMH) complemented by the transient maxima hypothesis (TMH). Foraging constraints of daily...
cropping (solid line) and digestion in frequently-burned (fine-dotted line) and infrequently-burned (dashed line) grassland that result in a foraging optima (arrows) at low-to-intermediate biomass. (Modified from Fryxell 1991).

Figure 2-2. Seasonal variation in forage properties at Konza Prairie, Manhattan, KS, U.S.A. (A) Variation (±95% CI) in the availability of standing grass biomass recorded along a 6m transect and averaged for upland and lowland areas in the three burn treatments used by bison. (B) Variation in grass biomass in frequently burned, ungrazed grasslands recorded along a 6m transect and averaged for upland and lowland topographical areas, 2011-2013. Data are shown with the monthly rainfall pattern; shaded bars indicate when burning occurred. (C) Percentage of crude protein in grass leaf tissue at feeding stations. (D) Percentage of lignin in grass leaf tissue at feeding stations. (E) Seasonal variation in the crude protein content of grass in the three grassland types available to bison recorded along a 6m transect and averaged for upland and lowland
topographical areas. (F) Seasonal variation in the lignin content of grass in the three grassland types.

Figure 2-3. Functional relationship of bite mass in relation to grass biomass at feeding stations. (A) Frequently-burned, (B) infrequently-burned, and (C) not-burned grasslands in the different seasons. Similar bite mass was obtained in (C) not-burned grasslands throughout the three seasonal periods, so a single line was fitted to these data. Functional relationship of bite rate in relation to grass biomass at feeding stations of (D) frequently-burned, (E) infrequently-burned, and (F) not-burned grasslands in the different seasons. Functional relationship of intake rate in relation to grass biomass at feeding stations of (G) frequently-burned, (H) infrequently-burned, (I) not-burned grasslands in the different seasons. Similar intake rate were obtained in (G) frequently-burned and (I) not-burned grasslands lands throughout the three seasonal periods, so a single line was fitted to these data.
Figure 2-4. Seasonal changes (±SE) in (a) mean bite mass; (b) mean bite rate; (c) mean intake rate across burn treatments by plains bison pooled across 2012-2013.
APPENDIX A

Temporal Variation in Grassland-type Biomass

Permanent sampling stations were established in the lowland and upland areas of all bison-grazed watersheds as well as two ungrazed watersheds (1D and K1B) located adjacent to the bison unit to measure variation in monthly vegetation biomass and height over the course of this two year study. The two ungrazed, annually burned watersheds were sampled to estimate differences in forage complexity between grazed and non-grazed units. Six swaths of 0.1 x 1 m of vegetation were clipped in both upland and lowland topographical areas. To avoid resampling recent plots, each new sample was located randomly approximately 5 m from samples taken the previous month. Twenty grass canopy height measurements were made along a 30 m transect running parallel to the clipped vegetation swath. Clipped samples were sorted into graminoids, forbs, and litter and each fraction dried and weighed. Vegetation biomass and grass height measurements were collected every two months during the non-growing season. For grazed watersheds, two of the six 0.1 x 1 m graminoid samples were randomly selected for nutrient analysis.
Table A.1.1. Results from a mixed linear model ANOVA for the effects of seasonal period, burn frequency, and year on total grass biomass as well crude protein content of grass shoots at Konza Prairie Biological Station, 2012-2013.

<table>
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<th>df</th>
<th>$F$</th>
<th>$P$</th>
<th>df</th>
<th>$F$</th>
<th>$P$</th>
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<td>2, 6.7</td>
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<td>0.52</td>
<td>4, 21.2</td>
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<td>Year</td>
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<td>0.78</td>
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<td>0.16</td>
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</table>
Figure A.1 1. Total grass biomass from permanent sampling stations pooled across 2012-2013 for each burn treatment by seasonal period at Konza Prairie Biological Station, Manhattan, KS, U.S.A.
Figure A.1 2. Crude protein content of grass leaf tissue from permanent sampling stations pooled across 2012-2013 for each burn treatment by seasonal period at Konza Prairie Biological Station, Manhattan, KS, U.S.A.
APPENDIX B

Functional Responses to Feeding Station Live Biomass

Bite mass
To test whether this trend between bite mass and available forage was observed in relation to live tissue availability by seasonal period we conducted ANCOVA with live grass mass. In all three treatments, a significant interaction between season and live grass mass did not occur in the bite mass ANCOVA (P>0.1); therefore we did not test whether the slope of bite mass with increasing live grass mass differed between seasons.

Bite rate
In frequently- and not-burned watersheds, a significant interaction between season and live grass mass did not occur in the bite rate ANCOVA (P>0.1); therefore we did not test whether the slope of bite rate with increasing live grass mass differed between seasons in these treatment types. A marginally significant interaction between season and live grass mass did occur for bite rate (slope, $F_{1,50} = 3.48$, $P=0.07$, intercept, $F_{1,50}=3.92$, $P=0.05$) in infrequently-burned watersheds with transitional season bite rate decreasing at a greater rate than the growing season.

Intake rate
In frequently- and not-burned watersheds, a significant interaction between season and live grass mass did not occur in the intake rate ANCOVA (P>0.1); therefore we did not test whether the slope of intake rate with increasing live grass mass differed between seasons in these treatment types. A significant interaction between season and live grass mass did occur for bite rate (slope, $F_{1,50} = 5.5$, $P=0.02$, intercept, $F_{1,50}=1.2$, $P=0.28$) in infrequently-burned watersheds with transitional season intake rate decreasing at a greater rate than the growing season.
Overall, we found significant differences in slopes of seasonal bite rate and intake rate with increasing total grass mass and live grass mass with transitional season rates decreasing at a greater rate than the growing season only in infrequently-burned watersheds.

Seasonal Trends in Feeding Measures

Mean bite mass increased with increasing grass biomass during spring in both years with an increase from 0.30 to 0.85 g in 2012 and from 0.20 to 0.40 g in 2013 across all three burn types (Fig. B1a). Thereafter, mean bite mass decreased to 0.45 g in 2012, whereas in 2013 it rose to 0.71 g until October. Mean bite rate remained between 33 and 38 bites min\(^{-1}\) from April to July in both years (Fig. B1b). Thereafter, mean bite rate remained at ~35 bites min\(^{-1}\) in 2012, whereas in 2013 it decreased to 22 bites min\(^{-1}\) in August then rose to ~38 bites min\(^{-1}\).

The mean grass intake averaged across burn types increased during spring in both years from 12 g min\(^{-1}\) to 27 g min\(^{-1}\) in 2012 and from 8 to 11 g min\(^{-1}\) in 2013. Thereafter, grass intake rate decreased to 15 g min\(^{-1}\) in 2012, whereas in 2013 it rose to 26 g min\(^{-1}\) during the transitional months of September and October (Fig. B1c). In 2013, the larger mean bite mass made possible by the generally more productive growing season led to an increase in the mean grass intake rate to over 19 g min\(^{-1}\) from September to November. Overall grass intake rate increased with grass biomass toward an asymptote of 31.4, 21.9, and 22.4 g min\(^{-1}\) during the growing \((F_{1, 90}=9.2, P=0.003)\), transitional \((F_{1,77}=5.93, P=0.017)\), and dormant seasons, respectively \((F_{1,35}=4.9, P=0.03)\) (Fig. B2).
Figure B.1. Monthly changes (±SE) in (a) mean bite mass; (b) mean bite rate; (c) mean intake rate by plains bison in 2012-2013 at Konza Prairie Biological Station, Manhattan, KS, U.S.A.
Figure B.1. 2. Non-linear relation between overall bison intake rate and feeding station biomass during the growing (April to mid-July), transitional (mid-July to early October), and dormant (mid-October to late March) seasons at Konza Prairie Biological Station, Manhattan, KS, U.S.A.
Multivariate Methods

Redundancy Analysis (RDA) was used to represent vegetation characteristics as a linear function of foraging behavior during the early growing season (April-June) and late summer (15 Aug-Oct); these periods reflect grass developmental and early-senescence periods when variation in grass quality is most pronounced. Values of the vegetation characteristic dataset were centered and standardized using z-transformation. Permutation tests were used to test the significance of the relationships between vegetation characteristics and foraging behavior variables (Ter Braak 1995). Canonical ordination analyses were performed using function rda in the labdsv package for Program R (v2.15).

Associations between vegetation characteristics and the foraging behavior variables were deduced from the RDA biplot. In RDA, response and explanatory variables are represented as vectors in a multidimensional space and the relative positions of these vectors indicate correlations (Makarenkov and Legendre 2002, Borcard et al. 2011). The ordination biplot reduced the multi-dimensional space to the two most differentiating dimensions. When the angle between the vectors of vegetation characteristics and foraging behavior variables in the horizontal plane was <45° and >135°, we inferred that variables were positively and negatively correlated, respectively. No correlation between variables was inferred when the enclosed angle lay between 45° and 135°. Significant factors were identified by a stepwise forward selection procedure.

Results

In spring, bite mass and bite quality averaged across years were associated with grass structure and grass chemistry, respectively (RDA, Fig. B3a). Bite mass was negatively associated with
grass structure, while bite quality was positively associated with grass nutrient content. Bite mass 
(P=0.01) and bite quality (P=0.01) were significantly correlated with forage nutrient 
concentrations and physical structure (Monte Carlo Permutation test), but bite rate was not 
significant (P=0.46) nor was it associated with bite mass or bite quality (Table B1). In late 
summer, bite mass, bite quality, and bite rate were associated with various measures of 
vegetation structure and grass foliar chemistry (RDA, Fig. B3b). The vectors representing bite 
mass and bite rate pointed to opposite quadrants of the RDA biplot, suggesting an inverse 
relationship between these variables and vegetation structure (Table B1). Bite quality was 
positively associated with grass nutrient contents. Bite mass (P=0.01), bite quality (P=0.01), and 
bite rate (P=0.01) were significantly correlated with vegetation nutrients and structure (Monte 
Carlo permutation test).
Table B.1. List of vegetation characteristics likely to be correlated with bite size and with bite quality as indicated by the spring and late summer RDA biplots (Fig.B1, B2) and the directions of the indicated correlation at Konza Prairie Biological Station, Manhattan, KS, U.S.A.

<table>
<thead>
<tr>
<th>Vegetation characteristic</th>
<th>Bite Mass</th>
<th>Bite Quality</th>
<th>Bite Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Spring</td>
<td>Late Summer</td>
<td>Spring</td>
</tr>
<tr>
<td>Total grass mass</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Live grass</td>
<td>-</td>
<td>+</td>
<td>%N</td>
</tr>
<tr>
<td>Dead grass</td>
<td>+</td>
<td>+</td>
<td>%P</td>
</tr>
<tr>
<td>Height</td>
<td>-</td>
<td>+</td>
<td>%NDF</td>
</tr>
<tr>
<td>No-grass mass</td>
<td>-</td>
<td>+</td>
<td>Lignin</td>
</tr>
<tr>
<td>%NDF</td>
<td>+</td>
<td>Total grass mass</td>
<td>-</td>
</tr>
<tr>
<td>Lignin</td>
<td>+</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure B.1. 3. (A) RDA biplot showing the relationship between foraging behavior variables and vegetation characteristics for bison grazing at Konza Prairie during the spring season (1 April to 20 June). Of the total variance in vegetation characteristics, 26% could be explained by foraging behavior variables. Of this variance, 22% is explained by the horizontal axis (axis 1 of the RDA), and another 4% by the vertical axis (axis 2). (B) RDA biplot showing the relationship between foraging behavior variables and vegetation characteristics for bison grazing during the late summer season, 1 August to 7 October. Of the total variance in vegetation characteristics, 24% could be explained by foraging behavior variables of which 16% is explained by axis 1 and another 8% by axis 2. Arrows indicate positions of foraging behavior variables.
Grazing Index

Grazing Activity Methods

An index of recent grazing activity established by Joern (2005) was used at forage sampling sites to estimate recent bison grazing. Joern (2005) classified an index of recent grazing activity based on an ordinal scale: 0 (ungrazed sites; no evidence of recent grazing because bison never present); 1 (no recent grazing but site located in grazed area); 2 (small amount of grazing evident, probably by one or two animals); 3 (moderate grazing from many animals; many grazed patches interspersed in ungrazed matrix, and evidence of relatively fresh dung); 4 (extensive grazing, but grazing lawn not yet developed; evidence of large herd grazing activity, including recent dung); and 5 (extensive grazing with much return grazing leaving a closely cropped site and little vertical structure).

Results

Mean grazing index for burn treatments were not different (p=0.53), while mean grazing index differed between seasons (p=0.001) with growing season having a lower index than the dormant season but not transitional period. A significant interaction (p=0.01) between burn frequency and season revealed unburned watersheds in the growing season had a lower index than in the dormant season. Sum of grazing index per sampling event indicate feeding stations in infrequently burned watersheds had the greatest grazing activity during the growing season (Fig. B4).
Figure B.1. 4. Sum of grazing index across season and burn treatments pooled from all feeding station sampling events at Konza Prairie Biological Station, Manhattan, KS, U.S.A.
Chapter 3 - Foraging decisions at the feeding-site and landscape scale in nutritionally heterogeneous grassland

ABSTRACT

When foraging in seasonal environments, herbivores select among plant patches that vary in standing crop and nutritional quality at several spatial and temporal scales. Although ruminants can maintain basic metabolic activity at marginal levels of forage quality, foraging tactics may shift to meet maintenance requirements during periods of plant dormancy. We investigated fine- and coarse-temporal scale foraging tactics of plains bison (Bison bison bison) throughout two growing seasons, hypothesizing that (a) forage quality will influence feeding-site selection at the fine, patch-scale, and (b) at the coarse, landscape-scale, avoidance of mature forage will decay as the growing season progresses. We investigated foraging behavior at two temporal scales throughout the growing season in a fire-dependent landscape – short-term foraging decisions in terms of feeding-site selection and coarse-scale foraging decisions in terms of time spent feeding over the growing season. In burned watersheds, bison feeding sites had higher a grass:forb ratio and forage quality, and lower forage quantity than measured at nearby random sites in the same habitat, especially in burned watersheds. Over the growing season, bison spent more time feeding in burned watersheds, and the diurnal time spent feeding increased from spring to fall as forage quality declined. An isotopic record of seasonal diet change from bison hair corroborated our fine-and coarse-scale findings that bison were moving into primarily unburned areas of high vegetation structure with C3, cool-season graminoids later in the season after C4 plants senesced. Our detailed foraging observations and stable carbon isotope records indicate that bison minimize time spent foraging by grazing in high-nutrient, burned grassland during the growing
season and shift foraging tactics by grazing in unburned grassland to meet nutrient requirements during periods of plant dormancy.

Keywords: *Bison bison*, Feeding-site Selection, Foraging, Mesic grassland, Scale, Stable Isotope

**INTRODUCTION**

For large mammalian herbivores, the spatial distribution of vegetation standing stock (stock or biomass) and nutritional quality are fundamental components affecting foraging behavior and resource-selection tactics (Wilmshurst et al. 1999a, b). Patterns of resource use reflect a hierarchy of scale-dependent limiting factors by foraging mammalian herbivores (Rettie and Messier 2000, St-Louis and Côté 2014). As plant cellulosic content increases over a growing season, plant nutritional quality in guiding foraging decisions can vary in a spatially dependent manner (Spalinger and Hobbs 1992, Fortin et al. 2002, Wallace and Crosthwaite 2005). In grassland ecosystems, forage abundance and quality are often inversely related because plant maturation increases fiber content in stems and leaves, thus lowering forage digestibility (McNaughton 1985, Van Soest 1994). Consequently, plants in low-stature vegetation patches such as in the early growing season may be more digestible than plants in patches with high vegetation stature (Miller et al. 1965). On the other hand, a mosaic of heterogeneous vegetation patches may be created with burning in response to simultaneous increased soil nutrient availability and release from light limitation, which can combine to increase both forage quantity and quality (Seastedt and Knapp 1993) especially in mesic grasslands. Herbivores thus face choices when foraging in a variable landscape of forage quantity and quality across several spatio-temporal scales, potentially leading to scale-dependent resource use patterns (Drescher et al. 2006, Hebblewhite et al 2008, St-Louis and Côté 2013).
Bovids can maintain metabolic function and cellulosic digestion at marginal levels of forage quality because nutrients from plants are extracted efficiently, in part due to the generally slow passage rate of plant materials in their digestive tract (Gilchrist and Clark 1957, Peden et al. 1974). In seasonal environments, forage resources are generally abundant, yet dependent on annual rainfall patterns. Therefore, resource selection tactics by foraging herbivores should reflect a strategy to maximize nutrient intake and minimize digestion constraints (Van der Wal et al. 2000). We expect grassland herbivores to forage in areas with high accessibility to young forage tissue to minimize foraging and digestion constraints (Fryxell 1991). Investigating patterns of patch selection will provide insight regarding the relative importance of forage availability and quality to modulate landscape-level distributions of ungulates throughout a year as patch selection drives choice of landscape features and foraging tactics may shift in response to availability of resources in the landscape.

Recently, quantitative information regarding bison grazing patterns in response to recently-burned grasslands has been primarily studied in tallgrass prairies, which are productive mesic grasslands in the North American continent (Vinton et al. 1993, Coppedge and Shaw 1998, Knapp et al. 1999, Allred et al. 2011a, b; 2013, Chapter Four, this thesis). In these studies, bison affinity for nutrient-rich, post-fire plant regrowth has been shown to drive their distribution across the landscape in space and time. However, little is known about how the increased forage quality and quantity associated with burned grassland will affect the behavioral mechanisms underlying bison attraction to recently-burned grassland. Finding and handling food normally dominates the activity budgets of ruminants (Beier and McCullough 1990), so an understanding of feeding-site selection and activity budgets of a wild bovid in fire-dependent, productive mesic
grasslands (e.g. tallgrass prairie) should shed light on how availability of forage resources of varying quality modulate the fire-grazer interaction at multiple spatiotemporal scales.

