

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

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## 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-equilibrium 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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# Chapter 1 - Introduction, Foraging Behavior, Fire-Grazer Interactions, and Animal Distribution

Understanding factors driving foraging decisions requires the elucidation of behavioral mechanisms involved in both the fine and broad scale distribution of animals (Senft et al. 1987, Edwards et al. 1994, Fortin et al. 2002, Fryxell et al. 2008, Boettinger et al. 2011). Acquiring a fully complementary and balanced diet, minimizing time spent acquiring a diet, and understanding constraints imposed by group living are crucial factors affecting decisions leading to habitat selection in animals (Charnov 1976, Illius and Gordon 1992, McNamara et al. 1993, Bergman et al. 2001, Farnsworth and Illius 1998, Babin et al. 2011, Merkle et al. 2015).

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

24 managed as a replicated watershed-level experiment where different watersheds are burned at  
25 varying frequencies. This mosaic of watersheds with different burn histories becomes the habitat  
26 mosaic available for grazing by plains bison (*Bison bison bison*; Knapp et al. 1999). The  
27 replicated fire treatments at KPBS allowed me to measure how bison foraging and space use  
28 patterns shift in response to plant abundance and nutritional content across a variety of spatial  
29 and temporal scales. In this study, I examined effects of fire-induced variation in forage  
30 resources on foraging and space use at multiple scales, from fine-scale foraging kinetics and  
31 patch selection to the broad-scale distribution of bison in nutritionally heterogeneous grassland.

## 32 **Theoretical Basis of Grazer Foraging**

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

43 The classical model describing food intake by predators hunting specific prey is Holling's  
44 Type II functional response: as prey density increases, predator intake also rises as a decelerating  
45 function and approaches to an upper asymptote (Gross et al 1993). The deceleration in predator  
46 intake rate results from a trade-off between searching for prey items and handling them after and

47 during capture. Therefore, the more prey a predator handles, the less time is spent searching for  
48 food. The asymptote in this model is set by the reciprocal of the handling time for each captured  
49 prey item, while the rate at which the curve rises to the asymptote results from the animal's  
50 searching efficiency (Holling 1959; 1965). Grazing herbivores also exhibit a similar functional  
51 response as vegetation availability increases, but the underlying assumptions of the model  
52 describing grazing intake rates differ from consumers such as carnivores. Focusing on herbivore  
53 grazers, Spalinger and Hobbs (1992) modified Holling's Type II functional response to include  
54 an herbivore's ability to search while still handling food. They demonstrated that post-capture  
55 handling time is not likely causing the deceleration in herbivore intake rate because most  
56 herbivores can continue searching for new bites as they crop and chew (handle) others, whereas  
57 most predators must consume their prey before starting a new search. Most studies of grazing on  
58 cultivated swards show bite mass and bite rate exhibit an inverse relationship with increasing  
59 forage abundance, which drives grazer forage intake rates (Spalinger and Hobbs 1992, Laca et al  
60 1994). Specifically, Gross et al. (1993) found an asymptotic response to bite size and an inverse  
61 relationship between cropping rate and bite size in feeding trials of several mammalian  
62 herbivores. Because larger bites require an herbivore to invest more effort in mastication before  
63 swallowing, and because chewing movements cannot occur simultaneously as cropping  
64 movements, they hypothesized that cropping rate declines with increasing bite size. Empirically,  
65 the Gross et al. (1993) model accounted for 77% of the variability in herbivore intake rate and  
66 strongly supported the hypothesis that competition between cropping and chewing (processing)  
67 is responsible for the Type II functional response observed in herbivores. These results provide  
68 the theoretical foundation for predicting how variation in plant morphology and vegetation  
69 structure can influence fine-scale foraging strategies and inevitably influence coarse-scale



70 distribution of large mammalian herbivores. How do disturbances such as fire that initiate  
71 variation in forage quality and quantity affect grazer foraging behavior?

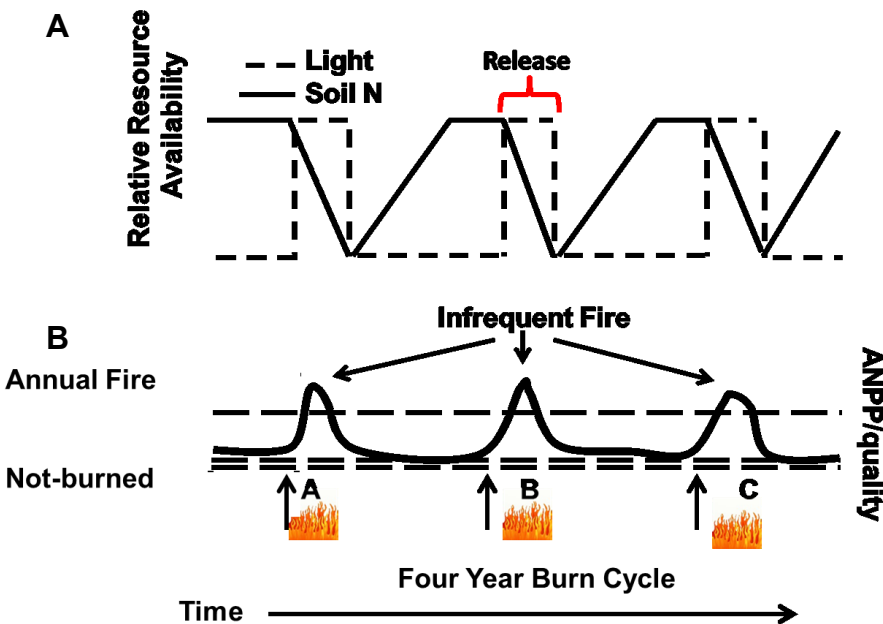
## 72 **Animal Distribution and Space Use**