In this study, we investigated factors influencing foraging behavior by plains bison in tallgrass prairie that is managed with spring-season prescribed-burning. Our main objectives were twofold: (1) to assess the effects of vegetation abundance and quality on feeding-site selection in bison, and (2) to determine if coarse-scale foraging behavior differs among burn treatments in response to whether they were burned or not early in the growing season. We evaluated how forage quality and quantity influenced the foraging behavior of bison at three temporal scales: (a) feeding site selection patterns at the patch-level, the intermediate level between the feeding-station and landscape levels in the ecological hierarchy of foraging in large herbivores (fine scale; Senft et al. 1987), (b) the percentage of time spent feeding per week by bison groups relative to total activity budgets (intermediate scale), and (c) shifts in diet selection based on isotopic record of C3-C4 plant composition over a year (coarse scale).

At the fine, temporal scale to assess the effect of vegetation abundance and forage quality on patterns of feeding site selection, we assessed selection among three vegetation groups (i.e. graminoids, forbs, and litter). Crude protein content of forage at feeding sites was used to index plant quality. Observations were made during summer and fall to assess seasonal variability in forage biomass and quality as they affect fine-scale, short-term foraging decisions. In a previous study, we showed that bison intake of forage increased at a greater rate in the early growing season than during the transitional mid-summer season only in recently-burned, highly-nutritious and digestible grassland (Chapter 2; Raynor et al. 2015). We therefore hypothesized that low-to-intermediate forage abundance would be a main factor driving forage selection at the feeding site. Accordingly, we hypothesized that (a) patches with low-to-intermediate vegetation biomass
should be used in greater proportion than their relative availability within the study area,
especially when plants are capable of regrowth, and (b) active feeding sites should contain forage
with higher crude protein content than that measured in forage from nearby, randomly selected
sites that were not grazed during short-term, group foraging bouts. Moreover, (c) as overall plant
biomass increases but quality declines throughout summer and fall, patterns of feeding-site
selection should be mostly driven by forage quality early during the growing season, and then
shift toward increased standing stock of vegetation as summer and fall progress.

At the intermediate, temporal scale, we considered the effect of the time of the day in our
analysis of weekly time spent-feeding in the daytime, since foraging may also be dependent on
daily patterns of temperature or daily movements (Berger and Cunningham 1994). In mesic
grasslands, large herbivores shift coarse-scale resource selection patterns with increasing
ambient temperatures (Maichek et al. 2004, Allred et al. 2013). Here, we hypothesized that (a) in
the growing season when temperatures are warmer, bison may spend more time feeding during
the morning and late afternoon than during the middle of the day. In addition, (b) the proportion
of time spent feeding should be negatively related to forage quality, and bison foraging activity
should track seasonal shifts in plant quality and spend a smaller proportion of their daily activity
budget feeding early in the summer when plants are most nutritious compared with later in
growing season when forage is less nutritious; thus more time feeding is required to meet
metabolic demands.

METHODS

Study Area

We conducted this study in spring-summer 2012 (April to September) and summer-fall 2013
(May to December) in a 1,040 ha enclosure at Konza Prairie Biological Station (KPBS), near
Manhattan, KS (USA). KPBS is a mesic tallgrass prairie landscape that experiences a variable, continental climate with warm, wet springs, hot summers and dry, cold winters. Mean annual precipitation is 826 mm with ~75% falling during the April-September growing season, which is characterized by increasing biomass and fiber content in graminoids. Moreover, seasonal precipitation and landscape features also contribute to the mosaic of vegetation patches that vary in abundance and quality throughout the growing season. The bison area at KPBS is managed using spring controlled-burning with a fully-replicated watershed level experimental design, where watersheds are burned at varying frequencies (1, 2, 4 and 20 years). This variable fire frequency affects forage availability and quality, which in turn strongly influences bison resource-selection strategies and foraging behavior over time. The current bison herd was established in 1987, and is currently maintained at a stocking rate of ~260 adult individuals, with ~90 calves born in each spring. This stocking rate of ~14.5 g bison m$^{-2}$ (~0.3 animals ha$^{-1}$) results in a target density that removes ~25% of the standing vegetation biomass annually (Knapp et al. 1999).

**Fine Temporal-scale Foraging Behavior: Feeding-site Selection**

To evaluate feeding-site selection at the fine temporal scale, we measured vegetation attributes at active feeding sites that we compared with nearby, randomly located sites located within the same watershed at least 50 m away. A group feeding site was defined as an approximately circular area where >50% of the bison in a group were observed feeding together for a minimum of 30 min). Bison observations were taken throughout the entire daylight period. Bison were approached on foot and observed at distances between 100 and 500 m. On those rare occasions when bison were disturbed, observations were started after they resumed their foraging activities. Vegetation characteristics at feeding-sites were sampled using three 1 m$^2$ plots, placed randomly
within a 25 m$^2$ radius circle adjacent to the feeding-site location (Schaefer and Messier 1995). In every plot, the percentage of graminoids, forbs and litter was estimated visually for each vegetation group in 10% classes. We repeated the same sampling design at sites not grazed during feeding observations in a random direction from each feeding site at a distance of 50-75 m for comparison with feeding sites. To estimate plant biomass, we clipped individual plants 2 cm above the ground in each of the three plots next to each feeding site and in nearby, random locations. Plant samples were dried in the field in paper bags, and then oven-dried for 48 h at 60 °C and weighed using a 0.1 g precision scale. Because graminoids comprise 98% of the year-round diet of bison in tallgrass prairie (Coppedge et al. 1998), all graminoids, irrespective of photosynthetic pathway, were separated from clipped vegetation samples and then analyzed for nitrogen content. For each foraging observation sample and nearby, random location, two of the three clipped graminoid samples were randomly selected for nutrient analysis. Samples were dried, ground to a 1mm particle size in a ball mill, and analyzed by Dairyland Laboratories Inc. (Arcadia, WI) on a Foss model 5000 NIR instrument. Graminoid crude protein was determined using NIRS (Near Infrared Spectroscopy) analysis. Crude protein was estimated as “% N in plant tissue * 6.25” for 2-3 samples at each feeding site and the nearby, random location. Observations were delineated to three seasonal periods: growing (April 15-June 30), mid-to-late summer transition (July 1-October 14), and dormant (October 15 – December 31); periods of generally young, transitioning, and senesced plant tissue in order to understand shifts in foraging tactics as overall plant quality declined over the growing season. 

Intermediate Temporal scale Foraging Behavior: Scan Sampling
To monitor the proportion of time spent feeding by bison during daylight, we conducted repeated
scan sampling of bison groups of at least two individuals (Altmann 1974), performed every 15
min. Bison observations spanned the entire daylight period (0600–2000 h). Each observation
period lasted between 1 and 12 h. Bison activity was divided into four categories: (1) feeding, (2)
standing, (3) lying, and (4) walking. Scan observations yielded the proportion of time a group
spent feeding, which corresponds to the coarse temporal scale of foraging behavior. Records
without full information on group composition and when behavior of every individual’s behavior
could not be accounted for were not included in analysis. We followed 283 groups between 1
and 12 h, for a total of 577 h of observation throughout the study.

Data Analyses

Feeding-site selection
We compared feeding sites to paired random sites using conditional (i.e., case-controlled)
logistic regression, using the LOGISTIC procedure and the STRATA statement in SAS version
9.1 (SAS Institute Inc. 2003). Because we hypothesized that plant quality and composition could
both influence the selection of feeding sites, we considered the following covariates to explain
the use of feeding sites relative to random sites: (i) percentage of green foliage, (ii) grasses, (iii)
litter, and (iv) forbs. Because we had no a priori information on how these factors would
influence the selection of feeding sites, alternate candidate models were built to include the
following: a full model, a null model (without covariate), a model for every single covariate, and
a set of models comprising multiple combinations of two covariates. Models were ranked based
on Akaike’s information criterion corrected for small sample size (AICc; Burnham and Anderson
2002). For each candidate model $i$, we calculated the difference between the AICc of model $i$ and
the AICc of the best model (AICc), Akaike weight ($\omega_i$), and the evidence ratio, expressed as the
ratio between the $\omega_i$ of the best model and the $\omega_i$ of model $i$. This ratio indicates how the first
model (i.e., with the lowest AICc value) is likely to be the best model compared with model $i$.

For the best model, we calculated the McFadden’s adjusted $r^2$ (Compton et al. 2002):

McFadden’s adjusted $r^2 = 1 - \left( \frac{\text{LL covariate} - k}{\text{LL without covariate}} \right)$, where LL is the log-likelihood
and $k$ is the number of parameters. Models with $\Delta$AICc less than 2 were considered to have
substantial empirical support, $\Delta$AICc 4-7 considerably less, and $\Delta$AICc >10 essentially no
support (Burnham and Anderson 2002).

Intermediate Temporal-scale Foraging Behavior: Weekly Time Spent Feeding

The percentage of time that bison groups spent feeding was calculated as the proportion of scans
where more than 50% of the individuals were observed feeding relative to the total number of
scans completed on a specific group. To account for potential diurnal patterns in activity budgets,
we first divided our observations into three periods: 0600 to 1000 (morning), 1000 to 1500 (mid-
day), and 1500 to 2000 (evening). Since there was a difference in the time spent feeding between
morning and mid-day ($t_{1,134} = -2.34, P = 0.02, N = 266$) and mid-day and evening ($t_{1,157} = 7.44,
P<0.0001$), we performed our analyses using the three daily periods. To take into account the
potential influence of group size on foraging behavior, we analyzed the influence of group size
on time spent feeding using a GLM, which was not significant ($z_{1,264} = -1.59, P = 0.11, N = 266$).
Therefore, we did not include group size in subsequent analyses. We used logistic regression to
assess the influence of burn type, date (number of days after 1 May), and period of the day on the
proportion of scans where bison were feeding. We first tested the effect of year on time spent
foraging for summers 2012 and 2013. Because there was no difference between the two summer
seasons ($t_{1,186} = -0.68, P = 0.50, N = 187$), we pooled the data for these 2 years. Moreover,
because the dates of observations in fall did not overlap with the dates of observations during
summers 2012–2013, the date was used as a surrogate for season, and the factor year was removed from the analyses (St-Louis and Côté 2012). We assembled candidate models to include combinations of all covariates and interactions between covariates that were biologically relevant to our initial hypotheses. Means are presented ±SE. Significance level was set at 0.05 for all statistical analyses.

**Coarse Temporal-scale Foraging Behavior: Seasonal shifts in diet using δ¹³C stable isotopes**

During annual bison roundup activities in late October, a tail hair was collected from each of the same four matriarchal female bison that were fitted with GPS-collars throughout 2010-2013 (Chapter 4). In the laboratory, hair samples were wiped with acetone to remove dirt, grit, and oils. Hair samples were serially sampled, with 1 sample collected from each 5-mm interval for δ¹³C analysis (Cerling et al. 2009).

We measured the stable carbon isotope ratios in the Stable Isotope Mass Spectrometry Laboratory (SIMSL) at Kansas State University. Samples were combusted with a CE1110 elemental analyzer (Carlo Erba Instruments, Milan, Italy) and coupled to a Delta Plus mass spectrometer (Thermo Electron Corporation, Bremen, Germany) for isotope analysis using a ConFlo II Universal Interface (Thermo Electron Corporation, Bremen, Germany). The isotopic ratio of samples was calculated using delta notation as:

\[
\delta = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000
\]  

(Equation 1)

where \( R \) is the ratio of the heavy to light isotope for the sample and standard, respectively. The within-run variability estimated as the standard deviation of working standards was always 0.05%, and the between run variability, estimated as the difference between the measured value of a working standard and its calibrated value, was always 0.05%.
Strongly delineated isotopic signals occur in the $\delta^{13}C$ ratios of plants, reflecting use of plants with $C_3$ and $C_4$ photosynthetic pathways. Most $C_4$ plants have $\delta^{13}C$ values between -11 and -14‰, whereas most $C_3$ plants have $\delta^{13}C$ values between -25 and -29‰ (Cerling et al. 2009). Therefore, we classify primarily $C_4$ plant diets as those represented by hair follicle $\delta^{13}C$ values above -14‰ and a value below -14‰ representing a mixed $C_4$-$C_3$ plant diet unless -25‰ was reached. Regression (linear, polynomial) was performed to assess the $\delta^{13}C$ distribution across the tail hair length. Non-linear patterns in $\delta^{13}C$ signatures throughout a year indicate a diet shift of plants from one photosynthetic pathway towards another. Log-likelihood estimates were compared for the linear or polynomial distributions for each tail hair. The distribution with the lowest AICc value was retained for interpretation. Because our annual average tail hair length was 11.72 ± 0.16 cm and cattle hair growth rate is ~2 cm per month (Schwertl et al. 2003), we presume our data encapsulate isotopic history spanning from late winter through summer for all four years in each animal.

RESULTS

Fine temporal-scale Foraging Behavior: Feeding-site Selection

Feeding-site grass:forb ratio
Sites grazed by bison showed a higher grass:forb ratio (9.4:1) than ungrazed sites (6.1:1; $t_{1,238}=-2.3$, $P=0.02$), while grass:forb ratios at sites that were burned (7.4:1) and not-burned (8.3:1) were not significantly different ($t_{1,170}=0.55$, $P=0.59$; Fig.1).

Growing season feeding-site selection
The percentage of forb and grass cover were the main variables explaining the selection of feeding sites during the growing season since they were the only variables common to the
models with $\Delta_i<2$ (model-averaged estimate for forb and grass cover: $-26.15\pm6.19$ and $-8.09\pm2.26$; Table 1). These results suggest that bison generally avoid areas containing both high forb and grass cover. The top model (forbs+grass+litter) explained 41% (McFadden’s adjusted $r^2$) of the observations.

**Transition season feeding-site selection**

The percentage of forb and grass cover were the main variable explaining the selection of feeding sites during the transitional season since they were the only variables common to the models with $\Delta_i<2$ (model-averaged estimate for grass and cover: $-12.23\pm2.75$ and $-3.95\pm1.28$; Table 2). These results suggest bison are less likely to use areas containing high forb and grass cover during the transition season than during the early growing season. The best model (forbs+grass) explained 18% (McFadden’s adjusted $r^2$) of the observations.

**Dormant season feeding-site selection**

The top model explaining feeding site selection during the dormant season was the null model. However, the model-averaged estimates for the models with $\Delta_i<4$, which contain some empirical model support (Burnham and Anderson 2002), were $-1.76\pm2.86$ and $-0.08\pm1.98$ for forb and grass cover, respectively (Table 3). These results suggest that bison are less likely to avoid areas containing high forb and grass cover during the dormant season than was observed during the early growing or transitional seasons.

**Factors associated with forage quality and quantity**

Higher crude protein content was found in graminoids during the growing season than was observed for either the transition or dormant season ($F_{2,244}=39.0$, $P<0.0001$; Fig. 2). A significant interaction between season and burn status revealed that graminoid crude protein content was greater in burned watersheds compared to not-burned watersheds during the growing (27%
higher) and transition (14%) seasons, but not during the dormant season (8%; $F_{2,244}=5.01$, $P=0.007$). Across seasons, graminoid crude protein at sites selected for grazing was higher than protein content at sites not selected for grazing ($F_{1,132}=24.9$, $P<0.001$). Selected areas were 15, 11, and 23% higher in crude protein content than sites not selected for grazing during the growing, transition, and dormant season, respectively. Interactions between feeding-site selection and season ($F_{2,132}=1.9$, $P=0.16$) or burn status ($F_{1,132}=0.10$, $P=0.76$) were not significant.

Overall, standing crop biomass was lower in the dormant season than the growing and transition seasons ($F_{2,254}=3.9$, $P=0.02$; Fig. 3). Standing crop biomass was also lower in burned watersheds than unburned watersheds ($F_{1,254}=8.6$, $P=0.003$). Across seasons, biomass at feeding sites was lower than that observed at nearby random locations ($F_{1,132}=11.0$, $P<0.0001$), probably reflecting effects of recent bison foraging.

**Intermediate temporal-scale Foraging Behavior**

**Time spent grazing**

The proportion of time spent feeding over the entire activity budget was explained primarily by whether the watershed used by grazers was burned or not ($\chi^2=6.6$, df=1, $P=0.01$, N=266), the period of the day ($\chi^2=15.0$, df=2, $P=0.0005$, N=266), and the date after 1 May ($\chi^2=36.3$, df=1, $P<0.0001$, N=266). This model had an Akaike weight of 0.74 and explained 23% of the variation in observations (McFadden’s adjusted $r^2$) (Table 4). The odds that bison were feeding in burned grassland were 2.5 times greater than the odds of bison feeding in unburned grasslands. The proportion of time spent feeding by bison was about 30% in early summer, increased to approximately 50% in late summer, and further increased to about 65% very late in the summer and during autumn (Fig. 4). Bison feeding during daytime and at the end of the afternoon were
about half the odds of feeding during morning (morning: 60 ± 1%; daytime: 28 ± 0.3%; late afternoon: 34 ± 0.4%).

Coarse Temporal-scale Foraging Behavior

Isotopic record of δ13C

The δ13C isotopic signature of tail hair indicated that the diet shifted from a strictly C₄ diet during the growing and transitional seasons to a mixed diet of C₃ and C₄ plants in the dormant season (Fig. 5). For three of four bison with tail hairs ranging from 6-14 cm in length the relationship between δ13C signature and hair follicle length was best fit by a second-order polynomial regression for 8 of the 12 tail hair samples. Bison #Y139 had tail hair lengths ranging from 14.5 to 21.5 cm during each collection time that were best fit by third-order polynomial regression in 2010 and 2012 and fourth-order polynomial regression in 2011 and 2013. Because cattle hair grows at a length of ~2.5 cm a month (Schwertl et al. 2003), we assumed hairs from bison #Y139 provide isotopic history spanning across an annual cycle or encapsulating two dormant seasons.

DISCUSSION

Integrating more than one temporal scale in ecological studies allows a better understanding of patterns, processes, and limiting factors determining resource use (Senft et al. 1987, Rettie and Messier 2000). To our knowledge, this is the first study to simultaneously evaluate feeding-site selection at the patch-scale and the activity budgets of bison at the landscape-scale across the growing season in the tallgrass prairie of North America. Previous studies documented that components of resource use in plains bison may be driven by both forage availability and quality (Vinton et al. 1993, Coppedge and Shaw 1998), but none considered a multi-scale approach. Our results support our hypothesis that resource use varies across seasons and temporal scales. At the
intermediate, weekly temporal scale, bison increased time spent feeding as plant quality declined with the approaching dormant season. At the fine, temporal scale, feeding-site selection in bison is dependent on plant regrowth during the growing season, then shifting towards areas of higher plant abundance as plant quality declines. At this fine scale, forage quality measured through crude protein content did not explain resource use in the dormant season, but its effect was higher throughout the growing season. We suggest that patterns of resource use by bison may reflect foraging tactics aimed at increasing nutrient intake while minimizing foraging effort in productive mesic grassland.

*Feeding-site Selection*

As seen in previous surveys of bison foraging at KPBS, bison grazed watersheds in a nonrandom fashion (Vinton et al. 1993). In the growing season, bison preferentially grazed recently burned watersheds, whereas their grazing was more evenly distributed among watersheds in the dormant season. Burning modifies the grazing habits of bison and other large herbivores (Allred et al. 2011a, Sensenig et al. 2010) by enhancing growth and accessibility to desired forage. Spring burning in tallgrass prairie increases productivity of dominant C_4 grasses, in part by eliminating detrital accumulation on plant growth (Knapp and Seastedt 1986), which likely aids grazers’ ability to find high quality food. In 1988, the year after bison were re-introduced to KPBS, feeding-site surveys of plant composition conducted in June revealed bison selected feeding sites with low forb cover (Vinton et al. 1993), a finding consistent with our result of selection for sites of lower forb cover than nearby available areas throughout the growing and transition season. Since their reintroduction to KPBS, significantly increased forb cover is found in the bison enclosure (Hartnett et al. 1996), yet our study demonstrates feeding-site selection is driven by
availability of low-to-intermediate cover of graminoids which suggests bison continue to avoid high-forb cover in their enclosure.

High densities of large herbivores can maintain patches of grassland in a state of low-to-intermediate forage quantity with increased production of young forage tissue (grazing lawns: McNaughton 1979). Thus avoidance of areas of high forage biomass can reflect feeding-site utilization and spatial distribution of grazers when forage regrowth is possible (Fryxell 1991, Wilmshurst et al. 1999b). In our study of a mesic grassland, bison grazed areas of lower biomass compared to sites available nearby. However, their avoidance of areas with high grass and forb cover seen early in the growing season diminished as the growing season progressed, eventually showing random selection during the dormant season. This suggests the availability of profitable areas of low-to-intermediate biomass decreased as plants senesced, which may explain the more random use of the landscape in the dormant season as observed by Vinton and others (1993).

Moreover, bison selected feeding sites based on forage quality (crude protein content) in all seasons in both burned and unburned watersheds at a fine spatial resolution (50 m scale). This suggests that they responded to local variations in forage quality within habitat types, potentially increasing their nutrient intake by selecting food patches with a high availability of protein (Spalinger and Hobbs 1992). At the landscape-scale, similar levels of forage protein content between burned and unburned watersheds during the dormant season may further explain a more random spatial distribution of grazing habits in colder months at KPBS (Chapters 2 and 4).

Intermediate, temporal-scale Foraging Behavior

Because post-fire regrowth in tallgrass prairie results in greater availability of high quality food patches, we hypothesized that bison would spend less time feeding early in summer after spring burns. In our study, bison spent a higher proportion of their time feeding in watersheds that
burned during the spring prior to the observation than in unburned watersheds, and the total time spent feeding throughout the growing season was at its minimum during the early spring. These results support our hypothesis that time spent foraging is inversely related to forage quality. Coppock and others (1983) conclude that increased graminoid production and higher live:dead tissue ratios resulting from spring burning are two important determinants of bison foraging habits. Preferential grazing of recently-burned watersheds on tallgrass prairie during the growing season likely reflects increased forage availability and accessibility. However, we posit that high quality forage content is a critical factor driving preferential grazing in burned grassland. Increased forage crude protein content and digestibility during the early growing season likely allow bison to maintain short-term nutrient intake while incurring reduced time spent feeding (Chapter 2; Raynor et al. 2015). High availability of highly digestible, protein-rich forage likely allows bison to allocate time to activities related to reproduction (e.g. milking calves and increased vigilance of lactating females). Therefore, our findings shed light on the underlying behavioral mechanisms responsible for large herbivore resource use that drives their attraction to recently-burned grasslands.

Our hypothesis that time spent feeding would be highest in the morning and late afternoon was partly supported. To reduce thermoregulatory stress from high ambient temperature and heat production from rumination (Galbraith et al. 1998), bison reduce overall daily activity (Belovsky and Slade 1986) and decrease daily foraging and intake (McHugh 1958). Bison are known to seek woody cover at extreme temperatures (>35°C; Allred et al. 2013) and increase foraging activity as daytime temperatures decrease (Collins and Smith 1989, Rutley and Hudson 2001). Thus, we expected bison to begin feeding in the late afternoon. Because bison increase nocturnal foraging in periods of increased ambient temperature (Hudson and Frank...
we presume that increased nocturnal feeding occurred during our study as ambient temperature was well above the study area’s mean (KNZ LTER). Several nocturnal surveys indicated bison were feeding at night although our restricted ability to observe foraging activity and small sample size limited our ability to draw inferences. Future studies of direct effects of ambient temperature on large herbivore behavior and physiological adaptations and responses are warranted as temperatures increase globally (Maichek et al. 2004, Allred et al. 2013).

Seasonal fluctuations in diets of large herbivores can arise from variation in temporal and spatial resource quality and abundance (Stearns 1992). At KPBS, the most infrequently burned watersheds support a high proportion of cool-season C\textsubscript{3} grasses (Gibson and Hulbert 1987, Vinton et al. 1993). During the dormant season, observational studies and distribution of GPS-collared bison show bison prefer watersheds that are not burned in the spring (Vinton et al. 1993, Chapter 4, this thesis). Our limited stable isotope record of δ\textsuperscript{13}C using tail hairs of GPS-collared matriarchal female bison indicates their attraction to not-burned watersheds in the dormant season is driven by the availability of cool-season C\textsubscript{3} grasses. Moreover, watersheds not-burned the previous spring contain high vegetation structure during the colder months (Chapter 2; Raynor et al. 2015) that may reduce the foraging efficiency of bison that occurs in highly accessible and nutrient-rich patches in the growing season. Cool-season C\textsubscript{3} graminoids tend to occur in unburned tallgrass prairie with high vegetation structure (Coppedge and Shaw 1998, Stueter and Hidinger 1999, Rosas et al. 2005), which likely decreases the accessibility of these forage resources and reduces foraging efficiency. During this period, we surmise that bison were compensating for low protein availability in forage by consuming higher amounts of low-quality
forage although this strategy may reduce short-term nutrient intake as observed in other studies (Laca et al. 1994, Laca et al. 2001).

**Implications**

Plant phenology and environmental conditions strongly influence physiological balance and the foraging behavior of herbivores living in seasonal environments (Moen et al. 2006, Shrader et al. 2006). The observation that bison closely adjust their foraging behavior to the seasonal patterns of plant phenology and select patches with respect to foliar-N concentrations suggests that plant quality is an important driver of their foraging ecology. Unlike tropical systems, where plant regrowth after grazing occurs almost year round (Fryxell 1991), availability of high quality forage is seasonal in temperate grasslands. At KPBS, bison selected feeding sites of low vegetation stature during the early growing season when regrowth was possible and then shifted to high vegetation stature patches in the dormant season where more effort is likely expended to reach nutrient requirements. Thus, large herbivores in seasonal environments select food resources on the basis of both forage quantity and quality using different tactics to increase nutrient intake at several temporal scales as predicted by the forage maturation hypothesis (Fryxell 1991). In particular, bison experience a shifting mosaic of habitat quality within and among seasons and years, and can track such variability in resource availability at multiple spatiotemporal scales.

**LITERATURE CITED**


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1991 microbiology of the rumen. Journal of the South African Veterinary Medical Association
1995 49:413-4200.
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Table 3-1. Candidate models and parameter estimates for feeding-site selection of bison at Konza Prairie, Manhattan, Kansas in spring 2012-2013, where selection for feeding sites were compared with random sites located in a random direction 50 m away.

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<thead>
<tr>
<th>Model</th>
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<th>Grass</th>
<th>Litter</th>
<th>Green</th>
<th>df</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>ω_i</th>
<th>Evidence Ratio</th>
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Table 3-2. Candidate models and parameter estimates for feeding-site selection of bison at Konza Prairie, Manhattan, Kansas in summer 2012-2013, where selection for feeding sites were compared with random sites located in a random direction 50 m away.

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<th>ΔAICc</th>
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Table 3-3. Candidate models and parameter estimates for feeding-site selection of bison at Konza Prairie, Manhattan, Kansas in fall 2012-2013, where selection for feeding sites were compared with random sites located in a random direction 50 m away.

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<th>Litter</th>
<th>Green</th>
<th>df</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>( \omega_i )</th>
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<td>6.65</td>
</tr>
<tr>
<td>I + Grass + Green + Litter</td>
<td>0.56</td>
<td>-1.77</td>
<td>-0.47</td>
<td>-1.00</td>
<td></td>
<td>3</td>
<td>81.00</td>
<td>4.07</td>
<td>0.04</td>
<td>7.65</td>
</tr>
<tr>
<td>I + Grass + Green + Litter</td>
<td>-0.18</td>
<td>0.17</td>
<td>0.65</td>
<td></td>
<td>-0.74</td>
<td>3</td>
<td>81.20</td>
<td>4.29</td>
<td>0.03</td>
<td>8.54</td>
</tr>
<tr>
<td>I + Forb + Grass + Litter</td>
<td>2.07</td>
<td>-3.52</td>
<td>-2.28</td>
<td>-3.60</td>
<td></td>
<td>4</td>
<td>82.00</td>
<td>5.10</td>
<td>0.02</td>
<td>12.81</td>
</tr>
<tr>
<td>I + Forb + Litter + Green</td>
<td>0.35</td>
<td>-2.79</td>
<td></td>
<td>-2.14</td>
<td></td>
<td>4</td>
<td>82.30</td>
<td>5.34</td>
<td>0.02</td>
<td>14.44</td>
</tr>
<tr>
<td>I + Forb + Grass + Green</td>
<td>0.90</td>
<td>-3.52</td>
<td>-1.00</td>
<td></td>
<td></td>
<td>4</td>
<td>82.70</td>
<td>5.76</td>
<td>0.02</td>
<td>17.81</td>
</tr>
<tr>
<td>I + Grass + Litter + Green</td>
<td>0.35</td>
<td>-0.51</td>
<td>-2.22</td>
<td></td>
<td></td>
<td>4</td>
<td>83.00</td>
<td>6.06</td>
<td>0.01</td>
<td>20.70</td>
</tr>
<tr>
<td>I + Forb + Grass + Litter + Green</td>
<td>2.77</td>
<td>-6.08</td>
<td>-3.27</td>
<td>-4.15</td>
<td></td>
<td>5</td>
<td>83.50</td>
<td>6.52</td>
<td>0.01</td>
<td>26.05</td>
</tr>
</tbody>
</table>
Table 3-4. Models explaining the proportion of time spent feeding by bison groups during scans at Konza Prairie, Manhattan, Kansas (2012–2013, N = 282). The models are ranked according to their AICc values.

<table>
<thead>
<tr>
<th>Model</th>
<th>df</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>ωi</th>
<th>Evidence ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>I + Burn + Period + Date</td>
<td>5</td>
<td>267.7</td>
<td>0</td>
<td>0.741</td>
<td>1.00</td>
</tr>
<tr>
<td>I + Burn + Period + Period*Burn + Date</td>
<td>7</td>
<td>270.4</td>
<td>2.68</td>
<td>0.194</td>
<td>3.82</td>
</tr>
<tr>
<td>I + Period + Date</td>
<td>4</td>
<td>272.6</td>
<td>4.87</td>
<td>0.065</td>
<td>11.42</td>
</tr>
<tr>
<td>I + Burn + Date</td>
<td>3</td>
<td>292.4</td>
<td>24.65</td>
<td>0</td>
<td>225257.62</td>
</tr>
<tr>
<td>I + Date</td>
<td>2</td>
<td>300.4</td>
<td>32.65</td>
<td>0</td>
<td>12298649.28</td>
</tr>
<tr>
<td>I + Period</td>
<td>3</td>
<td>314.7</td>
<td>46.95</td>
<td>0</td>
<td>15669782293.28</td>
</tr>
<tr>
<td>I + Burn + Period</td>
<td>4</td>
<td>316.6</td>
<td>48.91</td>
<td>0</td>
<td>41751449241.00</td>
</tr>
<tr>
<td>I + Burn + Period + Period*Burn</td>
<td>6</td>
<td>318.9</td>
<td>51.16</td>
<td>0</td>
<td>128603517418.86</td>
</tr>
<tr>
<td>I (null)</td>
<td>1</td>
<td>336.8</td>
<td>69.09</td>
<td>0</td>
<td>1006243011958810.00</td>
</tr>
<tr>
<td>I + Burn</td>
<td>2</td>
<td>338.3</td>
<td>70.61</td>
<td>0</td>
<td>2151625504512620.00</td>
</tr>
</tbody>
</table>

I: intercept; burn types: burned that year, not-burned that year; period of the day: morning, daytime, evening; date: number of days since 1 May.
Figure 3-1. Mean grass:forb ratio (±SE) at feeding sites and nearby, available sites located 50 m away in watersheds that burned that year and watersheds that did not burn that year from 2012-2013 at Konza Prairie Biological Station, Manhattan, Kansas.
Figure 3-2. Mean graminoid crude protein content (±SE) at feeding sites and nearby, available sites located 50 m away in watersheds that burned that year and watersheds that did not burn that year from 2012-2013 at Konza Prairie Biological Station, Manhattan, Kansas.
Figure 3-3. Mean standing crop biomass (±SE) at feeding sites and nearby, available sites located 50 m away in watersheds that burned that year and watersheds that did not burn that year from 2012-2013 at Konza Prairie Biological Station, Manhattan, Kansas.
Figure 3-4. Mean percentage of time spent feeding (±SE) per week by bison in relation to date from 2012-2013 (pooled) at Konza Prairie Biological Station, Manhattan, Kansas.
Figure 3-5. δ13C ‰ of composite hair profile in relation to hair follicle length (cm) averaged over 2010-2013 for four matriarchal female bison fitted with GPS-collars. Beginning of hair follicle is when hair was plucked from bison tail during management activities in late October of each year. Dashed line indicates separation of mostly C₄ plant diet and mixed C₃-C₄ diet.
Chapter 4 - Extending the transient maxima hypothesis to grazing: bison preferentially select infrequently burned watersheds in fire-managed mesic grassland

ABSTRACT

Consideration of fire-grazer interactions is critical for understanding grassland structure and function globally. In turn, grassland structure and function determines ungulate distributions and forage selection. We compared the preferential use of watersheds by bison in a tallgrass prairie landscape managed with different burn frequency treatments to understand the contribution of recent fire and burn history. Based on the Transient Maxima Hypothesis, one expects an increase in plant productivity and forage quality with increased time since the last burn. Accordingly, one expects bison to preferentially select infrequently burned watersheds in the year of burn over watersheds that were frequently burned or watersheds that were not burned that year. Using GPS collars, individual bison were tracked among experimental watersheds managed with four burn treatments (1-, 2-, 4-, and 20-year burn intervals), over a 7-year period at Konza Prairie Biological Station, Manhattan, KS (USA). Bison preferred recently burned watersheds during the growing season and unburned watersheds during winter periods. In accordance with predictions of the transient maxima hypothesis, the strength of selection by bison in the year a watershed burned increased as the time since a watershed last burned increased. Space use had a positive relationship with the availability of recently burned watersheds that had not burned in four years, where the strength of attraction attenuated with time and disappeared by the end of the growing season. Moreover, the availability of watersheds that did not burn the previous spring was the strongest predictor of space use during the non-growing, dormant season. Our study applies resource utilization function methodology to a large herbivore population in
response to the availability of grassland burned at varying frequencies, and our results provide new quantitative insights into the spatial ecology of the consumer processes behind the fire-grazer interaction in a mesic grassland ecosystem.

Keywords: GIS, GPS collars, resource ecology, transient maxima hypothesis, resource utilization functions (RUF), ungulate space use, utilization distributions (UD)

INTRODUCTION

Understanding the grazer-plant interaction as affected by fire in a tallgrass prairie ecosystem is central for understanding mesic, grassland ecosystems. Along with climate, fire and especially the fire-grazer interaction are key drivers of grassland ecosystem function and structure (Archibald et al. 2005, Anderson et al. 2007, Fuhlendorf et al. 2009, Allred et al. 2011a, Allred et al. 2014). Effects of the fire-grazer interaction include altered vegetation quality and primary productivity (Bond and Keeley 2005, Anderson et al. 2007), increased plant, arthropod, and vertebrate species richness (Collins et al. 1998, Joern 2005, Fuhlendorf et al. 2012), and increased woody encroachment in response to long burn intervals where grasslands could become increasingly woody and ultimately no longer grasslands in its absence (Ratajczak et al. 2014). In this context, it is important to understand how fire affects landscape-level distributions of ruminant grazers, in time and space, in their quest to track and use food resources of the highest available quality (Archibald and Bond 2004, Archibald et al. 2005, Anderson et al. 2007, Prins and van Langevelde 2008). This becomes a bigger challenge for ungulates foraging in heterogeneous landscapes as food often can be of substandard quality and the best quality food is distributed spatially in a patchy configuration that varies over time as a shifting mosaic (Augustine and McNaughton 1998, Augustine and Frank 2001, Augustine and Derner 2014). In turn, the spatial and temporal heterogeneity of forage quality dictates the spatial distribution and movement kinetics of large herbivores at the landscape level, although predation risk or physical
features of the environment can also affect habitat use (Fryxell 1991, Fryxell et al. 2005, Anderson et al. 2010). Moreover, large herbivores can themselves alter the spatial heterogeneity of forage resources through their significant levels of forage consumption and effects on subsequent fuel loads, because of their relative large individual and population sizes. Accurate spatial memory allows large ungulates to anticipate the heterogeneous distribution of food resources that coupled with their high mobility increases the likelihood they will select sites with high forage quality (Prins and van Langevelde 2008, Augustine and Derner 2014, Merkle et al. 2014). Although the study of foraging and distribution of grazers in time and space requires an understanding of herbivore-plant interactions at multiple scales (Senft et al. 1987), other aspects of the landscape may also contribute to ungulate distributions, including topography, availability of soil mineral nutrients (Tracy and McNaughton 1995), distance to water, risk of predation, and physical factors (e.g., temperature, soil water) (Anderson et al. 2010, Allred et al. 2013).