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

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

92 **Non-equilibrium Forage Dynamics**

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



103

104 **Figure 1-1. Diagram of ‘pulsed’ release of soil nutrients from light-limitation (above)**  
105 **induced by fire and response in ANPP and forage quality in infrequently-burned,**  
106 **frequently-burned, and unburned watersheds (below). (A) Diagram of the transient**  
107 **maxima in resource availability: the increased levels of soil Nitrogen content (solid black**  
108 **line) which is made available to plants after fire releases the light-limited canopy (dashed**  
109 **black line) from previous years’ dead plant tissue. Soil Nitrogen declines after the release**

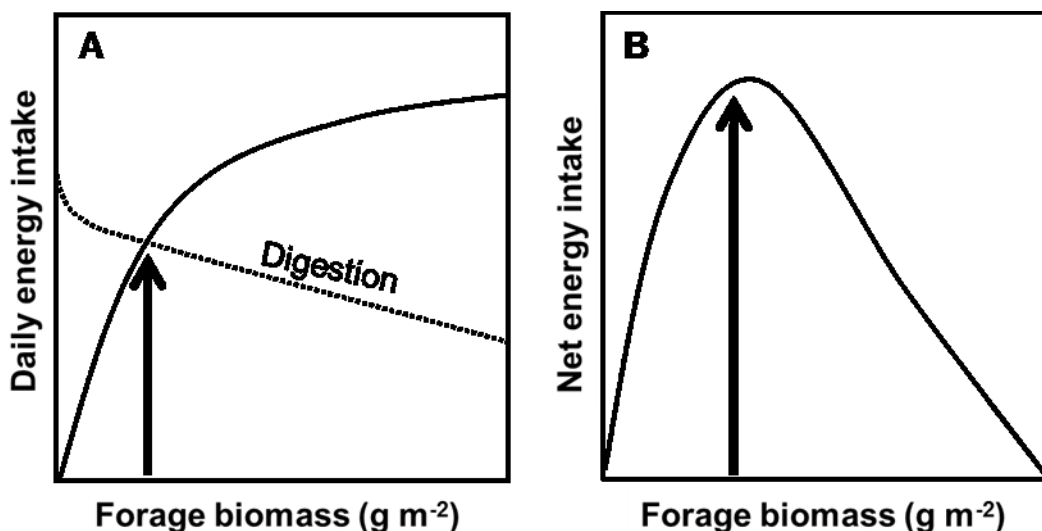
110 **due to use by aboveground plant processes and canopy light-limitation again occurs as fire**  
111 **is suppressed. (B) Variation in grassland aboveground resource availability based on burn**  
112 **frequency: the pulsed response in resource availability of infrequently-burned grassland in**  
113 **year of burn (solid black line), the static response of frequently-burned grassland burned**  
114 **that year, which is not light-limited and therefore supports lower soil N content, and no**  
115 **response in grassland that is not-burned which is dominated by light limitation and offers**  
116 **little green tissue. Modified after Seastedt and Knapp (1993), Blair (1997).**

117  
118

## 119 **The Forage Maturation Hypothesis**

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

137 Illius and Gordon 1991). The negative relationship between forage quantity and forage quality in  
138 natural grasslands results in a digestion rate of forage, which is commonly found to be a negative  
139 function of forage quantity. Therefore, the potential daily intake rate is limited by the constraints  
140 of forage ingestion and digestion (Drescher et al. 2006). In patches of intermediate forage mass,  
141 the intersection of the forage ingestion and digestion constraints is where the maximum net  
142 intake rate is found (Fig. 2b; Fryxell 1991).



143  
144 **Figure 1-2. Schematic showing general mechanisms of the forage maturation hypothesis**  
145 **(FMH). (a) Foraging constraints of daily cropping (solid line) and digestion (fine-dotted**  
146 **line) that result in a foraging optima (arrows), where optimal energy/nutrient assimilation**  
147 **occurs, at low-to-intermediate biomass. (b) The arrow indicates maximization of**  
148 **energy/nutrient intake by foraging in patches of low-to-intermediate forage quantity over a**  
149 **coarser time period. Modified after Fryxell 1991, Drescher et al. 2006.**

## 151 **Variation in Forage Resources Driven by Prescribed Burning**

152 Fire plays a critical role in driving spatio-temporal variation in forage quality, forage  
153 quantity, and structure of patches (Briggs and Knapp 1995, Archibald et al. 2005, Anderson et al.  
154 2007). Fire homogenizes forage quality and quantity in grasslands (Hobbs et al. 1991, Briggs and  
155 Knapp 1995); providing highly-nutritional forage (Coppock et al. 1983) and increased quantities  
156 (Wallace et al. 1995) throughout the burned landscape for ungulate grazers. Numerous studies