As critical ecological drivers, fire and grazing influence habitat heterogeneity and vegetation community composition, productivity, and physical structure especially in mesic grassland ecosystems. Consumer diversity and abundance also respond accordingly (Hobbs 1996, Adler et al. 2001, Fuhlendorf and Engle 2004, Derner et al. 2009). As is seen for grazing systems elsewhere, plains bison (Bison bison) in North American grasslands both respond to and contribute to the creation of spatial heterogeneity in forage quality and standing crop (Fuhlendorf and Engle 2001). Vegetation regrowth after fire is very nutritious and highly sought by large grazers (Archibald and Bond 2004, Archibald et al. 2005, Murphy and Bowman 2007, Allred et al. 2011a,b, Eby et al. 2014). In turn, recent grazing decreases the likelihood that a patch will burn again for a period of time, leading to relatively decreased forage quality during the inter-burn intervals, increased low-quality biomass, and reduced foraging activity until there is enough
regrowth to carry the next fire (Archibald et al. 2005, Fuhlendorf and Engle 2001, Raynor et al. 2015). Ultimately, this fire-grazing interaction leads to the establishment of spatially heterogeneous patches of forage quality that exhibit shifting-mosaic dynamics over time, where patches representing different times since the last burn co-mingle in space.

Like ungulate grazers worldwide, bison preferentially select recently burned over unburned habitats during the growing season (Coppock and Detling 1986, Shaw and Carter 1990, Nellis and Briggs 1997, Coppedge and Shaw 1998, Biondini et al. 1999, Wallace and Crosthwaite 2005, Schuler et al. 2006, Allred et al. 2011a). Fire significantly alters nutrient concentrations in post-fire regrowth, resulting in increased concentrations of leaf nutrients (Blair 1997, van de Vijver et al. 1999, Oliveras et al. 2012) and removal of older, non-palatable tissues (Knapp 1985, Pfeiffer and Hartnett 1995). Unanswered at this time is whether variable time since the last burn differentially alters resource quality, and if so, what is the significance to an ungulate consumer? The non-equilibrial “transient maxima hypothesis” (TMH) (Seasteadt and Knapp 1993) posits that vegetation responses (e.g. ANPP and foliar quality) in tallgrass prairie are co-limited by multiple factors (light, energy and soil nutrients) that vary with time since the last fire. After periods without fire and the accumulation of litter, vegetation becomes light-limited and soil nutrients accumulate to relatively high levels (Blair 1997). With frequent fire, soil nutrients become limiting to plant growth, even while sufficient light exists to promote growth. Enhanced ANPP is seen immediately following infrequent fires (e.g. 4 years) that lasts over a relatively short non-equilibria transition stage (e.g., one growing season) in response to the relatively high availability of both light and soil nutrients in areas burned at intermediate frequencies compared with sites burned annually or left unburned for long periods. Here, the ecosystem switches from primary light limitation to one of soil-nutrient limitation. High levels of ANPP of high nutritional
quality result only during this transient period when neither light or soil nutrients are limiting
(Blair 1997, Chapter 2; in bison unit).

Most available studies of the responses to fire by ungulate grazers are usually represented in a simple binary fashion – i.e., burned vs. not-burned sites. However, the time since the last burn potentially can increase the expected strength of ungulate responses to vegetation in accordance with TMH (Seastedt and Knapp 1993, Blair 1997). With time, soil-N availability following fire will decline to intermediate levels with plant growth, and continue to decline with successive annual burns (Blair 1997), leading to lower quality forage overall for grazers in annually burned vs. infrequently burned sites in the year of the burn. Moreover, net N-mineralization rates and plant-tissue-N content both decline with successive annual burning, which ultimately reduces foliar nutritional quality available to grazers. Unburned sites provide less palatable forage as well (Vinton et al. 1993, Pfeiffer and Hartnett 1995, Knapp et al. 1999).

Our overarching goal in this paper is to understand changes in bison distribution and movement patterns with respect to effects of fire-frequency in the context of the transient maxima hypothesis. We examine the relative distribution and movement of bison in a continental tallgrass prairie in response to controlled spring fires at different burn frequencies. Our study takes advantage of the experimental design at Konza Prairie Biological Station (hereafter, KPBS) (Kansas, USA) that allows us to track bison preferences among watersheds with different burn-interval treatments as they change from year to year. At KPBS, bison can move freely among watersheds that are burned at 1-, 2-, 4-, and 20-year intervals, a process that sets up fire-grazing interactions that underlie the development of highly variable grassland structure and resource distribution. From 2007-2013, we tracked the movements of selected female bison fitted with GPS collars to determine how bison used the habitat in response to
spring prescribed burning treatments. The TMH predicts spatially-explicit differences in resource quality in response to fire that should influence the distribution of grazers if plant quality is a key factor underlying space use by bison. Key questions and predictions include: (1) Bison will prefer recently burned watersheds to unburned watersheds during the growing season, where the spatial pattern shifts in space following different sequences of controlled burning at the watershed level. (2) Because of seasonal drops in foliage quality, bison preferences for recently burned watersheds will decay as the season progresses, and no difference in use is expected between burned and unburned watersheds during the non-growing season. And, (3) the TMH predicts that bison will prefer recently burned watersheds with longer burn intervals compared to recently burned watersheds with short burn intervals (e.g., annual burns) during the growing season in years that watersheds are burned.

METHODS

Study system
Our study was conducted at Konza Prairie Biological Station (KPBS) (Knapp et al. 1998), a 3,487-ha native tallgrass prairie preserve located in the Flint Hills grassland near Manhattan, Kansas (39°05'N, 96°35'W; Fig. 1). Vegetation is mostly tallgrass prairie dominated by C₄ grasses (Andropogon gerardii, Schizachyrium scoparium, Sorghastrum nutans, and Panicum virgatum) along with a diverse mixture of warm- and cool-season graminoids. Forbs constitute ~75% of species richness (575 species) and vegetation biomass is >75% from grasses (Towne 2002, Collins and Calabrese 2012). Average monthly temperatures range from -2.7° C (January) to 26.6° C (July). Average annual precipitation is ~835 mm, with 75% falling during the growing season. A drought occurred from mid-summer of 2011 to the beginning of the growing season in
2013, and ANPP in an ungrazed watershed, 1D, was 19% lower than the long-term average at KPBS (Chapter 2, Fig 2).

KPBS is divided into replicated, watershed-level experimental treatments that cross bison grazing with fire frequency; ungrazed sites are not considered further. Bison at KPBS have free access to 10 experimental watersheds over approximately 1040 ha (Fig.1) subjected to 1-, 2-, 4-, and 20-year burn-interval treatments. All prescribed management burns in the bison-grazed watersheds are conducted in the spring (mid-March to end of April in the year of burning). Watersheds are labeled according to fire frequency (1, 2, 4, 20 years between burns); all watersheds included here are part of the bison unit (labeled as N, native grazer). A watershed label indicates replicate number (A–D). For example, N04D is replicate-D of a bison grazed watershed (N) burned every 4 years. Individual replicate watersheds with the same fire frequency are burned in different years (additional information regarding watershed treatments found at kpbs.konza.ksu.edu). Watersheds in the bison unit studied here were burned in the spring according to the schedule shown in Knapp et al. (1998, pp.9-11). We refer to watersheds that were burned in the spring in the year in question as “recently burned”.

The current bison herd was established in 1987, and is currently maintained at a stocking rate of ~260 adult individuals, with ~100 calves born in each spring. This stocking rate of ~14.5 g bison/m² (~ 0.3 animals ha⁻¹) results in a target density that removes ~25 of the standing vegetation biomass annually (Knapp et al. 1999); the actual %-loss rate depends on precipitation and forage quality. Individuals are weighed and general health assessed at an annual round-up of all animals in late October/early November; some individuals are culled at this time to maintain prescribed stocking densities. Young animals (>1 y of age), old animals, and excess males are removed from the herd to maintain the stocking rate stated above, resulting in a sex ratio of
mature females to mature males of approximately 4:1. All males are removed from the herd at age 8, while females may remain until the age of 15 or older (Ungerer et al. 2013). Natural mineral soil licks and artificial mineral supplements are available in the enclosure and the corral, respectively, throughout the year (Tracy and McNaughton 1995).

Data collection

Individual bison were tracked using Telonics TGW-3700 GPS collars during 2007-2013. Four individuals were tracked in 2007, 7 in 2008-2009, 11 in 2010, 13 in 2011, 12 in 2012, and 11 in 2013. All individuals fitted with collars were older, matriarchal females; no males were collared. Collars were fitted or replaced annually at the bison roundup, using the same individuals in consecutive years when possible. Collars in the early part of the study (2007-2009, 5 individuals in 2010) collected location data at intervals of two hours, while later collars (6 individuals in 2010, all individuals in 2011-2013) collected data at one-hour intervals during the dormant season and at thirty-minute intervals during the growing season. Only 3D fixes with a DOP of less than 3.5 were used for the analyses; ~98% of fixes met these criteria. Two-hour collar fixes were used for all individuals in analyses described here. Data from twice-yearly periods during which bison movement was restricted for herd management activities (October-November) and other scientific work taking place on the site (March) were excluded from analyses to avoid distortion of behavioral analyses. Estimates indicate that collared animals are often accompanied by about 30-40 individuals (Raynor, personal observations).

Landscape attributes for use in the analysis were generated using ArcMap v10.1 with shape files that included polygons of each watershed-type. A 30 x 30 m grid was overlain over the bison enclosure to investigate how space use by bison changed with landscape characteristics.
We obtained topographic information (elevation and slope) from a digital elevation model ($2\text{m}^2$ resolution) for each grid cell.

Utilization distributions (UD) and resource utilization functions (RUF)

Separate utilization distributions (UD) were calculated for monthly distributions of each individual bison using the biased-random bridge (BRB) method (Benhamou and Cornélis 2010; Behamou 2011). All individuals for each month met the minimum number of 200 locations recommended for UD analysis (Millspaugh et al. 2006; Benhamou and Cornélis 2010). The diffusion coefficient was calculated using the function BRB.D (Benhamou 2011) in the package ‘adehabitatHR’ for Program R (Calenge 2006). The shapefile containing the UD for each individual was loaded into ArcMap together with landscape attributes for the enclosure. Any points with a UD>99 were excluded so that only grid squares with a 99% probability of use are analyzed. Landscape attributes for each 30 x 30 m grid cell was extracted using the Spatial Analyst Extraction tool for ArcGIS v10.1 to create spatially explicit data files for the package ‘ruf’ for Program R (Kertson and Marzluff 2010). The package ruf, version 1.5.2 (Handcock 2012), was used to analyze the UD. Resource utilization functions (RUF) were calculated for each female bison to investigate the relationship between space use and landscape attributes on a cell-by-cell basis (Marzluff et al. 2004). RUFs use a multiple regression approach to relate multiple landscape variables of watershed-type, elevation, and slope, to a continuous measure of the UD height. The resulting RUF coefficients indicate the contribution of each landscape variable to the variation in the UD. To account for the spatial autocorrelation generated by natural environmental autocorrelation (Schiegg 2003), the RUF uses a maximum likelihood procedure with a Matern correlation function (Marzluff et al. 2004). Because we were interested in how space use may change from month-to-month between burn periods, our analyses are
based on each individual’s monthly UD$s for each burn period from April (post-burn) to February (pre-burn). Indicator categories were created for the three watershed-types that burned that spring. For each year, watersheds that did not burn that spring were combined into one class (not-burned) and were used as a reference category against which two annually burned, one biannually burned, and one watershed burned every four years were compared. Because a twenty-year watershed was burned in 2012, the additional indicator variable “20y burned watershed” was incorporated into analyses for April 2012 to February 2013 only. The continuous landscape characteristics, elevation and slope, were not transformed. Log (100-UD) was used as the response variable to give a normal distribution (Kertson and Marzluff 2010; Papworth et al. 2012). We estimated RUFs with standardized and unstandardized β coefficients to investigate the influence of landscape attributes on bison space use within the enclosed experimental landscape at KPBS and the potential for interactions with prescribed fire management activities (Marzluff et al. 2004; Kertson et al. 2011).

To develop population level inferences, we calculated mean standardized β coefficients (\(\bar{\beta}\)) and variance for each landscape attribute by monthly period (Marzluff et al. 2004). Standardized β coefficients were used to compare the relative importance of landscape factors on the concentration of use by each bison:

\[
\bar{\beta}_j = \hat{\beta}_j^* \frac{S_{ij}}{S_{RUF}},
\]

(Equation 1)

where \(\hat{\beta}_j^*\) is the maximum likelihood estimate of the partial regression coefficient from the multiple regression estimate (unstandardized β), and \(S_{ij}\) is the standard deviation of the UD values (Marzluff et al. 2004). Standardized β coefficients allow comparisons between the relative
importances of landscape characteristics despite differences in quantifying scales. For both individual and population level inferences, standardized coefficients with 95% confidence intervals that did not overlap zero were significant predictors of space use (Marzluff et al. 2004). If a resource coefficient was significantly different from zero, we inferred that resource use was greater than (+) or less than (-) that expected based on the availability of the resource within the enclosure (Marzluff et al. 2004). We ranked the relative importance of significant landscape attributes using the absolute value of their mean standardized β coefficients. To assess heterogeneity among individuals, we used individual standardized β coefficients and associated 95% confidence intervals to quantify the number of female bison with significant positive or negative relationships with each of the landscape attributes. Relative use of watersheds (sum UD values within the watershed divided by the area (m²) of that watershed) was tested for significance using an analysis of variance (ANOVA), with post hoc Tukey’s HSD tests when appropriate (Marzluff et al. 2004). All means are given ±SE. Significance level was set at 0.05 for all statistical analyses. SAS version 9.2 (SAS Institute Inc. 2011) was used for the ANOVA.

RESULTS

Landscape-scale resource use
In the growing season, bison used recently-burned watersheds more frequently than watersheds not-burned that year (ANOVA of sum UD by watershed type area; F₃,1586=177.3, P<0.0001; Fig. 3a). Watersheds that burned during spring and that had not burned for two or four years previously experienced higher relative use by bison than annually-burned watersheds (Tukey mean difference=0.01, P<0.0001). The relative use of biannually-burned watersheds in the year of a spring burn did not differ from use of watersheds burned after four years of not-burning (Tukey mean difference=-0.005, P=0.18). We had one opportunity to examine responses to
burning after 20 years of not burning in N20A, which burned in 2012. In 2012, bison used recently-burned watersheds more frequently than watersheds not-burned the previous spring \((F_{4,355}=125.9, \ P<0.0001)\). The four-year watershed burned in spring 2012 had higher use than all other watersheds burned that spring (Tukey mean difference=0.035, \(P<0.0001\)). In 2012, the sum UD \(\text{m}^2\) averaged across the early growing season was 0.045, 0.045, 0.081, and 0.046 for annual, biannual, four, and twenty-year watersheds burned that spring, respectively.

During the transitional mid-summer season when plant growth slows and begins to senesce, all burn-type comparisons met our predictions that bison used recently-burned watersheds more frequently higher use than watersheds not burned in the current year, and use of recently-burned watersheds use was highest in watersheds with the longest elapsed time (4 y) since they were last burned \((F_{3,1526}=384.8, \ P<0.0001; \text{Fig.3b})\). In 2012, use of all recently-burned watersheds was greater than watersheds not-burned the previous spring. However, unlike responses seen in other years, use of biannually-burned (sum UD \(\text{m}^2 = 0.055\)) and four-year (0.055) watersheds did not differ from bison use of annually-burned (0.047) watersheds in 2012. Post-hoc comparisons showed that bison use of N20A (0.06), the watershed that burned after twenty years of no burning, was greater than that observed in the annually-burned watersheds (Tukey mean difference=0.01, \(P=0.012\)). Bison use of N20A did not differ from biannually-burned and four-year watersheds \((P=0.91)\), nor did the biannually-burned and four-year watersheds differ in relative use during the transitional season of 2012 \((P=0.99)\).

In the dormant season, overall differences in relative use among burn-types were significant \((F_{3,1476}=25.5, \ P<0.0001; \text{Fig.3c})\), and differed from those seen during the growing season. Watersheds not burned the previous spring had higher use by bison in the dormant season than did annually-burned and biannually-burned watersheds that were burned the pervious spring.
(Tukey mean difference=0.01, P<0.0001). The use of watersheds that burned after four years of no burning did not differ from use of not-burned watersheds in the dormant season (Tukey mean difference=0.002, P=0.49), although bison used four-year watersheds more often in the dormant season than their use of recently burned annually- and biannually-burned watersheds (Tukey mean difference=0.006, P<0.01). Use of recently-burned biannually- and annually-burned watersheds was not different (P=0.99). In 2012, overall differences in relative use among burn-types were significant in the dormant season ($F_{4,345}=14.8$, $P<0.0001$). Use of watersheds not-burned the previous spring was higher than all recently-burned watersheds (Tukey mean difference=-0.01, $P<0.001$), except the biannually-burned watershed (Tukey mean difference=0.001, $P=0.99$). The biannually-burned watershed that burned the previous spring had higher use than all recently burned watersheds during the dormant season (Tukey mean difference=-0.01, $P≤0.049$).

**Drivers of space use**

Areas highly utilized by bison were associated with a greater availability of grassland burned in the spring after two and four years without burning as compared to habitat not burned throughout the growing season, while areas highly utilized in the dormant season were associated with greater availability of unburned grassland as compared to all watershed types burned the previous spring (Table 1). Throughout the dormant season, frequently-burned (annual and biannual burns) watersheds were avoided to greater extent than watersheds that burned after four years without burning, whereas the watershed that burned in 2012 after twenty years of no burning had the highest level of avoidance as compared to unburned watersheds.

We used standardized $\beta$ coefficients to compare the relative importance of landscape factors on the concentration of use by individual bison in each month of the study. Areas that were
highly used by collared bison were associated with a greater proportion of recently-burned grassland compared to not-burned grassland from May to September. During the dormant season, bison preferentially used watersheds that did not burn the previous spring. Relative use of recently-burned watersheds that burned at varying frequencies decayed as time since burn increased (Fig 4). Bison showed higher use of burned watersheds than of watersheds not-burned the previous spring in the growing and transitional seasons, but not during the dormant season.