157 have assessed floristic heterogeneity in landscapes resulting from fire-grazing interactions  
158 (Hartnett et al. 1996, Fuhlendorf and Engle 2001, Collins and Calabrese 2012), although the  
159 spatio-temporal patterns of grazing in response to recent burning has only been assessed at broad  
160 spatial and temporal scale investigations in burned or unburned grassland (Vinton et al. 1993,  
161 Coppedge and Shaw 1998, Allred et al. 2011). For example, Coppedge and Shaw (1998) studied  
162 the impact of burn-type (dormant and growing season) of grassland sites on seasonal bison  
163 grazing activity and herd composition, while Vinton et al. (1993) examined bison grazing  
164 patterns in relation to burning regime and graminoid-type ( $C_3$  vs.  $C_4$ ) at the watershed-scale.  
165 Furthermore, neither study focused on fine-scale foraging behavior by bison such as forage  
166 intake rate relative to recent burning or addressed how behavior may vary when grazing in  
167 grassland burned at different frequencies over the extent of a growing season. The foraging  
168 kinetics responsible for this marked response to burning remains unexplored and the  
169 experimental setting at KPBS has been ideal for such an investigation. Heterogeneity of resource  
170 abundance in seasonal burns during their first and subsequent growing seasons likely influences  
171 bison foraging strategies both temporally and spatially. I found that the impetus behind these  
172 responses to fire-induced nutrient enhancement in forage by large herbivores may be found by  
173 investigating activities at the micropatch (feeding station [Chapter 2]) and patch (feeding area  
174 [Chapter 3]) scales. I hypothesized that adjustments in fine-scale feeding rates to control energy  
175 and nutrient intake and to potentially maximize time in non-feeding activities may be an outcome  
176 of a grazer's strong response to recently burned areas. Such adjustments may be modulated by  
177 the grassland's time since last burn, which impacts forage quality and quantity (Seastedt and  
178 Knapp 1993, Blair 1997). Consequently, a response in fine-scale foraging behavior to grassland

179 offering differing levels of resource availability due to burn frequency may dictate landscape-  
180 level space use.

## 181 **Grazer Distribution in a Nutritionally Heterogeneous Landscape**

182 Understanding the grazer-plant interaction as affected by fire in a tallgrass prairie  
183 ecosystem is central for understanding mesic grassland ecosystems. Along with climate, fire and  
184 especially the fire-grazer interaction are key drivers of grassland ecosystem function and  
185 structure (Archibald et al. 2005, Anderson et al. 2007, Fuhlendorf et al. 2009, Allred et al. 2011,  
186 Allred et al. 2014). Effects of the fire-grazer interaction include altered vegetation quality and  
187 primary productivity (Anderson et al. 2007), increased plant, arthropod, and vertebrate species  
188 richness (Collins et al. 1998, Joern 2005, Fuhlendorf et al. 2012), and increased woody  
189 encroachment in response to long burn intervals where grasslands could become increasingly  
190 woody and ultimately no longer grasslands in its absence (Ratajczak et al. 2014). In this context,  
191 it is important to understand how fire affects landscape-level distributions of ungulate grazers in  
192 time and space as they track and use food resources of the highest available quality (Archibald  
193 and Bond 2004, Archibald et al. 2005, Anderson et al. 2007, Prins and van Langevelde 2008).  
194 This becomes a bigger challenge for ruminants foraging in heterogeneous landscapes as food  
195 often can be of substandard quality and the best quality food is distributed spatially in a patchy  
196 configuration that varies over time as a shifting mosaic. In turn, the spatial and temporal  
197 heterogeneity of forage quality dictates the spatial distribution and movement kinetics of large  
198 herbivores at the landscape level, although predation risk or physical features of the environment  
199 can also affect habitat use (Fryxell 1991, Fryxell et al. 2005, Anderson et al. 2010, Ford et al.  
200 2014). Moreover, large herbivores can themselves alter the spatial heterogeneity of forage  
201 resources through their significant levels of forage consumption and effects on subsequent fuel

202 loads, because of their relative large individual and population sizes. Accurate spatial memory  
203 allows large ungulates to anticipate the heterogeneous distribution of food resources that coupled  
204 with their high mobility increases the likelihood they will select sites with high forage quality  
205 (Prins and van Langevelde 2008, Merkle et al. 2014, Merkle et al. 2015). Although the study of  
206 foraging and distribution of grazers, in time and space, requires an understanding of herbivore-  
207 plant interactions at multiple scales (Johnson 1980, Senft et al. 1987, Levin 1992), other aspects  
208 of the landscape may also contribute to ungulate distributions, including topography, availability  
209 of soil mineral nutrients (Tracy and McNaughton 1995), distance to water or shade, risk of  
210 predation, and physical factors (e.g., temperature, soil water) (Anderson et al. 2010, Allred et al.  
211 2013).

212         The final portion of this dissertation, Chapter 5, incorporates a recent development in the  
213 field of movement ecology: the development of quantitative tools to identify landscape features  
214 that constrain movement by taking into account the relative utility of both the habitat where the  
215 animal currently resides and that of where it is moving (Potts et al. 2014, Beyer et al. 2014).  
216 Extrinsic biases to bison movement were evaluated using a comparison between observed and  
217 random steps through the heterogeneous landscape. The statistical approach used here is based  
218 on conditional logistic regression analysis, and was inspired by resource selection studies based  
219 on a case-control design (e.g. Compton et al. 2002, Boyce et al. 2003). In contrast, I used an  
220 approach that compares landscape ‘segments’ instead of individual GPS-locations (Arthur et al.  
221 1996, Boyce et al. 2003) or areas (Johnson et al. 2002). Consequentially, I explicitly considered  
222 landscape characteristics that bison would have been likely to encounter along their path (a step  
223 selection function design; Fortin et al. 2005). This procedure is novel, however, because  
224 estimating the movement and habitat preference models simultaneously facilitates unbiased

225 parameter estimation (Beyer et al. 2014), and it is applied to a system with an intact fire-grazer  
226 interaction, which is a first, to my knowledge.