The most frequent, significant predictor of space use during the early growing season by bison was the proportional availability of watersheds burned after 4 years without burning compared to not burned watersheds ($\bar{\beta} = 0.27$; ranging from -0.22 to 0.71; Fig. 5, Table 2). Space use was significantly positively related to watersheds burned after four years compared to all not-burned watersheds in 77% (149 of 195) of individuals in all growing season months (Table 2). During the mid-summer transitional period, the most frequent significant predictor of space use by female bison was the availability of watersheds burned after 4 years without burning compared to all not-burned watersheds ($\bar{\beta} = 0.29$; ranging from 0.07 to 0.53). Space use was significantly positively related to watersheds burned after four years compared to all not-burned watersheds in 91% (172 of 189) of individuals in all transitional season months. In contrast, the most frequent significant predictor of space use during the dormant season was the proportional availability of watersheds not-burned the previous spring compared to annually-burned watersheds ($\bar{\beta}$ ranging from -0.31 to 0.08). Space use was significantly negatively related to watersheds burned annually compared to all not-burned watersheds in 69% (125 of 181) of individuals in all dormant season months. Elevation was the strongest topographical predictor of space use during the transitional season months ($\bar{\beta} = 0.26$; ranging from -0.35 to 0.62), while elevation was less important as a predictor during the growing ($\bar{\beta} = 0.16$; ranging from -0.15 to
0.47) and dormant season months ($\bar{\beta} = 0.07$; ranging from -0.18 to 0.38; Table 2). Slope was most frequently a significant topographical predictor of space use during the dormant season months when behavioral avoidance was evident ($\bar{\beta} = -0.02$; ranging from -0.05 to 0.006; Table 2). Space use was significantly negatively related to slope in 16% (29 of 181) of individuals in all dormant season months, while a positive relationship between space use and slope for individual female bison occurred during the growing season (5%[9 of 195]) and transitional season months (1%[1 of 189]).

**DISCUSSION**

In this study, we focused primarily on how fire modulates the spatial and temporal dynamics of bison distribution in response to forage quality affected through soil-plant interactions. Bison at KPBS are not subject to predation, the physical features of the site have only a small impact on their distribution (this study, Vinton et al. 1993), and a range of fire frequencies are manipulated experimentally at the watershed level; therefore, this site provides a unique opportunity to tease apart their landscape-level distribution in response to fire-induced variation in forage quality and quantity.

To test our primary hypotheses, we quantified space use by bison in response to fire frequency using the probabilistic utilization distribution (UD) and its correlation with landscape characteristics (Resource Utilization Function, RUF; Marzluff et al. 2004). UDs quantify an animal’s relative use of space in terms of a probabilistic density function (Van Winkle 1975), removing pseudoreplication without presuming equal usage across the entire available habitat. This approach accommodates statistical issues that arise from the repeated collection of GPS collar relocation points from the same animal. UDs were used to quantify space use in relation to categorical and continuous resource variables using resource utilization functions. The
significance of regression coefficients was calculated for each animal and across individuals to test key individual-and population-level hypotheses.

Bison track recently burned watersheds, a response that has been observed repeatedly. During the growing season, bison preferentially use watersheds burned in the spring of that year over unburned ones, a finding consistent with other studies of bison habitat use in response to fire (Coppock and Detling 1986, Shaw and Carter 1990, Vinton et al. 1993, Nellis and Briggs 1997, Coppedge and Shaw 1998, Biondini et al. 1999, Wallace and Crosthwaite 2005, Schuler et al. 2006, Allred et al. 2011a). Different burn schedules at different sites lead to the same qualitative conclusions, indicating the generality of the pattern. For example, at the Tallgrass Prairie Preserve (TPP) in Oklahoma (Coppedge and Shaw 1998, Wallace and Crosthwaite 2005, Schuler et al. 2006, Allred et al. 2011a), bison preferentially selected burned patches distributed randomly on the landscape that differ in size and season burned (Allred et al. 2011a). While bison-grazed watersheds at KPBS are only burned in the spring at set burn frequency treatments, both schedules yielded similar outcomes. Our study builds on such fire-driven responses and assesses the effect of different fire frequencies at the watershed-level to bison responses. We link differential responses to prescribed burning at different frequencies to a possible ecosystem level mechanism – the transient maxima hypothesis and the creation of spatially-explicit, shifting mosaics of forage suitability.

Bison distribution and the Transient Maxima Hypothesis

Clear distinctions in bison habitat use were affected by watershed burn intervals. Among recently burned watersheds, bison preferentially used watersheds with higher burn intervals (2, 4 or 20 years) compared to annually burned watersheds; space use was graded among 1, 2 and 4-year intervals with the highest use observed for watersheds burned at 4 year intervals. At KPBS,
soil nitrogen is more limiting to vegetation growth in annually burned watersheds, while light limitation becomes more important in unburned watersheds with litter buildup (Blair 1997). Infrequently burned watersheds at KPBS typically show increased aboveground net primary productivity (ANPP) and foliar-N concentrations compared with annually burned watersheds in the growing season following a burn (Seastedt et al. 1991, Seastedt and Knapp 1993, Blair 1997, Raynor et al. 2015). This increase in ANPP for infrequently-burned watersheds during a burn year when light is no longer limiting is linked to the transient high availability of soil-N after several years without fire and the accumulation of litter (leading to light limitation) relative to annually burned watersheds (Blair 1997). Furthermore, because annually burned sites are more likely to be N-limited than are infrequently burned sites in the year of burn, foliar-N is higher in plants in the recently burned sites subjected to longer burn interval watersheds (Blair 1997). The high ANPP in recently burned plots with longer burn intervals combined with higher, foliar nitrogen content likely explains why bison select these watersheds (Coppock et al. 1983, Allred et al. 2011a).

Mechanisms underlying how non-equilibrial forage resources should direct grazer resource utilization largely reflect the importance of forage quality. The TMH was originally proposed as a soil-plant-light interaction, with an emphasis on explaining vegetation responses (Seastedt and Knapp 1993, Blair 1997). Increased ANPP and foliar-N was observed in the year of burn compared to unburned sites, with the magnitude of the response increasing with elapsed time since the watershed’s last burn (Blair 1997). Because bison and other ungulate grazers routinely respond positively to forage with higher protein content (Allred et al. 2011a,b), and actively select the highest quality patches (Archibald and Bond 2004, Ranglack and du Toit 2015, Raynor Chapter 4, this thesis) as long as sufficient vegetation standing stock exists, one
expects that the strength of behavioral selection for watersheds should track vegetation recently released from light- and soil-N limitation. Our results indicate this occurs during the growing season in the year of burn as bison preferentially select infrequently burned watersheds over frequently burned watersheds, and select burned watersheds over unburned ones. Moreover, the KPBS management plans for prescribed burning results in a shifting mosaic of recently burned watersheds among years, changing the spatial relationships of where the most profitable, nutrient-laden watersheds are each year. Bison reliably track the shifting mosaic of watershed forage quality as expected.

In all cases, effects of elevated forage quality on bison foraging as predicted by the transient maxima hypothesis last about one growing season for all burn histories. However, the effects of recent burning on elevated space use of watersheds reflected burn histories that extended into September in 4-y burned watersheds, but ended in August for those that were annually or biannually burned. We presume the 20-year watershed, N20A, that burned in spring 2012 was not the strongest predictor of space use during that growing season because almost half of this watershed was ungrazable due to woody vegetation cover (J. Briggs, personal communication). The effect of woody encroachment on ungulate space use remains mostly unexplored in mesic grasslands (but see Allred et al. 2013), which is cause for concern as this biome is facing a major risk of conversion to woodland (Ratajczak et al. 2014 and references therein). Moreover, campaigns in the Great Plains to limit woody encroachment using altered fire regimes and implementation of prescribed-burning programs (Twidwell et al. 2013), such efforts may benefit from our record of native grazer space use in mesic grassland managed with prescribed-burning under varying temporal frequencies.
Previous work elsewhere has shown that large grazer responses to burning can be short-lived (i.e. ~1 month; Augustine and Derner 2014). In this study, we found use of burned areas compared to not-burned areas lasted an entire growing season (May to September). We surmise that the plant productivity of this tallgrass prairie interacted with soil-N availability in recently-burned watersheds to maintain the availability of high quality forage well into mid-summer. In infrequently-burned watersheds, the availability of high quality forage has been shown to last through the transitional season (Raynor et al. 2015), thus we expected bison to respond to the resources throughout the summer. Furthermore, recent studies have demonstrated that grazers track the availability of high forage quality in efforts to ensure reproductive success (Bischof et al. 2012, Si et al. 2015).

**Seasonal space use in response to fire**

In recently unburned watersheds, bison exhibit a pattern of very low use (avoidance) during the growing season and relatively higher use during the dormant season. This pattern was evident in the 20-year burns during our study, with relatively high dormant season use in N20B in particular. Bison may be attracted to low burn frequency watersheds because these plots tend to have higher concentrations of cool season, C_{3} grasses, which have higher digestibility during the dormant season (Vinton et al. 1993, Steuter and Hidinger 1999, Post et al. 2001). Moreover, as the dominant C_{4} forage matures at KPBS, bison may shift foraging strategies to locate C_{3} grasses in unburned watersheds (Vinton et al. 1993, Raynor Chapter two).

In semi-arid rangeland, however, cattle actively select recently burned areas during the period of rapid vegetation growth, but to a lesser degree than that observed in highly, productive mesic grasslands such as KPBS; topography becomes important after greening periods end (Augustine and Derner 2014). Furthermore, Augustine and Derner (2014) also quantified the
amount of time cattle were grazing in burned areas, the only way a behavioral response to fire could be detected unlike other studies in mesic grasslands that did not account for foraging-specific resource selection (Allred et al. 2011a, Augustine and Derner 2014).

Differences in woody vegetation cover are possible explanations for the higher use of individual watersheds with similar burn histories, and ways of factoring these into analysis need to be developed further. In the growing season, cattle and bison seek thermal refugia in wooded areas as air temperature increases, which may be compounded by predicted warming in the Great Plains (Allred et al. 2013). Understanding how grazer space use differs in grasslands with varying woody vegetation cover is critical because their affinity for thermal refugia in periods of extreme air temperature may drive reductions in riparian vegetation productivity and increases of nonpoint source pollution (Belsky et al. 1999, Bailey 2005, Allred et al. 2013).

Our study only utilized adult female bison, but space use and movement patterns may vary by sex and developmental stage (Ruckstuhl and Neuhaus 2000). For example, work by Coppedge and Shaw (1998) show that bulls do not prefer spring burned areas during the growing season, but mixed-sex herds do. Thus, we posit that male bison groups may not need to track high quality forage because they are not nursing offspring. KPBS bulls are known to have lower quality diets than calves, cows, and juveniles (Post et al. 2001).

Management implications
Managing for habitat heterogeneity is a conservation strategy that can increase taxonomic diversity in grassland systems (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006, Engle et al. 2008). Managing grasslands by allowing large herbivores to choose among patches of varying burn frequency in the landscape, thus interactively influences vegetation heterogeneity through grazing of burned and unburned patches, is a means to sustain grassland heterogeneity, form, and...
function (Fuhlendorf et al. 2006, 2012). Many grassland bird populations are generally declining, and increasing habitat heterogeneity may be an especially important conservation practice for maintaining grassland bird populations (Fuhlendorf et al. 2006). For example, insectivorous Upland Sandpiper (Bartramia longicauda) select grazed watersheds at KPBS (Sandercock et al. 2015), which offer higher densities of grasshoppers than ungrazed watersheds (Joern 2004). Understanding how bison use habitats in response to fire frequency and distribution will be key for implementing management regimes that conserve grassland systems and lead to increased diversity. Although the generality of these results to other grasslands remains to be tested, we anticipate that this interaction between nonequilibrial forage resources and ungulate foraging behavior is a key driver for ungulate distributions in fire-prone systems generally. Because grazing can modulate plant species diversity while concomitantly enhancing invertebrate abundance and diversity when interacting with fire (Collins et al. 1998, Joern 2004; 2005, Collins and Calabrese 2012), our findings may improve land-use practices dedicated to maintaining landscape heterogeneity.

Conclusions
Our project is the first quantitative examination of the spatial ecology of native grazer herd in response to varying burn frequencies in tallgrass prairie, one that provides a direct link to the transient maxima hypothesis for consumers. We found that the mean space use of watersheds burned at different yearly intervals followed a graded pattern of low to high use across a spectrum of watersheds burned annually to every four years. Although use of a watershed that burned after twenty years of no burning was greater than annually-burned watersheds, its lack of grazable area due to woody encroachment likely kept it from being used more than a watershed burned after four years without burning. We observed that the strongest predictor of space use
throughout the growing season was the availability of grassland burned after four years of no
burning over unburned watersheds, whereas the availability of grassland not-burned the previous
spring over annually-burned was the best predictor during the dormant period. Moreover,
preference for four-year burns compared to not-burned watersheds lasted longer into the growing
period than frequently-burned watersheds; thus suggesting soil-N availability for grazing-
induced graminoid regrowth in infrequently-burned grassland may indirectly sustain grazer use
in the year that watershed-type burns at a higher level than frequently-burned grassland. Our new
understanding of bison space use could be used to inform management of grassland with intact
fire-grazer interactions. The resource utilization function approach was developed to allow
researchers to investigate why animals use resources and space disproportionately within their
available landscape (Marzluff et al. 2001). Our use of this approach provides insight into spatial
and temporal dynamics of bison behavioral ecology in relation to landscape characteristics and
management-induced variation in resource availability that can be targeted in management and
assessment of large herbivore land use dynamics (Boyce et al. 2002, Millspaugh et al. 2006).

LITERATURE CITED

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Raynor, E. J. Chapter 5, this thesis.


Si, Y., Q. Xin, W.F. deBoer, P. Gong, R.C. Ydenberg, and H.H.T. Prins. 2015. Do Arctic breeding geese track or overtake a green wave during spring migration? Scientific Reports 5: 8749; DOI:10.1038/srep08749.


Table 4-1. Mean unstandardized coefficients (\( \bar{\beta} \pm SE \)) for resource utilization functions (RUFs) calculated for female Plains Bison (\textit{Bison bison bison}) from 2007-2013 at Konza Prairie Biological Station. Burn-types (annual, biannual, four, twenty) modeled in response to not-burned grassland availability, showing how space use by bison differs between months in the study area. Positive coefficients indicate that use increases with increasing availability of the resource.

<table>
<thead>
<tr>
<th>Month</th>
<th>n</th>
<th>Intercept</th>
<th>Annual</th>
<th>Biannual</th>
<th>Four</th>
<th>Twenty*</th>
<th>Elevation</th>
<th>Slope</th>
</tr>
</thead>
<tbody>
<tr>
<td>April</td>
<td>65</td>
<td>0.675 (0.657)</td>
<td>0.02 (0.145)</td>
<td>-0.204 (0.237)</td>
<td>-0.122 (0.241)</td>
<td>0.058 (0.073)</td>
<td>0.006 (0.002)</td>
<td>0.003 (0.001)</td>
</tr>
<tr>
<td>May</td>
<td>59</td>
<td>0.366 (0.398)</td>
<td>1.029 (0.089)</td>
<td>1.32 (0.191)</td>
<td>1.306 (0.229)</td>
<td>1.206 (0.051)</td>
<td>0.005 (0.001)</td>
<td>0.002 (0.001)</td>
</tr>
<tr>
<td>June</td>
<td>62</td>
<td>-0.914 (1.145)</td>
<td>0.849 (0.14)</td>
<td>1.325 (0.255)</td>
<td>1.448 (0.217)</td>
<td>1.391 (0.017)</td>
<td>0.009 (0.003)</td>
<td>0.002 (0.001)</td>
</tr>
<tr>
<td>July</td>
<td>61</td>
<td>-1.886 (1.932)</td>
<td>0.677 (0.157)</td>
<td>1.125 (0.244)</td>
<td>1.245 (0.168)</td>
<td>0.959 (0.035)</td>
<td>0.012 (0.005)</td>
<td>0.001 (0.001)</td>
</tr>
<tr>
<td>August</td>
<td>65</td>
<td>-3.743 (1.532)</td>
<td>0.427 (0.196)</td>
<td>0.907 (0.255)</td>
<td>1.0 (0.161)</td>
<td>0.623 (0.047)</td>
<td>0.017 (0.004)</td>
<td>0.002 (0.001)</td>
</tr>
<tr>
<td>September</td>
<td>60</td>
<td>1.412 (1.061)</td>
<td>0.21 (0.131)</td>
<td>0.474 (0.233)</td>
<td>0.672 (0.143)</td>
<td>0.122 (0.096)</td>
<td>0.004 (0.003)</td>
<td>-0.001 (0.001)</td>
</tr>
<tr>
<td>December</td>
<td>65</td>
<td>2.436 (0.978)</td>
<td>-0.543 (0.066)</td>
<td>-0.503 (0.099)</td>
<td>-0.246 (0.162)</td>
<td>-0.449 (0.168)</td>
<td>0.001 (0.002)</td>
<td>-0.004 (0.001)</td>
</tr>
<tr>
<td>January</td>
<td>64</td>
<td>0.817 (1.013)</td>
<td>-0.252 (0.112)</td>
<td>-0.398 (0.143)</td>
<td>-0.26 (0.235)</td>
<td>-0.789 (0.183)</td>
<td>0.005 (0.003)</td>
<td>-0.003 (0.001)</td>
</tr>
<tr>
<td>February</td>
<td>64</td>
<td>1.708 (0.974)</td>
<td>-0.286 (0.091)</td>
<td>-0.499 (0.242)</td>
<td>-0.178 (0.177)</td>
<td>-1.425 (0.124)</td>
<td>0.003 (0.002)</td>
<td>-0.004 (0.001)</td>
</tr>
</tbody>
</table>

*N20a was burned only in 2012; number of collared bison per month: 12, 12, 12, 12, 12, 13, 10, and 11.
Table 4-2. Standardized $\beta$ RUF coefficients for female bison for each month. The table illustrates the standardized coefficient averaged across the study period and the number of significant coefficients (where the 5-95% confidence intervals did not include 0) for each RUF variable in each month. The highest standardized $\beta$ coefficient for each bison is the best predictor of space use. Boldface indicates variable with the greatest number of times individual bison had significant selection coefficients per month in that season.