## 227 **Research Objectives**

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

- 245 • (Chapter 2) can show increased feeding rates in the early growing season only in  
246 infrequently-burned watersheds burned that year and shift forage kinetics to optimize nutrient  
247 intake in times of low forage quality,



- 248 • (Chapter 3) select feeding sites of high protein content and low forage stature as long as plant  
249 regrowth is possible then shift foraging behavior and diet in order to attain forage resources  
250 in times of uniformly low forage quality at the cost of spending more of the daytime feeding,
- 251 • (Chapter 4) disproportionately utilize infrequently-burned watersheds throughout the  
252 growing season (May to September) then shift to using watersheds that did not burn that  
253 previous spring while simultaneously avoiding annually-burned watersheds during the  
254 dormant season (December to February),
- 255 • (Chapter 5) respond to the underlying dynamic forage resources and static landscape  
256 characteristics of the shifting mosaic of vegetation quantity and quality at KPBS by selecting  
257 areas of high foliar protein and low herbaceous biomass content, while mostly avoiding low  
258 elevations, steep slopes, and non-south facing areas.

259

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

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509           **Abstract**

510           Foraging decisions by native grazers in fire-dependent landscapes modulate the fire-  
511   grazing interaction. Uncovering the behavioral mechanisms associated with the attraction of  
512   grazers to recently burned areas requires understanding at multiple spatial scales in the  
513   ecological foraging hierarchy. This study focused on feeding in the area between steps in a  
514   foraging bout, the feeding station, as forage chemistry and vegetation architecture play central  
515   roles in these fine-scale, feeding-station decisions. The forage maturation hypothesis (FMH) uses  
516   the temporal dynamics of forage quality and quantity in grasslands to explain the distribution of  
517   large herbivores, but does not address herbivore responses to inter-patch variation caused by fire-  
518   induced nutrient increases of forage quality. Using an experimental setting with contrasting fire  
519   treatments we describe the effects of variable burn history on foraging kinetics by bison at Konza  
520   Prairie Biological Station (KPBS). We assessed the potential to link the FMH in a  
521   complementary fashion to the transient maxima hypothesis (TMH) to explain temporal variation  
522   in bison responses to grassland forage quality and quantity in response to burning at different  
523   temporal frequencies. Forage attributes met predictions of the TMH that allowed us to  
524   investigate how forage maturation affects feeding station foraging behavior across watersheds

525 with varying burn frequency. At sites burned in the spring after several years without burning,  
526 both bite mass and intake rate increased with increasing biomass at a greater rate during the  
527 growing season than during the transitional mid-summer seasonal period. In these infrequently  
528 burned watersheds, early growing season bite mass ( $0.6 \pm 0.05$ ), bite rate ( $38 \pm 1.5$ ), and intake  
529 rate ( $21 \pm 2.3$ ) was reduced by ~15, 13, and 29% during the mid-summer transitional period. A  
530 behavioral response in foraging kinetics at the feeding station occurred where a non-equilibrium  
531 pulse of high quality resource was made available and then retained by repeated grazing over the  
532 growing season. Our results provide the first experimental evidence for demonstrating the fine-  
533 scale behavioral response of a large grazer to fire-induced changes in forage attributes, while  
534 linking two prominent hypotheses proposed to explain spatial variation in forage quality and  
535 quantity at local and landscape scales.

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

## 538 **INTRODUCTION**

539 In grasslands, spatial and temporal variation in forage quality and quantity results from multiple  
540 interacting abiotic factors such as precipitation, topography, and soil nutrients, which in turn  
541 affect the foraging behavior of grazing ungulate herbivores (Owen-Smith 2002, Prins and  
542 Langevelde 2008). Equally important, such heterogeneity in forage quantity and quality in a  
543 landscape also reflects recursive fire-grazer interactions (Milchunas et al. 1988, Fuhlendorf and  
544 Engle 2001, Archibald et al. 2005, Anderson et al. 2007). Fire in grasslands creates an  
545 “ecological magnet” for many grazer species (Archibald et al. 2005), resulting in heavy selection  
546 and sustained use of regrowth in post-burned areas (Coppedge and Shaw 1998, Sensenig et al.  
547 2010, Eby et al. 2014). In turn, recent grazing negatively reduces fuel and the likelihood a patch

548 will burn in the near future. While the spatial distributions and movement patterns of large  
549 herbivores in response to recent fires are increasingly understood at coarse-scale landscape levels  
550 (Vinton et al. 1993, Schuler et al. 2006, Allred et al. 2011*a, b*, Augustine and Derner 2014),  
551 much remains to be learned about how fire-grazing interactions affect foraging at fine-scales, i.e.  
552 the feeding station level. A feeding station is defined as the forage available to an herbivore  
553 without moving its front feet during a foraging bout (Bailey et al.1996). The feeding station is  
554 the spatial unit of finest ecological resolution in the ecological hierarchy where foraging  
555 decisions are made that can affect coarser-scale distributional decisions (Morris 1987, Senft et al.  
556 1987).

557 Fryxell (1991) modeled the forage maturation hypothesis (FMH) (McNaughton 1986,  
558 Hobbs & Swift 1988) as a trade-off between forage quality and quantity to evaluate grazer  
559 behavior at multiple scales, providing a framework to understand patch use and the spatial and  
560 temporal distributions of grazing herbivores (Wilmschurst et al. 1999, Hebblewhite et al. 2008,  
561 Dancose et al. 2011, Bischof et al. 2012). In this model, optimal intake rates by foragers occur at  
562 low to intermediate levels of forage biomass. FMH posits that aggregations of large herbivores  
563 reflect optimal combinations of forage quality and quantity to maximize intake rate (Fryxell  
564 1991). In turn, collective consumption pressure at intermediate to high grazer densities may  
565 maintain vegetation in a state of low to intermediate forage quantity but high quality through  
566 regrowth of young forage tissue (McNaughton 1979, Fryxell 1991); i.e., seasonal maturation to  
567 high biomass is repressed by repeated foraging pressure.

568 Fire is a major ecosystem driver in many grasslands, where it leads to spatially  
569 heterogeneous distributions of forage quality, appearing as a shifting mosaic within and among  
570 years depending on the time since a patch last burned. Fire significantly increases leaf nutrient



571 concentrations in post-fire growth (Blair 1997, van de Vijver et al. 1999) while removing older,  
572 non-palatable tissues (Pfeiffer and Hartnett 1995). Complementary to direct grazer-vegetation  
573 interactions and the FMH, the Transient Maxima Hypothesis (TMH) (Seastedt and Knapp 1993,  
574 Blair 1997) describes the development of a shifting mosaic of vegetation quantity and quality in  
575 response to fire-mediated release from resource limitations in tallgrass prairie with great  
576 potential to influence grazer-fire interactions. In tallgrass prairie, primary productivity is often  
577 co-limited by light, energy and soil nutrients, with the relative importance of individual resources  
578 dependent on time since last fire (Blair 1997). Annually burned grassland receives sufficient  
579 light and temperatures are non-limiting, but soil nitrogen becomes limiting. For unburned  
580 grassland when litter accumulates, light / temperature is limiting, and available soil-N increases  
581 with time as it is not fully used by plants.

582       A post-fire “pulsed” increase in ANPP occurs in vegetation that is released from an  
583 extended period of fire suppression. An abrupt release of light limitation coupled to the  
584 availability of increased accumulation of available soil nitrogen leads to a short-lived, non-  
585 equilibrium pulse in ANPP. This non-equilibrium period is referred to as a “transient maxima” –  
586 when availability of both potentially limiting factors is sufficient to support increased ANPP  
587 (Seastedt and Knapp 1993). In tests of the TMH in tallgrass prairie, Blair (1997) found increased  
588 ANPP and higher concentrations of shoot tissue nitrogen (N) in years with burning when  
589 vegetation was exposed to intermediate fire frequencies (e.g. every several years) compared to  
590 annual burning or long periods of fire suppression (Fig. 1a; Blair 1997). Enhanced ANPP and  
591 plant tissue-N content following an infrequent fire derive from the ability of vegetation to exploit  
592 higher soil inorganic and mineralizable-N accumulated in the absence of fire, under new high-  
593 light conditions. Moreover, net N-mineralization rates and foliar-N content both decline with

594 successive annual spring burning, ultimately reducing nutritional quality available to grazers;  
595 unburned sites provide less palatable forage because of the significant proportion of mature, low  
596 quality leaf tissue in standing vegetation (Vinton et al. 1993, Pfeiffer and Hartnett 1995, Knapp  
597 et al. 1999). Consequently, a shifting mosaic of areas of varying fire frequency can modulate the  
598 spatial and temporal distribution of large herbivores through combined effects on forage quality  
599 and quantity (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2009) similar to the FMH.  
600 Differences in nutrient value and palatability of forage available in areas burned frequently,  
601 infrequently, and not burned should alter foraging behavior at the feeding station level where diet  
602 selection occurs (Senft et al. 1987).

603         The overall significance of the fire-grazing interaction can be determined by examining  
604 how fire influences grazing behavior, the key to understanding the link between fire and grazing  
605 (Fuhlendorf and Engle 2004, Allred et al. 2011*a*). Although it is well known that large grazers  
606 are attracted to recently burned grassland, the mechanisms drive forage nutrient availability and  
607 resulting fine-scale foraging behavior after a fire remain unexplored. For example, the initial  
608 post-fire surge in forage nutrient availability in infrequently burned grassland (TMH) may  
609 interact with subsequent concentrated grazing pressure (FMH) to maintain grassland in an ideal  
610 state of forage quality and quantity, where large herbivores realize short-term benefits in nutrient  
611 acquisition (Fig 1b). The shifting mosaic from both fire-induced and concomitant grazing  
612 enhanced forage quality is well known (Schuler et al. 2006, Allred et al. 2011*b*, Eby et al. 2014).  
613 Here, we hypothesize that mechanisms underlying FMH and TMH interact as two  
614 complementary diet optimization drivers that guide bison distributions during short-term periods.  
615 Because protein (i.e. N content) is often a limiting factor for ungulate performance (Van Soest

616 1996), foraging responses to variable fire frequency and associated plant responses will provide  
617 insight into how frequent and infrequent fires impact bison behavior.

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

634 An inverse relationship between leaf development stage and protein content and forage  
635 digestibility (Waite et al. 1963, Miller et al. 1965), predicts a positive feedback between grazing  
636 activity and forage palatability (Archibald et al. 2005, Verweij et al. 2006, Kerby et al. 2007) – a  
637 tenet of FMH. Forage quantity influences grazer foraging behavior at the feeding station scale

638 (Ruyle et al 1987, Drescher et al. 2006), outcomes that are sure to be influenced by fire-induced  
639 alterations in forage quality are in need of study.