<table>
<thead>
<tr>
<th>Month</th>
<th>Annual</th>
<th>+_</th>
<th>Best</th>
<th>Biannual</th>
<th>+_</th>
<th>Best</th>
<th>Four</th>
<th>+_</th>
<th>Best</th>
<th>Twenty</th>
<th>+_</th>
<th>Best</th>
<th>Elevation</th>
<th>+_</th>
<th>Best</th>
</tr>
</thead>
<tbody>
<tr>
<td>April</td>
<td>0.01</td>
<td>13</td>
<td>36</td>
<td>1</td>
<td>-0.06</td>
<td>21</td>
<td>27</td>
<td>1</td>
<td>-0.04</td>
<td>25</td>
<td>29</td>
<td>3</td>
<td>0.01</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>May</td>
<td>0.44</td>
<td>60</td>
<td>0</td>
<td>1</td>
<td>0.44</td>
<td>58</td>
<td>0</td>
<td>3</td>
<td>0.41</td>
<td>60</td>
<td>3</td>
<td>3</td>
<td>0.33</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>June</td>
<td>0.36</td>
<td>61</td>
<td>1</td>
<td>0</td>
<td>0.43</td>
<td>58</td>
<td>1</td>
<td>3</td>
<td>0.44</td>
<td>64</td>
<td>3</td>
<td>3</td>
<td>0.41</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>Growing</td>
<td>0.27</td>
<td>134</td>
<td>37</td>
<td>2</td>
<td>0.27</td>
<td>137</td>
<td>28</td>
<td>7</td>
<td>0.27</td>
<td>149</td>
<td>32</td>
<td>9</td>
<td>0.25</td>
<td>27</td>
<td>1</td>
</tr>
<tr>
<td>July</td>
<td>0.28</td>
<td>59</td>
<td>2</td>
<td>0</td>
<td>0.36</td>
<td>57</td>
<td>1</td>
<td>2</td>
<td>0.36</td>
<td>64</td>
<td>0</td>
<td>2</td>
<td>0.28</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>August</td>
<td>0.18</td>
<td>44</td>
<td>10</td>
<td>0</td>
<td>0.29</td>
<td>53</td>
<td>3</td>
<td>2</td>
<td>0.30</td>
<td>60</td>
<td>2</td>
<td>2</td>
<td>0.19</td>
<td>10</td>
<td>2</td>
</tr>
<tr>
<td>September</td>
<td>0.09</td>
<td>35</td>
<td>13</td>
<td>0</td>
<td>0.15</td>
<td>38</td>
<td>14</td>
<td>3</td>
<td>0.19</td>
<td>48</td>
<td>3</td>
<td>2</td>
<td>0.05</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Transition</td>
<td>0.18</td>
<td>138</td>
<td>25</td>
<td>0</td>
<td>0.27</td>
<td>148</td>
<td>18</td>
<td>7</td>
<td>0.29</td>
<td>172</td>
<td>5</td>
<td>6</td>
<td>0.17</td>
<td>29</td>
<td>4</td>
</tr>
<tr>
<td>December</td>
<td>-0.21</td>
<td>0</td>
<td>52</td>
<td>4</td>
<td>-0.14</td>
<td>9</td>
<td>38</td>
<td>1</td>
<td>-0.05</td>
<td>11</td>
<td>34</td>
<td>0</td>
<td>-0.13</td>
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<td>9</td>
</tr>
<tr>
<td>January</td>
<td>-0.10</td>
<td>10</td>
<td>39</td>
<td>1</td>
<td>-0.11</td>
<td>8</td>
<td>40</td>
<td>1</td>
<td>-0.05</td>
<td>11</td>
<td>35</td>
<td>2</td>
<td>-0.21</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>February</td>
<td>-0.11</td>
<td>6</td>
<td>34</td>
<td>0</td>
<td>-0.12</td>
<td>14</td>
<td>35</td>
<td>4</td>
<td>-0.04</td>
<td>20</td>
<td>23</td>
<td>0</td>
<td>-0.34</td>
<td>11</td>
<td>1</td>
</tr>
<tr>
<td>Dormant</td>
<td>-0.140</td>
<td>16</td>
<td>125</td>
<td>5</td>
<td>-0.120</td>
<td>31</td>
<td>113</td>
<td>6</td>
<td>-0.046</td>
<td>42</td>
<td>92</td>
<td>2</td>
<td>-0.226</td>
<td>3</td>
<td>29</td>
</tr>
<tr>
<td>Total</td>
<td>0.12</td>
<td>288</td>
<td>187</td>
<td>7</td>
<td>0.15</td>
<td>316</td>
<td>159</td>
<td>20</td>
<td>0.18</td>
<td>363</td>
<td>129</td>
<td>17</td>
<td>0.07</td>
<td>59</td>
<td>34</td>
</tr>
</tbody>
</table>

Slope was not the best predictor of bison space use throughout the study; the number of individual bison with significant positive slope coefficients were 7,1,1,0,1,0,0,0,0 and significant negative slope coefficients were 0,0,0,0,0,0,0,9,9 for April, May, June, July, August, September, December, January, and February, respectively.
Figure 4-1. Map of bison enclosure at Konza Prairie Biological Station, Manhattan, KS.
Figure 4-2. Cumulative growing season (Mar-Oct) precipitation (blue line) with 30-year mean of cumulative growing season precipitation (dashed blue line), annual net primary productivity (ANPP) averaged across ungrazed watersheds: 04B, 1D, 20B (green line) with 29-year mean (dashed green line; Konza-LTER dataset PAB01), and average growing season ambient temperature (°C; red line) with 32-year mean (dashed red line) during 2008-2013 at Konza Prairie Biological Station, Manhattan, Kansas, U.S.A.
Figure 4-3. Differences in levels of mean relative use of available burn-types from 2007-2013 at Konza Prairie Biological Station excluding 2012 when a twenty-year burn occurred. Relative use was calculated from the sum of UD values within habitat divided by area (m$^2$) of that habitat for each month within a season.
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Figure 4-5. Monthly population-level standardized β coefficients (95% CI) for female bison resource utilization functions by burn-type in response to not-burned watersheds from 2007-2013 at Konza Prairie Biological Station, near Manhattan, Kansas, U.S.A.
ABSTRACT
Maintaining the fire-grazer interaction in grasslands requires a mechanistic understanding of the effects of landscape heterogeneity on grazer movements and habitat selection. Using an analytic framework for simultaneously quantifying the effects of habitat preference and intrinsic movement on space use, we examined how native grazers assess the forage quantity-quality tradeoff at the landscape-scale. We evaluated the association of dynamic, biotic forage resources and static, abiotic landscape features with movement and habitat selection in an experimental landscape, where forage resources vary in response to prescribed burning, grazing by a native grader (*Bison bison bison*), and variable weather. Our overarching goal was to determine how biotic and abiotic factors govern habitat preference and movement of plains bison in nutritionally heterogeneous grassland with an intact fire-grazer interaction. We integrated spatially-explicit relocations of GPS-collared bison and vegetation surveys to link bison distribution in a landscape with an intact fire-grazer interaction. High-quality upland habitat constrained bison movement rates during the growing season, while selection for slope and aspect did not limit movement. Preference for habitat with high foliar crude content and low stature forage structure was consistent across years, although substantial variation in the magnitude of selection for high quality forage occurred among years. In years of below-average plant productivity, the strength of selection for high foliar crude protein content was greater than in years of normal to above average plant productivity. Avoidance of areas with high herbaceous biomass content was strongest during years of low plant production. The inverse relationship in selection between forage quality and quantity varied in magnitude across years. Climatic interactions in plant
quality and quantity seemingly shaped female bison distribution as they sought to maximize nutrient gains by selecting areas containing immature plants of high nutrient value. Our results provide experimental evidence for documenting a key behavioral mechanism that drives fine-scale movement of a large grazer in response to fire- and local-climate-induced changes in forage attributes. Combined, results elucidate a complex strategy that promotes nutrient acquisition and illustrates the utility of linking foraging theory with insights from consumer resource, movement, and fire ecology. Keywords: animal movement, habitat preference, forage quantity, local climate, protein content, step selection

INTRODUCTION

Many animals respond to environmental heterogeneity by fostering selectivity in their choice of habitats to best fulfill basic nutritional requirements. Habitat selection is the process whereby individuals preferentially use a nonrandom set of available habitats (Morris 2003) that result from habitat-specific variation in fitness and have important implications for population dynamics (Fretwell and Lucas 1970, Holt 1985, Pulliam 1988). Movement is a behavioral mechanism employed by animals to mediate trade-offs in life-history requirements arising from heterogeneous distribution of forage resources. Therefore, understanding how animal movement and habitat preference patterns respond to the interaction of biotic and abiotic processes as they influence forage attributes in heterogeneous environments is paramount to evaluating ecosystem structure and function. The interactions between various biotic and abiotic processes are complex and dynamic over time, and initial movement patterns may not reflect long-term responses and dynamics to biotic or abiotic drivers. Therefore, long-term data and experimental manipulations are needed to assess how multiple drivers interact to affect animal distribution and space use over the long term.
Animal distribution is considered to be fitness-based as all animal movements incur a cost to an individual in terms of energy/nutrient resources, time (opportunity cost), and exposure to risk (Ricketts 2001, Baker and Rao 2004, Fahrig 2007). For example, the cost of movement to an ungulate moving through a nutritionally heterogeneous grassland may be influenced by topographic variation (reducing movement rate and increasing the energy cost of movement) compared to moving in a habitat with less topographical relief, limited availability of high-quality forage (opportunity cost relative to occupying homogeneous, low quality habitat), and possibly an increased risk of predation arising from the increased likelihood of encountering predators when covering more geographic space (mortality risk). Reduced movement rates should result in areas where energetic costs are low, predation risk is minimal, and diet optimization is likely.

Because foraging goals (e.g. intake of protein and energy) dictate diet choices, an initial step to understand food-motivated animal distribution is to identify the objective that foragers pursue. For example, ruminants can maximize their instantaneous intake rate of digestible energy by consuming large plants that result in rapid satiation but reduced digestibility compared to feeding on small plants (Illius et al. 1999). Alternately, foragers can maximize their daily intake of digestible energy by foraging on small and/or immature plants, which demand longer cropping times and extended time to satiation, but ultimately provide more digestible energy due to their higher digestibility than large plants (Wilmshurst et al. 1999a, Bergman et al. 2001, Shipley 2007). Few studies have assessed the dynamic forage quantity-quality tradeoff experienced by ungulates to meet nutritional and energetic requirements. Plains bison (*B. bison bison*) in boreal forest and meadows dominated by C₃ vegetation make foraging decisions that maximize their instantaneous intake rate of digestible energy at the cost of reduced daily energy gains (Bergman
et al. 2001, Fortin et al. 2002, Babin et al. 2011); these studies did not examine responses to protein. Because nitrogen (protein) content in forage is often limiting to herbivores, diets deficient in protein can delay growth and loss of body condition (Van Soest 1994). Animals may adopt a foraging strategy that yields rapid nutrient assimilation and energy intake to meet daily nutrient requirements for basic metabolic function (Owen-Smith and Novellie 1982), especially where nutrients are limited, which can shape herbivore distribution across a landscape (McNaughton 1988). Yet, the impact of the forage quantity-quality tradeoff on large herbivore distribution in fire-dependent, C₄ forage-dominated landscapes remains to be examined.

Our general goal was to determine how biotic and abiotic factors govern habitat preference and movement of plains bison in nutritionally heterogeneous grassland dominated by warm season (C₄) graminoids subject to a variable continental climate. Our study area, Konza Prairie Biological Station (KPBS), is a tallgrass prairie research tract where experimental watersheds are managed with varying temporal frequencies of prescribed-fire. During the growing season, bison are attracted to recently-burned sites over those not burned during the spring burning period (Vinton et al. 1993, Chapter 4, this thesis), and the magnitude of this attraction to recently-burned grassland depends on the watershed’s burn history (Chapter 4; this thesis). Here, we assess biotic and abiotic environmental variables related directly (forage biomass and quality) or indirectly (landscape topography) to the use of a location by bison (Beyer et al. 2010). Specifically, we investigate the effect of topography along with forage quantity (herbaceous biomass) and quality (foliar protein) on bison habitat preference and movement patterns. Our primary objective was to assess habitat selection patterns at the landscape level along the forage quantity-quality resources gradient and in response to topographical characteristics that are dynamic or static in time, respectively (Beyer et al. 2014).
Protein was used to represent forage quality as this biomolecule is integral for maintenance of intrinsic biological processes in adults and nursing offspring (Van Soest 1994). Because the collared animals studied here were reproductive females, we predicted that grass protein content would be an important driver of habitat selection or habitat types would be strongly preferred if they offer optimum levels of forage and quantity.

Developing tools that help predict animal distributions in the face of environmental change is integral to understanding ecosystem function. Fundamental knowledge of resource use decisions should provide stronger quantitative grounds for projecting future ecological scenarios (Coreau et al. 2009). Our dynamic vegetation modelling approach incorporates vegetation responses to prescribed burning and precipitation in the growing season so that inferences made from movement modelling in this study reflect large herbivore responses to fire- and precipitation induced variation in forage quantity and quality, and thus describes the fire-grazer interaction, a critical ecological process within tallgrass prairies (Fuhlendorf and Engle 2001, Allred et al. 2011a). The need to predict future ecosystem states has been growing in recent years (Coreau et al. 2009), so insight gained from this long-term study can inform managers of fire-grazer systems about large grazer response to variation in local climate as well as fire-induced variation in forage resources.

METHODS

Study Area and Bison Population

Our study was conducted at Konza Prairie Biological Station (KPBS) (Knapp et al. 1998), a 3,487-ha native tallgrass prairie preserve located in the Flint Hills grassland near Manhattan, Kansas (39°05'N, 96°35'W). Because the Flint Hills are steep and rocky and largely unsuitable for row crop farming, the region is used primarily for cattle production (Launchbaugh and
Owensby 1978). Flint Hills bedrock is composed of alternating layers of shale and limestone, leading to topography with a "stair-step" appearance including steep slopes and shallow soils forming over limestone and shallow slopes with deep soils over shale (Schimel et al. 1991). The most elevated areas of the “stair-step” shaped topography are flat, bench-like areas with shallow soils, while the least elevated areas are riparian habitat with deeper soils. Topographic relief from lowland to upland is about 100 m. Vegetation is mostly tallgrass prairie dominated by C₄ grasses *(Andropogon gerardii, Schizachyrium scoparium, Sorghastrum nutans, and Panicum virgatum)* along with a diverse mixture of warm- and cool-season graminoids. Short-statured, stoloniferous and grazing-tolerant graminoids found in in flat, upland areas include *Bouteloua dactyloides* and *Bouteloua gracilis*, respectively. Forbs constitute ~75% of species richness (575 species) and vegetation biomass is >75% from grasses (Towne 2002, Collins and Calabrese 2012). Average monthly temperatures range from -2.7° C (January) to 26.6° C (July). Average annual precipitation is ~835 mm, with 75% falling during the growing season. A drought occurred from mid-summer of 2011 through the growing season in 2012 (Fig. 1).

KPBS is divided into replicated, watershed-level experimental treatments that cross bison grazing with fire frequency; ungrazed watersheds are not considered further here. Bison at KPBS have free access to 10 experimental watersheds over approximately 1040 ha (Fig. 2) subjected to 1-, 2-, 4-, and 20-year burn-interval treatments. All prescribed management burns in the bison-grazed watersheds are conducted in the spring (mid-March to early May in the year of burning). Watersheds are labeled according to fire frequency (1, 2, 4, 20 years between burns); all watersheds included here are part of the bison unit (labeled as N, native grazer). A watershed label indicates replicate number (A–D). For example, N04D is replicate-D of a bison grazed watershed (N) burned every 4 years. Individual replicate watersheds with the same fire frequency
are burned in different years (additional information regarding watershed treatments are found at kpbs.konza.ksu.edu). Watersheds in the bison unit studied here were burned in the spring according to the schedule shown in KPBS-LTER.

The KPBS bison herd was established in 1987, and is currently maintained at a stocking rate of ~260 adult individuals, with ~80 calves born in each spring. This stocking rate of ~14.5 bison/m^2 (~ 0.3 animals ha^{-1}) results in a target density that removes ~25% of the standing vegetation biomass annually (Knapp et al. 1999); the actual %-loss rate in a specific year depends on precipitation and forage quality. Individual bison are weighed and their general health assessed at an annual round-up of all animals in late October/early November; some individuals are culled at this time to maintain prescribed stocking densities. Young animals (>1y of age), old animals, and excess males are removed from the herd to maintain the stocking rate stated above, resulting in a sex ratio of mature females to mature males of approximately 4:1. All males are removed from the herd by age 8, while females may remain until the age of 15 or older (Ungerer et al. 2013). Natural mineral soil licks and artificial mineral supplements are available in the enclosure and the corral, respectively, throughout the year (Tracy and McNaughton 1995).

Individual bison were tracked using Telsonics TGW-3700 GPS collars during 2008-2013. Seven individuals were tracked in 2008-2009, 11 in 2010, 14 in 2011, 13 in 2012, and 11 in 2013. All individuals fitted with collars were older, matriarchal females; no males were collared. Collars were fitted or replaced annually at the bison roundup, using the same individuals in consecutive years when possible. Handling procedures were approved by KSU-IACUC and in accordance with the guidelines established by American Society of Mammologists. Only 3D fixes with a DOP of less than 3.5 were used for the analyses; ~98% of fixes met these criteria. Two-hour collar fixes collected during 1 April to 30 September were
used for all individuals in analyses described here. Estimates indicate that collared animals are often accompanied by roughly 30-40 individuals (Raynor, unpublished data), a value that fluctuates somewhat and depends on whether the herd has coalesced or fragmented at the time.

Forage quality
The quality of the forage was estimated from grass nitrogen measured at 1,039 locations that were opportunistically selected between the 2011-2013 growing seasons and distributed throughout the different watershed burn types at KPBS. The aboveground grass biomass was clipped in 25 × 25 cm plots at each of the 1,039 locations (pooling all graminoid species) and air dried, ground to a 1-mm particle size, and analyzed by Dairyland Laboratories (Arcadia, Wisconsin, USA) on a Foss model 5000 Near Infra-Red (NIR) spectrophotometer (Foss, Hillerød, Denmark). Crude protein (%) was estimated as %−N in plant tissue * 6.25.