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

658     **METHODS**

659     *Study Area*

660     Konza Prairie Biological Station (KPBS) is 3487 ha of native, C<sub>4</sub>-dominated grassland in the  
661     Flint Hills of northeastern Kansas (39°05'N and 96°35'W), located approximately 13 km south of  
662     Manhattan, KS. The site is representative of Flint Hills tallgrass prairie with a variable  
663     continental climate with warm, wet springs, hot summers and dry, cold winters. The 32 year  
664     mean annual precipitation (1982 to 2013) is 832.9 ± 61.1 mm with ~75% falling during April to  
665     September. KPBS experienced below average precipitation in 2012 (568.9 mm, a deviation of -  
666     46% from the annual average precipitation), while 2011 (814 mm, -2% from the annual average  
667     annual precipitation) and 2013 (783.4 mm, -6% from the annual average precipitation) were near  
668     average precipitation. Vegetation is mostly native tallgrass prairie (>90%) dominated by C<sub>4</sub>  
669     perennial grasses (*Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, and  
670     *Schizachyrium scoparium*) where interstitial forbs constitute >75% of species richness (~575  
671     species) (Towne 2002). Bison have access to a contiguous 1,012 ha fenced enclosure comprising  
672     10 hydrologically-delineated watersheds with different fire treatments. Two replicate watersheds  
673     each have been burned in the spring since 1988 at one of three fire frequencies (1, 2, and 20  
674     years), while four watersheds have been burned once every four years. Hereafter, we refer to  
675     watersheds with fire frequencies of 1-2 years and that *did* burn in the spring (late March-early  
676     April) prior to focal animal observations (late April to December) as frequently-burned  
677     watersheds (n= 3 in both years). Watersheds with fire frequencies of 4 or 20 years and that  
678     burned in the spring prior to focal animal observation are referred to as “infrequently-burned”  
679     watersheds (n=2 in 2012, 1 in 2013). Watersheds that were not burned (n=5 in 2012, 6 in 2013)  
680     in the spring prior to our observations are referred to as “not-burned” sites in this study,

681 regardless of the historical burn frequency. Bison stocking rate is currently maintained at ~260  
682 adults (plus ~100 spring-born calves) annually or ~ 14.5g bison / m<sup>2</sup> resulting in a target density  
683 that removes ~25 of the ANPP.

#### 684 *Focal Sampling*

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

#### 695 *Vegetation Surveys at Feeding Stations*

696 Following each observation of bison feeding, forage attributes were measured using three  
697 quadrats at arbitrary locations parallel to the foraging area monitored during the 5 min foraging  
698 bout. Quadrats consisted of 1m<sup>2</sup> sampling frames split into five 0.2 m<sup>2</sup> sub-plots placed within a  
699 10 m radius circle centered on the feeding location (Schaefer and Messier 1995). In every sub-  
700 plot, plant cover and percentage of green material was estimated visually using 10% classes in  
701 four vegetation groups: grasses and sedges, forbs (all herbaceous dicots), litter (previous year's  
702 dead grass), and bare ground. Mean grass height was calculated by measuring three  
703 representative plants to the nearest cm at twenty points along a 30-m transect running parallel to

704 the grazed path. Total dry plant biomass (B, in grams per square meter) was estimated by  
705 clipping standing biomass to 1 cm height from a 0.1-m<sup>2</sup> sampling frame placed parallel to the  
706 foraging path. Three 0.1-m<sup>2</sup> swaths were clipped and adjusted to 1 m<sup>2</sup>. Total biomass was then  
707 multiplied by proportions of graminoids, forbs, and litter determined from visual percent cover  
708 estimates to estimate biomass of the three vegetation elements. To estimate forage quality at  
709 feeding stations, three swaths of vegetation within 2 m parallel to the foraging path were clipped  
710 to 1 cm height from a 0.1 m<sup>2</sup> sampling frame (< 24 hr since grazed).

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

725 *Estimation of bite size*

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

#### 736 *Ingestion Time*

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

744 Instantaneous forage intake rate was calculated as the product of bite rate and bite size.  
745 Because intake rate of dry matter at feeding stations by ungulates is limited by ingestion time  
746 (Spalinger and Hobbs 1992), we used functional responses estimated during foraging bouts to  
747 determine the ingestion time of forage. We determined dry matter forage intake rate (I; g/min) by  
748 multiplying the bite rate (BR; bites/min) derived from analysis of foraging videos by bite mass



749 (BM; g/bite). Forage intake rate was then related to forage biomass ( $B$ ) using the Michaelis-  
750 Menten form of the type II functional response:  $\frac{MB}{\beta+B}$ , where  $M$  is the maximum feeding rate  
751 (g/min) and  $\beta$  is the half-saturation constant (g/m<sup>2</sup>). Appendix B summarizes the methodology  
752 for estimation of recent grazing activity.

753

#### 754 *Data Analysis*

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

760 Satterwaite's approximation was used to calculate effective degrees of freedom of a linear  
761 combination of independent sample variances.