Forage quantity
The quantity of forage was estimated at 16,792 locations that were opportunistically selected between the 2011-2013 growing seasons and distributed throughout different watershed burn types at KPBS. Total dry plant biomass \((B; \text{grams/m}^2)\) was estimated using a calibrated pasture disk meter that measured the height (cm) to which a plastic disk of constant weight could be supported as it settled on top of the canopy (Vartha and Matches 1977). Height was related to total plant biomass by regressing pasture meter readings on plots that were subsequently harvested to determine dry biomass, leading to the following regression models:

\[ y=3.778406x+6.175267, \quad R^2=0.63, \quad P<0.0001, \quad n=55 \text{ for 2012, a drought year and} \]

\[ y=2.398824x+3.697927, \quad R^2=0.85, \quad P<0.0001, \quad n=35 \text{ for 2013, a normal year for precipitation.} \]

The calibration for 2013 was used to estimate herbaceous biomass at sites from 2011 because 2011 ANPP was similar to 2013 ANPP.
Describing vegetation dynamics

We used Random Forest regression models to estimate grass nitrogen and herbaceous biomass in watersheds as a function of cumulative precipitation in that year, time since burn, and site topography. The Random Forests approach is a regression tree technique in which many regression trees are generated from random subsets of the available observations and predictor variables (Liaw and Weiner 2012, Bohrer et al. 2014). The response variable is then predicted from the combination of all regression trees. This approach performs well when modeling non-linear relationships between predictors and the response and accommodates complex interactions among predictors (Bohrer et al. 2014). These model properties are important for modeling forage quality and quantity relationships across space because nutritive and structural values of plants are spatially heterogeneous (e.g. along environmental gradients; Adler et al. 2001). As such, interactions between spatial (e.g. topography) and temporal (e.g. cumulative precipitation and time since burn) predictors can be effectively incorporated into the model (Prasad et al. 2006, Vincenzi et al. 2011). The topographical characteristics assigned to each site sampled during the growing seasons of 2011-2013 included: the sine and cosine of aspect (radians), slope (degree), and scaled elevation (m) extracted from a digital elevation model (DEM, with spatial resolution of 2 × 2 m; ~333-443 m a.b.s.l) (KPBS LTER). Cumulative daily precipitation (mm) collected from KPBS headquarters and the number of days since the sampling area burned (KPBS LTER) was assigned to each sampling event in the training set. Accounting for topographic variation and meteorological events are important parameters for determining aboveground herbaceous biomass at KPBS (Briggs and Knapp 1995). The number of times the watershed had burned since 1980 and type of burn schedule assigned to the watershed if it burned in a particular year (Frequent [1-2 year], Infrequent [4-20], or Not-burned that Year) were additional predictors incorporated into the Random Forest models for forage quality and quantity. We trained the
model on a randomly-selected set of data comprising 33% of the sites, “the out-of-the-bag” sample, and withheld the remaining 67% to test model performance. Performance was assessed using the root mean squared error of log-transformed response variable. This validation procedure was repeated 10 times and model performance was characterized using the average root mean squared error from the 10 random validation datasets. Random Forests models were fit using the randomForest library in the R statistical language (Liaw and Wiener 2015).

The grass nitrogen and herbaceous biomass models described above were used to project grass nitrogen and herbaceous biomass across a 10 m grid of points throughout the bison enclosure, excluding points known to occur within 5 m radius of known shrub cover identified from a 1 x 1 m resolution raster map from summer 2011 (Ling et al. 2014). For this extrapolation, the model was trained on the entire 2011-2013 dataset (as opposed to the 33% used for model validation described in the previous section). Year was not used as a predictive variable in the Random Forest model. Instead, cumulative precipitation since 1 March and time since burn variables substituted for the temporal aspect of the projection model. This allowed us to predict spatial and temporal coverage of forage quality and quantity across the entire bison enclosure at bi-weekly intervals from 15 April to 15 October in the 2008 to 2013 growing seasons. Bi-weekly raster projections of grass crude protein content and herbaceous biomass were generated across the entire enclosure using the raster package in Program R for use in bison movement modelling (Fig. 3).

**Modelling effects of environmental variables on movement**

Our starting point for understanding drivers underlying movement follows the framework of Rhodes et al. (2005) and Forester et al. (2009), which defines the probability that an animal
moves from location a to location b (a ‘step’) in a given time interval and conditional on habitat covariates, X, at location b to be:

\[
 f(b|a, X) = \frac{\phi(a, b, \Delta t; \theta) \omega(X_b; \beta)}{\int_{c \in D} \phi(a, c, \Delta t; \theta) \omega(X_c; \beta) dc},
\]

(Equation 1)

where \( \phi(a, b, \Delta t; \theta) \) is defined as a habitat-independent movement kernel (HIMK, sometimes referred to as the resource-independent movement kernel) describing how the animal would move over time interval \( \Delta t \) in the absence of habitat influences, and \( \omega(X) \) is the resource selection probability function and X is a matrix of habitat covariates (including a column of one’s representing the intercept term (Manly et al. 2002, Lele and Kiem 2006). ‘Use’ refers to habitat that has been encountered and selected, while ‘availability’ defines the habitat that could potentially be encountered by the animal (Lele et al. 2013). The shape of the HIMK is determined by parameter vector \( \theta \), while parameter vector \( \beta \) represents the habitat preferences.

The numerator is normalized by the denominator, integrated over all locations, c, with the spatial domain, D. Each observed step (segments of the landscape; N~1,000) was paired with 100 random steps, and landscape characteristics of observed and random steps were contrasted using conditional logistic regression. We simultaneously estimated the habitat-independent movement kernel and habitat preference by fitting \( f(b|a, X) \) (eqn 1) to the location data. The model was fit using the ‘optim’ function in R (R Development Core Team 2015). Confidence intervals for the parameter estimates were calculated from the Hessian matrix (±1.96 times the square roots of the diagonal elements of the covariance matrix (Beyer et al. 2014). Habitat covariates included elevation (m), slope (degrees), cosine of aspect (radians), grass crude protein content (% CP), and herbaceous biomass content, all of which were raster format data sets with a spatial resolution of 10 x 10 m. Parameters were back-transform after fitting. The habitat selection function was modelled as:
\( \omega(X_b; \beta) = \exp(\beta_1 ELEV + \beta_2 SLOPE + \beta_3 \text{Cos}(\text{ASPECT}) + \beta_4 \text{PROTEIN} + \beta_5 \text{BIOMASS} + \beta_6 \text{PROTEIN} \times \text{BIOMASS}). \)

We used a generalized linear mixed model to test differences between years among habitat selection and movement kernel coefficients generated from the mechanistic movement model. We included a random effect for individual bison in the model to account for the repeated sampling of some animals across years. We used the R-package \textit{lme4} to analyze these data (R Development Core Team 2015).

**RESULTS**

*Forage quality and quantity*

The out-of-bag estimates of the error rate were used to select the optimum Random Forest parameters (trees=1000, terminal node size=5). The root mean square error averaged across the 10 random validation datasets was 1.47 for herbaceous biomass (n=5541 samples) and 1.03 (n=343 samples). For the training dataset, the Random Forest model explained a large proportion of the variance of the grass protein content (pseudo \( R^2 = 0.72 \)) and herbaceous biomass (pseudo \( R^2 = 0.49 \)). Figure 2 shows the ranking of predictors by their importance. Only a few of the descriptors contributed substantially to the estimation of crude protein content, namely elevation, slope, and days since burn. In decreasing order of importance, the other predictors included in the RF model were: cosine of aspect, cosine of day, times watershed burned, sine of day, sine of aspect, cumulative precipitation (mm), and watershed burn type. For herbaceous biomass, descriptors that contributed substantially to its estimation included: cosine of day, day since burn, sine of day, and cumulative precipitation (mm). In decreasing order of importance the remaining predictors included: elevation, times watershed burned, watershed burn type, slope, sine of aspect, and cosine of aspect.
Bison habitat preference

Topography

Habitat preference for elevated habitat at KPBS was evident, where 61 of 63 bison favored higher elevation relative to available elevation although preference differed among years (F_{5,26}=35.01, P<0.0001; Fig. 4, Fig. 5a). In 2012, two individuals did not select higher elevation relative to availability and the overall preference for high elevation was the lowest in this year (Fig. 4, 5a). All bison avoided steeper slopes in all years, but the strength of avoidance differed subtly among years (range 0 to -0.05), F_{5,26}=3.92, P=0.009; Fig. 5b, 6b). Preference for a southerly aspect was evident in 37 of 63 individuals (58.9%; Fig. 4), while confidence intervals were wide and overlapped 0 for the other 26 individuals (Fig. 5c). Only three individuals showed any preference for non-southerly aspect although their selection coefficients overlapped 0 (Fig. 4, 5c). Variation in selection for southern aspect was evident across years (F_{5,26}=5.60, P=0.001) with selection for southerly aspect in 2011 being greater than 2012 (t_{26}=-2.22, P=0.035; Fig. 5c).

Forage resources

A significant interaction occurred between biomass and protein selection in 16 of 63 individuals (25.4%; Fig. 4). Significant interactions revealed that 11 individuals selected areas of high biomass and high protein, while 5 individuals selected areas of low biomass and low protein (Fig. 4). Overall, selection for herbaceous biomass was negatively correlated with selection for foliar crude protein content (linear regression, F_{1,61}=26.3, P<0.0001, adjusted R^2=0.29; Fig. 6d).

Graminoid crude protein content

During this study, all individuals favored habitat with high foliar protein content relative to available habitat (Fig. 4,5d). The strength of selection for areas of high foliar protein content varied among years (F_{5,26}= 28.36, P<0.0001; Fig. 6e). Selection for foliar protein was not
different between 2008 and 2009 ($t_{1,26}=-0.09$, $P=0.93$; Fig. 6e). In contrast, selection for high
foliar protein was greater in 2010 than 2009 ($t_{1,26}=7.55$, $P<0.00001$) and the strength of selection
dropped from 2010 to 2012 with years being significantly different from one another in a
descending manner ($P≤0.0001$), while selection was not different between 2012 and 2013 ($t_{1,26}=-0.81$, $P=0.42$; Fig. 6e).

**Herbaceous biomass**

During the study, 54 of 63 individuals (78.3%) favored areas of lower herbaceous biomass
during the growing season (Fig. 4, 5e). In 2013, eight individuals did not select areas of different
herbaceous biomass content relative to availability, whereas one individual showed high biomass
preference in 2008. The strength of avoidance for areas of high herbaceous biomass content
generally varied among years ($F_{5,26}=32.42$, $P<0.0001$; Fig. 6f). Preference for areas of low
herbaceous biomass content was highest in 2010 through 2012 ($P≤0.02$), while 2008 and 2009
marginally differed in selection for herbaceous biomass ($t_{1,26}=1.98$, $P=0.06$; Fig. 6f).

**Movement**

A normal distribution was used to describe the habitat-independent movement kernel (HIMK; for
movements at 4 hr intervals) for all 63 individuals (Fig. 4, 5f). In 2009, movement rates were
lower than the other years in this study ($F_{5,26}=11.3$, $P<0.0001$; Fig. 6g). The distribution of step
lengths (movement) moderately decreased as a function of preference for elevation (linear
regression, $F_{1,61}=11.55$, $P=0.001$, adjusted $R^2=0.15$; Fig. 6h) and weakly decreased as a function
of preference for herbaceous biomass ($F_{1,61}=2.45$, $P=0.12$, adjusted $R^2=0.02$). Distribution of step
lengths was not explained by slope ($P=0.70$) or aspect ($P=0.79$). In contrast, step length
distribution was positively related to strong selection for grass protein content ($F_{1,61}=5.57$,
$P=0.02$, adjusted $R^2=0.07$).
Our results demonstrate that resource-driven movement patterns of bison are shaped by the forage quantity-quality tradeoff and site topography. Combined, these comprise the grazer component of the so-called “shifting mosaic” of the fire-grazer interaction (Knapp et al. 1999).

Multiple biotic and abiotic attributes of landscape heterogeneity influenced the movements of bison, which were not static from year-to-year and likely related to local weather in addition to fire management on the landscape. Movement patterns reflected trade-offs between individual goals such as the need for accessible high quality forage, and fitness-based selection for topography with low potential for insect harassment (e.g., wind-prone southern facing areas) and less energy-demanding locomotion (e.g., steep slopes).

Landscape attributes influencing bison habitat selection at KPBS

Fire-induced changes in plant quality modulate bison forage behavior and space use at KPBS (Chapter 2 & 4, this thesis), yet identification of the dynamic forage and static topographical resources driving movement patterns remain unclear. Mechanistic movement modelling developed in this chapter identified multiple dynamic (biotic) and static (abiotic) features of the environment influencing movements of female bison at KPBS. First, the strength of selection for elevation was greatest in upland areas of high elevation relative to available elevations throughout the enclosure. Also, the strength of selection for elevation actually constrained movement by placing greater relative weight on the RSPF compared with the HIMK.

Furthermore, strength of selection for high elevation decreased with increasing growing season temperatures, suggesting that bison were seeking water or shade in response to increased temperatures (Allred et al. 2013 and references therein). However, bison attain substantial amounts of water from wallows and forage after recent precipitation at KPBS (Nippert et al.)
The presence of steep slopes decreased the probability of selection, and bison generally avoided habitat that did not face south. Both of these behavioral responses to static environmental features could be fitness-based. Locomotion on steep slopes increases energy expenditure as compared to level areas in mountain ungulates (Hudson and White 1985, Dailey and Hobbs 1989). Some slopes in the KPBS bison enclosure are fairly steep, with areas of exposed soil and rock and high woody cover that reduces the probability that fire would carry across them completely to affect quality (Collins and Calabrese 2012), thus possibly making them less desirable to bison as grazing sites as the energetic demands that it would take to utilize these areas may outweigh the benefits from the forage consumed. Moreover, selection for steep slopes was strongest in years of low forage availability, which suggests steep slopes may prove useful as a source for forage in periods of low food availability. Selection of non-southerly aspects was highest during the drought year (2012), which further corroborates the view that shifts of habitat preference in drought years maybe food driven; areas of non-southern aspect may provide more forage than the highly utilized areas facing south. We hypothesize that the propensity for parasitic insect avoidance is likely a result of overall preference for southerly aspect as prevailing southern winds may reduce avoidance behavior. Macroparasites can cause subclinical consequences to fitness that manifest when hosts experience additional energetic or nutritional demands associated with immunological responses, reduced food intake, or increased movement and avoidance behaviors (Lima and Dill 1990, Lochmiller and Deerenberg 2000, Gunn and Irvine 2003, Fitze et al. 2004). However, high temperatures during the growing season may also be driving bison to seek elevated areas for greater exposure to wind at KPBS.

Movement paths of bison were influenced by the spatial distribution and variation in forage quality and quantity. Habitat with graminoids of high crude protein content was the
strongest dynamic driver of forage resource selection across all summers. Crude protein content of graminoids is inversely related with time since fire in tallgrass prairie, while forage quantity is positively related (Allred et al. 2011a). At KPBS, resource utilization functions based on GPS collared-female bison confirmed the preference for infrequently-burned watersheds over frequently-burned and not-burned watersheds from May to August (Chapter 4, this thesis). When infrequently-burned tallgrass prairie is released from light-limitation through prescribed burning in the presence of increased soil nutrients (transient maxima hypothesis), prolonged high quality forage is the result (Blair 1997), and bison maintain the habitat in a state of low-to-intermediate quantity throughout the remainder of the growing season (Chapter 2). Throughout the growing season, fine-scale patch selection is driven by availability of low stature, easily accessible and high quality forage (Chapter 3, this thesis). Foraging in such habitats allows ruminants to maximize daily intake rate of digestible energy (Bergman et al 2001, Shipley 2007). Because forage maturation stages are distributed variably in space and time, our approach of modelling bi-weekly changes in forage quality and quantity captures spatio-temporal variation in forage maturation in response to prescribed burning and climate.

The strength of selection and relative avoidance of areas containing high grass crude protein content and herbaceous biomass, respectively, varied from year to year. During this study, weak avoidance for areas of high herbaceous biomass coincided with above-average annual net primary productivity (ANPP), whereas avoidance of areas of high herbaceous biomass was slightly stronger in years of average-to-below average ANPP. On the other hand, the strongest selection for foliar crude protein content occurred during the less productive years of this study. The inverse relationship between selection for foliar quality and quantity observed in this study occurred in both climatic extremes studied that led to above and below average
plant productivity at KPBS. Because foliar protein concentration in grasses often increases in years of reduced precipitation (plant stress hypothesis; Jones and Coleman 1991, Milchunas et al. 1995, Joern and Mole 2005), daily nutrient gains could be maximized by selecting areas containing small plants of high nutrient value as long as young forage tissue was available through regrowth. Bison remember pertinent information about location and quality of forage resources, and may use this information to selectively move to areas of higher profitability (Merkle et al. 2014). A possible reason for favoring the long-term intake strategy of using areas where satiation may take longer to achieve but more digestible nutrients may be attained is that our study occurred in a predator-free system. Without the risk of predation, more time could be spent foraging instead of performing antipredator behavior (Creel et al. 2014). Also, mature group members seem to dictate bison herd movements (McHugh 1958). Therefore, because our study animals are mature and highly fecund (~66% had offspring throughout the study), gaining the most digestible food in the least amount of time (i.e. maximizing short-term instantaneous intake) might not be favored by individuals that are likely group leaders. They may not be as prone to interruptions during foraging bouts in efforts to maintain group membership as observed in non-group leaders (Fortin and Fortin 2009, Babin et al. 2011). In a boreal forest-meadow matrix in Saskatchewan in the presence of wolves, bison are time-spent- grazing minimizers (Babin et al. 2011) and rely on group familiarity with the site coupled to their knowledge of local foraging options and recently sampled resource quality when deciding to follow or leave a group – this tactic leads to resource-rewarding movements (Merkle et al. 2015). In the predator-free southern Great Plains, however, bison space use may be dictated by fire-enhanced forage availability and concomitant graminoid regrowth following grazing by large herbivores although the fission-fusion dynamics in these grazer populations remain to be evaluated.
Extrinsic biases to bison movement were evaluated through a comparison between observed and random steps through the heterogeneous landscape. The statistical approach used here is based on conditional logistic regression analysis, and was inspired by resource selection studies based on a case-control design (e.g. Compton et al. 2002, Boyce et al. 2003). In contrast, our approach compares landscape segments instead of locations (Arthur et al. 1996, Boyce et al. 2003) or areas (Johnson et al. 2002). Consequentially, we explicitly considered landscape characteristics that animals would have been likely to encounter along their path (a step selection function design; Fortin et al. 2005). Our procedure is novel, however, because estimating the HIMK and habitat preference models simultaneously facilitates unbiased parameter estimation (Beyer et al. 2014), and we apply this framework to a system with an intact fire-grazer interaction. Thus we determined movement patterns in relation to forage resource variability driven by landscape-level disturbance processes arising from fire frequency and local weather.

Growing season movement rates (realized distribution of step lengths) were generally consistent across our female study animals with the exception of 2009, when movement rates were lower than that observed in other years of this study. We surmise that the combined ideal rangeland conditions of below average temperature and above average rainfall during the 2009 growing season may be responsible (Pyke et al. 2002). Instead of spending more time seeking shade or water (Allred et al. 2013), large herbivores can use this time to seek a more diverse diet (Bailey et al. 2015). Because of high selection for the upper bench habitat at KPBS, the distribution of step lengths (e.g., movements) was increasingly limited by this habitat preference (Beyer et al. 2014). The highly profitable, infrequently-burned uplands at KPBS (Schimel et al. 1991, Blair 1997) may have provided suitable forage (e.g. *Bouteloua spp.*) to the extent that leaving uplands was minimal during this season. Additionally, shallow, upland soils at KPBS
lead to stressed plants of lower biomass, which in turn results in high protein availability in forage (Schimel et al. 1991, Koricheva et al. 1998). This result of movements being constrained by elevated habitat selection aids us in meeting our prediction that movement would be guided by preference for areas of high protein availability, such as the upper bench habitat. However, as grass regrowth likely became limited in years of low ANPP, bison distribution seemingly shifted to alternate topography away from these upper bench habitats to attain resources.

*Synthesis*

This study provides the first empirical evidence for documenting the trade-off between resource selection and realized movement distribution of a large grazer in response to dynamic forage availability and static landscape characteristics in a landscape with an intact multi-frequency fire-grazer interaction. Our framework brings together recent advances in movement modeling including the development of mechanistic movement models (Rhodes et al. 2005, Moorcroft et al. 2006, Moorcroft and Burnett 2008) to quantify the effects of dynamic and static environmental variables on movement and habitat selection. Moreover, the availability of a long-term GPS dataset in this study allowed us to assess habitat selection in response to local climate-driven variation in critical forage resources.

Understanding how the forage quality-quantity tradeoff dictates large herbivore habitat use when resources are plentiful or scarce in the Great Plains is critical to sustainable rangeland management. Warming and drying are anticipated to reduce both plant production and nutritive content in the southern Great Plains (Briske et al. 2015). These climatic changes are likely to negatively affect rangeland economics by reducing stocking rates and total livestock production (Polley et al. 2013). Furthermore, warmer temperatures will likely improve winter survival and increase abundance of macroparasites that will further suppress livestock performance (Briske et
Moreover, the impact of fire on over-wintering macroparasite populations may further the complexity of understanding what is driving space use and movement in systems with intact fire-grazer interactions. Our results shed light on native grazer preference for both dynamic forage resources and static land characteristics in a period encapsulating relatively normal and reduced plant production. Although food quality is influential in resource selection and movement, understanding actual bison distribution and movement is multifactorial.

Our investigation of fine-scale movements of a native grazer in mesic grasslands when fire results in markedly different nutritional levels provides baseline information for forecasting animal movement in other fire-prone ecosystems that support ungulate populations. While grassland fires can have pronounced effects on landscape scale distributions of large herbivores (Sensenig et al. 2010, Allred et al. 2011a, b), the underlying dynamic forage resources responsible for these distributions have previously remained unexplored. Our data suggest that fire induced heterogeneity coupled with climatic responses in vegetation quality are an important landscape-scale process that helps promote nutrient attainment in large herbivores and illustrates the utility of linking optimal foraging theory with insights from resource, movement, and fire ecology.

**LITERATURE CITED**


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Table 5-1. Maximum likelihood parameter estimates (\(\bar{x}\pm95\%\) CI) among all animals and years with for movement, intercept, elevation, slope, cosine of aspect, grass crude protein content, and herbaceous biomass content from 2008-2013 at KPBS.
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Figure 5-1. Cumulative growing season (Mar-Oct) precipitation (blue line) with 30-year mean of cumulative growing season precipitation (dashed blue line), annual net primary productivity (ANPP) averaged across ungrazed watersheds: 04B, 1D, 20B (green line) with 29-year mean (dashed green line; Konza-LTER dataset PAB01), and average growing season ambient temperature (°C; red line) with 32-year mean (dashed red line) during 2008-2013 at Konza Prairie Biological Station, Manhattan, Kansas, U.S.A.
Figure 5-2. Variable importance plots for (a) grass nitrogen content and (b) herbaceous biomass content generated by the random forest algorithm included in the `randomForest` package for R software. The plot shows the variable importance measured as the increased mean square error (%IncMSE), which represents the deterioration of the predictive ability of the model when each predictor is replaced in turn by random noise. Higher %IncMSE indicates greater variable importance. Variables include cosine of day, days since last burn of watershed, sine of day, cumulative precipitation since March 1, elevation (m; scaled), number of times burned since 1980, burn type [frequent, infrequent, not-burned that year], slope (degrees), sine of aspect (radians), and cosine of aspect (radians).
Figure 5-3. Map showing the prediction of (a) grass crude protein content (10 m resolution) in the Konza Prairie Biological Station bison enclosure obtained by the application of the random Forest model for May 2012, (b) with movement path of bison #W674 for May 2012, (c) map showing the prediction of herbaceous vegetation content (10 m resolution), and (d) with movement path of bison #W674 for May 2012.
Figure 5-4. Maximum likelihood parameter estimates among all animals with mean (circle), 95% confidences (lines) and 0 (no selection) as the redline for (a) elevation, (b) slope, (c) cosine of aspect, (d) grass crude protein content, (e) herbaceous biomass content, (f) protein-biomass interaction, and (g) habitat-independent movement kernel parameter. Points that are green are positively associated with the variable, purple are negatively associated with the variable, and blue are not different from random.
Figure 5-5. Distributions of maximum likelihood parameter estimates among all animals with mean (solid gray), 95% confidences (dashed lines) and 0 (no selection) as the redline for (a) elevation, (b) slope, (c) cosine of aspect, (d) grass crude protein content, (e) herbaceous content, and (f) habitat-independent movement kernel parameter.
Figure 5-6. Boxplots of maximum likelihood parameter estimates of selection averaged among all animals each year for (a) elevation, (b) slope, (c) cosine of aspect, (e) grass crude protein content, (f) herbaceous biomass content, and (g) habitat independent movement kernel. (d) Linear relationship between selection for protein and biomass and (h) change in the habitat independent movement kernel (specifically, the standard deviation describing a normal distribution; y axis) as a function of strength of selection for elevation based on individual bison movement paths (points) of length ~1,000 steps. The habitat independent movement kernel (HIMK) is a normal distribution with standard deviation 1.0. As the strength of selection increases, movements become increasingly limited by the effect of habitat selection (Beyer et al. 2014).
Chapter 6 – Epilogue

This study offers insights on the foraging behavior, habitat selection, and landscape-level distribution of bison that can help answer the seemingly simple question raised in the dissertation prologue: how does foraging behavior and space use respond to varying grassland burn frequencies? Bison prefer recently-burned watersheds that are burned every four years. Here, forage items have greater protein content than watersheds burned more frequently. Selection of foraging areas is related to high foliar crude protein content and low vegetation structure at the patch spatial scales. This dissertation further outlines the importance of the degree of disturbance in terms of prescribed fire intervals on habitat selection and resource use by a large, ruminant ecological engineer.

Fine-scale foraging behavior

Active selection of forage at the fine scale as a function of nutritional quality is the most immediate response in the foraging hierarchy. In Chapter 2, I first investigated the plant-bison interaction by examining feeding station intake rates for the area in between steps in a foraging bout (Bailey et al. 1996). During short foraging bouts, bison increased their intake rate with increasing availability of grass biomass at a greater rate in the early growing season compared to the mid-summer transitional season in infrequently-burned watersheds, whereas the slope of intake rate was gradually increasing with grass biomass in watersheds that did not burn that previous spring or burned that previous spring and are annually or biannually burned. This early growing season behavior corresponds with a time-minimizing short-term feeding strategy (Bergman et al. 2001, Fortin et al. 2002). When forage is in a state of greatest nutritional value, foragers may intensely utilize this resource as a means to free time for non-foraging behavior activities (e.g. social activities or nursing young). However, as the growing season progressed
and bison remained in this habitat, a shift towards a long-term feeding strategy, where daily
nutrient gains may be maximized by feeding in nutrient-laden, low-stature vegetation, likely
occurred.

My primary field seasons in 2012 and 2013 included a drought and non-drought period,
respectively, when ANPP was well below-average and average for the KPBS LTER long-term
mean. The contrasting ANPP that resulted from these periods allowed me to assess potential
differences in late growing season foraging behavior at the feeding station-scale. When
precipitation is markedly reduced in a growing season, grass protein concentrations increase
(Milchunas et al. 1995, Joern and Mole 2005). To determine if feeding station foraging behavior
responds to this climate-driven variation in forage resource I compared bite mass and
instantaneous intake rate at the end of the two growing seasons as this is the period when
nutrient-levels would be most reduced prior to the dormant season. Both feeding measures were
greater in 2013 than 2012. This result suggests bison may have been compensating for lower
nutrient availability in forage by taking larger bites and ingesting more grass as the dormant
season approached (Chapter 2).

Animals often face temporal and spatial heterogeneity in the distribution of resources,
and the decision of where to forage can influence the spatial dynamics of consumer-resource
processes. Optimal diet theory reworked for grazing provides a useful theoretical framework to
understand how and why animals include prey items in their diet (MacArthur and Pianka 1966,
is temporally stable, forage attributes such as protein concentration may be consistently
responsible for feeding-site selection during that season. Despite the variation in forage quality
among watersheds burned at different frequencies, I found plant-form characteristics guiding
feeding-site selection to be generally static within seasons (Chapter 3). Bison grazed preferentially in areas of higher foliar protein content, higher grass: forb ratio, and lower herbaceous biomass content than observed in nearby, randomly-selected locations in the early growing and mid-summer transitional seasons. However, bison grazed selectively in areas of higher uniformity in vegetation structure between used and available locations during the dormant season in primarily unburned watersheds. This suggests that the availability of forage irrespective of quality, which was uniformly low in this period, was driving feeding-site selection during periods of plant dormancy. In contrast, when plant regrowth was possible, bison were likely re-using previously grazed sites that could still offer higher quality forage items than that available in randomly selected areas nearby. Furthermore, diurnal time spent feeding increased as the dormant season approached, which suggests that bison’s ability to locate high-quality forage decreases as high quality foraging items became scarcer. Moreover, the isotopic history of diet selection for collared female bison documents a shift from a pure warm-season grass diet to a mixed diet of warm- and cool-season plants in the dormant season. Study animals disproportionately used unburned habitat during this period, which bolsters an environmentally-induced shift in diet and foraging behavior in response to reduced availability of high-quality forage during periods of plant dormancy.

These findings are consistent with predictions for the forage maturation hypothesis, which posits that aggregations of large herbivores reflect optimal combinations of forage quality and quantity to maximize net intake rate (Fryxell 1991). In turn, collective consumption pressure at intermediate to high grazer densities may maintain vegetation in a state of low to intermediate forage quantity but high quality through regrowth of young forage tissue (McNaughton 1979, Fryxell 1991); i.e., seasonal maturation to high biomass is repressed by repeated foraging
pressure. McNaughton and Fryxell’s observations originated in stable, tropical environments but our findings extend the use of this hypothesis to temperate environments for predicting patch use and the spatial and temporal distributions of grazing herbivores when plant regrowth is possible during the growing season. Furthermore, these findings of fine-scale foraging behavior in plains bison show that the initial attraction to infrequently-burned watersheds burned that year in response to the pulse of high quality forage dictates growing season space use as long as regrowth is possible. This observation links two prominent ecological hypotheses, one developed in Africa (FMH; Fryxell 1991) and one developed and tested at KPBS (Seastedt and Knapp 1993, Blair 1997).

**Coarse-scale behavior**

Studies of large grazer responses to fire-induced variation in forage quality and quantity has primarily been conducted in reference to spatial extent of fire and binary applications of fire or the lack thereof—i.e., comparisons of reactions by herbivores to recently burned vs. not-burned sites (Archibald and Bond 2004, Allred et al. 2011). In this dissertation, I investigated large grazer response to shifting maxima in forage resources resulting from prescribed burning of watersheds at different frequencies, which provides insight into dynamic, temporally-based variation in ungulate response to fire. In Chapter 4, I investigated the likelihood of GPS-collared female bison occurring at any given location in their enclosure and linked the likelihood to watersheds burned at different frequencies. Then, I tested whether the likelihood of using different burn types was different from using unburned watersheds. Without the watershed-level experimental design in place in the KPBS bison enclosure, a long-term investigation of bison use of different burn frequencies of mesic grassland would not have been possible anywhere in the world. The finding that annually-burned watersheds are most strongly avoided compared to
unburned watersheds during the dormant season offers further evidence that this management
strategy in the Flint Hills of Kansas may not offer adequate forage cover for herbivore
consumers, especially in years of low ANPP. Furthermore, I demonstrated that infrequently-
burned watersheds were more extensively used by bison than not-burned or frequently-burned
watersheds throughout the growing season (May to September), which implies that infrequent-
burning of pasture may not only collectively offer suitable habitat for other wildlife species
(Fuhlendorf et al. 2009, McNew et al. 2015) but also for economically-important cattle (Limb et

Understanding how the biotic and abiotic environment affects the movement and
distribution of organisms is a central objective of resource and movement ecology. As discussed
in earlier chapters, digestive and time constraints faced by herbivores can limit rates of daily
these constraints on daily food intake, herbivores may select foraging areas in efforts to
maximize forage intake as seen in free-ranging domestic sheep (*Ovis aries*) or to simultaneously
feed and thwart predation as in roe deer (*Capreolus caprolus*) (Mysterud et al. 1999).

In Chapter 5, using a novel mechanistic movement model (Beyer et al. 2014), I
demonstrated that spatial and temporal variation in forage quality and quantity was a biotic
feature of the landscape that shaped the distribution of bison. In the predator-free system at
KPBS, it seems safe to assume that bison distribution is food-motivated. However, I also found
topography to be a driver of space use. Over several growing seasons, bison tended to prefer high
elevation, avoid steep slopes and areas that did not face south. These habitat preferences may be
fitness-based as locomotion on steep slopes is energy-demanding (Dailey and Hobbs 1989),
whereas wind-prone, elevated southern-facing areas offer relief from insect harassment and high
temperatures, which induce sub-clinical effects on fitness (Skarin et al. 2004, Witter et al. 2012). Moreover, the flat, upper bench habitat at KPBS offers high quality forage (Blair 1997) as well as relief from warm temperatures and insects that likely influences growing season space use in the Konza Prairie bison herd in addition to fire-induced variation in forage resources. These results suggest that management strategies should consider biotic and abiotic characteristics of the landscape in which preferred habitat features are found (Pearson et al. 1995).

**Ecological hierarchy of foraging**

Animals should select habitats that simultaneously satisfy several of their needs that may result in behavioral trade-offs, which may vary at different spatio-temporal scales (Johnson 1980, Allen and Starr 1982, Senft et al. 1987, Mysterud et al. 1999, Fortin et al. 2004, St-Louis and Cote 2012). Scale-dependence in trade-offs has been suggested by Senft et al. 1987 and Bailey et al. (1996), and observed in empirical studies such as these of Wallace et al. (1995), Schaefer and Messier (1995), and Fortin et al. (2003).

I found that bison distribution and resource use were influenced by both abiotic and biotic factors with variation of relative importance at different scales and time periods. Fire-induced enhancement of forage quality influenced feeding station- and landscape-level decisions. In response to this abiotic factor, bison increased feeding rates at a greater rate in the most nutritious grassland than grassland of lower nutritive value (Chapter 2). The feeding station is the finest resolution of the ecological hierarchy in foraging by large herbivores and is where the strength of the plant-herbivore interaction is strongest as diet is selected at this level (Senft et al. 1987, Bailey et al. 1996). As forage availability waned in the most profitable habitat by mid-summer, bison instantaneous intake responded by taking large bites of poorer quality forage in a year of average ANPP, 2013, or smaller bites of the more stressed yet higher quality forage in a
year of very low ANPP, 2012 (Chapter 2). At the intermediate level of the foraging hierarchy, the patch or feeding site scale, bison preferred to graze in burned areas of low vegetation structure (Chapter 3), where high quality items that maximize daily nutrient gains are easier to find (Fryxell 1991). Decreasing forage availability with the approaching dormant season, likely drove bison to feed in more homogenous, unburned areas where satiation was more likely although at the cost of reduced nutrient intake.

In response to fire-induced variation in forage quality and temporal forage availability, bison foraging tactics to meet metabolic requirements at two scales dictated space use in the landscape as predicted by Senft et al. (1987). At the landscape-level, bison shifted patterns of space use in response to fire-induced resource variability but topographical features of the landscape also affected space use (Chapter 4). Preference for the upper bench features of the enclosure, which offer flat terrain, southerly winds, and high-quality food, reduced movement during the growing season (Chapter 5). In this empirical study, I documented behavioral mechanisms driving resource use at each of the levels of the ecological hierarchy available at KPBS (feeding station to patch to landscape). These findings shed light on a historically, important consumer’s multi-scale behavioral tactics to maintain basic metabolic requirements in a nutritionally heterogeneous grassland managed to mirror ecological processes in tallgrass prairie with an intact-fire grazer interaction.

**LITERATURE CITED**