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

## 769 **RESULTS**

### 770 *Temporal Trends in Grass Availability*

771 Mean standing stock of live and dead grass biomass ( $\text{g m}^{-2}$ ) averaged across topographic  
772 positions was greater in not-burned, watersheds in comparison to frequently- and infrequently-  
773 burned watersheds burned the previous spring (Fig. 2a). However, grass biomass after the spring  
774 burn in 2013 for infrequently-burned, grazed watersheds reached similar levels to frequently-  
775 and not-burned watersheds by the end of the growing season, unlike the consistently low levels  
776 of grass biomass for infrequently-burned sites in 2012. Analyses of total grass biomass revealed  
777 significant main effects of seasonal period ( $F_{2,7.5}=7.5, P=0.02$ ) and burn treatment ( $F_{2,22.7}=8.11,$   
778  $P=0.002$ ) in addition to a significant year-by-season interaction ( $F_{2,25}=4.3, P=0.02$ ; Appendix A,  
779 Table A1). The transitional period had greater total grass biomass than the dormant period except  
780 in 2012; the transitional period and dormant period had similar levels of grass biomass.  
781 Frequently-burned and infrequently-burned watersheds had significantly less total grass biomass  
782 than not-burned watersheds during the study (Fig. A1), which is in accord with the prediction  
783 that initial attraction to high quality forage instigated repeated grazing (Fig. B4). In 2012, grass  
784 biomass sampled during the peak of production in an annually burned, ungrazed site (watershed  
785 1D), was 19% ( $320.3 \text{ g m}^{-2}$ ) below the annual mean of  $399.7 \text{ g m}^{-2}$  estimated from 1989 to 2013  
786 (mean grass biomass averaged over topographical positions, Konza-LTER dataset PAB01). In  
787 2011 this watershed had above average ANPP with  $540.6 \text{ g m}^{-2}$  (+37%). In 2013, grass biomass  
788 was 38% above the recorded average with  $551.2 \text{ g m}^{-2}$ .

789 Crude protein content of live forage at feeding stations declined as the season progressed in  
790 2012 (curvilinear regression,  $F_{1,100}=26.2, R^2=0.35, P<0.0001$ ) and 2013 (curvilinear regression,  
791  $F_{1,93}=229.3, R^2=0.8, P<0.0001$ ), although a substantial increase in protein content was evident in  
792 late summer 2012 (Fig. 2c,d). Lignin content increased with increasing day of the year in 2012  
793 (curvilinear regression,  $F_{1,100}=21.5, R^2=0.30, P<0.0001$ ) and 2013 (curvilinear regression,

794  $F_{1,93}=42.2$ ,  $R^2=0.48$ ,  $P<0.0001$ ; Fig. 2d). Crude protein content of forage peaked during the early  
795 growing season of both years and protein content of forage from infrequently- burned watersheds  
796 was generally higher throughout the study (Fig. 2e). Analyses of variation in crude protein  
797 content of grass shoots by burn treatment revealed a marginally significant difference  
798 ( $F_{2,21.1}=3.43$ ,  $P=0.05$ ) in addition to a marginally significant year-by-seasonal period interaction  
799 ( $F_{2,12.1}=3.67$ ,  $P=0.06$ ; Table A1, Fig. A2). Infrequently-burned watersheds had higher crude  
800 protein content of grass shoots than not-burned watersheds throughout the study (Bonferroni's  
801 least squared differences [lsd],  $P=0.01$ ), while frequently-burned watersheds had marginally  
802 lower crude protein content of grass shoots than infrequently-burned watersheds (lsd,  $P=0.1$ ; Fig.  
803 A2). The year-by-seasonal period interaction revealed crude protein content of grass shoots was  
804 lower in the 2012 dormant season than in the 2013 dormant season (lsd,  $P=0.009$ ).

#### 805 *Functional Responses to Feeding Station Biomass*

806 Bite mass increased linearly with increasing grass biomass across all treatments ( $F_{2,206}=32.39$ ,  
807  $P<0.0001$ ,  $R^2=0.14$ ). The mean bite mass relative to grass biomass level did not differ  
808 significantly among burn treatments ( $F_{4,198}= 1.32$ ,  $P=0.27$ ) or among seasons in watersheds that  
809 did not burn in the spring prior to observation (slope,  $F_{2, 76}=1.94$ ,  $P=0.15$ ; intercept,  $F_{1,76}=5.09$ ,  
810  $P=0.03$ , Fig. 3c). In infrequently-burned watersheds, there was a marginally significant  
811 interaction between season and grass biomass in the bite mass ANCOVA (slope,  $F_{1,50}=3.37$ ,  
812  $P=0.07$ , intercept,  $F_{1,50}=0.1$ ,  $P=0.75$ , Fig. 3b). Thus, we tested whether the slope of the  
813 relationship of bite mass with grass biomass differed between seasons. Bite mass differed  
814 significantly between growing and transitional seasons independent of differences in grass  
815 biomass with growing season bite mass increasing with grass biomass at a greater rate than the  
816 transitional season in infrequently- burned watersheds. Only five observations in infrequently-

817 burned watersheds for the dormant season were available and were not included in analyses. In  
818 frequently-burned watersheds, the relationship of bite mass to grass biomass did not differ  
819 significantly among seasons (slope,  $F_{2,67}=1.12$ ,  $P=0.33$ , intercept,  $F_{2,67}=1.25$ ,  $P=0.29$ , Fig. 3a).  
820 The upper envelope to the scatter of points suggests that maximum bite mass for each watershed  
821 type could be obtained from a feeding station biomass of  $40 \text{ g m}^2$ . Overall, the mean bite mass  
822 was similar among watersheds types: frequently-burned ( $\bar{x} \pm \text{SE}=0.58 \pm 0.1 \text{ g}$ ), infrequently-  
823 burned ( $\bar{x}=0.53 \pm 0.1 \text{ g}$ ), and not-burned ( $\bar{x}=0.64 \pm 0.1 \text{ g}$ ; Fig. 4a).

824 Bite rate declined significantly with increasing grass biomass at the feeding station,  
825 averaged across all three burn treatments ( $F_{2,206}=19.11$ ,  $P<0.0001$ ,  $R^2=0.08$ ). Bite rate did not  
826 differ significantly among burn treatments ( $F_{4,198}=0.30$ ,  $P=0.88$ ). A seasonal difference in bite  
827 rate was measured at feeding stations with similar grass biomass within treatment combinations  
828 as seen for frequently-burned watersheds (Fig 3d). Bite rate was greater in the dormant season  
829 than the growing season, but not different from the transitional season (slope,  $F_{1,67}=0.83$ ,  $P=0.44$ ,  
830 intercept,  $F_{2,67}=2.64$ ,  $P=0.08$ , Fig 3d). Because we found a marginally significant interaction  
831 between season and grass biomass for bite rate (ANCOVA,  $F_{1,53}=2.95$ ,  $P=0.09$ , intercept,  
832  $F_{1,50}=0.74$ ,  $P=0.39$ , Fig. 3e) in infrequently-burned watersheds, we tested whether the slope of  
833 bite rate with increasing grass biomass differed between seasons. Bite rate differed significantly  
834 between growing and transitional seasons independent of grass biomass differences with  
835 transitional season bite rate decreasing at a greater rate than the growing period in infrequently-  
836 burned sites. This meets our prediction of an inverse relationship between bite mass and bite rate  
837 at high quality feeding stations as biomass increases. In watersheds not burned the spring prior to  
838 observation, bite rate was similar among seasons although the slopes were marginally different  
839 with the dormant season having a positive slope while the growing and transitional season bite

840 rate decreased with increasing grass biomass (slope,  $F_{2, 71}=1.44$ ,  $P=0.08$ ; intercept,  $F_{1,71}=1.44$ ,  
841  $P=0.24$ ). Maximum bite rates  $\sim 55$  bites  $\text{min}^{-1}$  were observed in each watershed type on grass  
842 biomass up to  $40 \text{ g m}^{-2}$ . Mean bite rate in frequently-burned ( $\bar{x}=34 \pm 2.3$  bites  $\text{min}^{-1}$ ),  
843 infrequently-burned ( $\bar{x}=37 \pm 2.4$  bites  $\text{min}^{-1}$ ), and not burned grassland ( $\bar{x}=35 \pm 2.1$  bites  $\text{min}^{-1}$ )  
844 were similar (Fig. 4b).

845 Intake rate increased linearly with biomass availability at the feeding station across all  
846 three burn treatments ( $F_{2, 206}=8.15$ ,  $R^2=0.04$ ,  $P=0.005$ ). A maximum limit to the intake rate was  
847 reached at feeding stations of  $\sim 50 \text{ g m}^{-2}$  ( $40 \text{ g min}^{-1}$  in frequently-burned watersheds;  $35 \text{ g min}^{-1}$   
848 in infrequently-burned; and  $50 \text{ g min}^{-1}$  in watersheds not burned in the spring prior to  
849 observation). Intake rate relative to total grass biomass at feeding stations did not differ  
850 significantly among watershed types ( $F_{4, 206}=1.04$ ,  $P=0.36$ ) or among seasons for frequently-  
851 burned (slope,  $F_{1,67}=2.05$ ,  $P=0.14$ , intercept,  $F_{2,67}=2.37$ ,  $P=0.10$ ) and not-burned watersheds  
852 (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  
853 response in forage kinetics at feeding stations in frequently-burned watersheds and in not-burned  
854 watersheds, which exhibit similar patterns of productivity. In infrequently-burned watersheds, a  
855 significant interaction between season and grass biomass influenced intake rate (ANCOVA,  
856 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  
857 slope of the relationship between intake rate and grass biomass differed between seasons. At  
858 infrequently-burned sites, intake rate differed significantly between growing and transitional  
859 seasons independent of grass biomass with intake rate during the growing season increasing at a  
860 greater rate relative to biomass than during the transitional season. This result met our prediction  
861 that a behavioral response in foraging kinetics would occur where a pulse of available nutrients  
862 was utilized following infrequent fire. Seasonal intake rate relative to feeding station grass

863 biomass levels remained similar ( $F_{4, 198}=0.64, P=0.64$ ). Overall, the mean intake rate was similar  
864 among grassland types: frequently-burned ( $\bar{x}\pm 95\% \text{ CI}= 19.1 \pm 2.5 \text{ g min}^{-1}$ ), infrequently-burned  
865 ( $\bar{x}=19.0 \pm 3.2 \text{ g min}^{-1}$ ), and not-burned watersheds ( $\bar{x}=21.7 \pm 2.6 \text{ g min}^{-1}$ ; Fig. 4c). Results of  
866 feeding measures across seasons by burn treatment with increasing live grass mass, feeding  
867 measures across seasons irrespective of burn treatments, and patterns in grazing activity are  
868 summarized in Appendix B.

## 869 **DISCUSSION**

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

### 883 *Fine-scale foraging behavior and fire frequency*

884 Fine-scale feeding behaviors ultimately contribute to coarse-scale foraging decisions and  
885 landscape distribution by large herbivores (Senft et al. 1987). We assessed how fine-scale

886 feeding behaviors by bison in recently-burned watersheds responded to fire frequency in tallgrass  
887 prairie. Observational and experimental data indicate that variation in fire frequency plays a  
888 significant role for understanding seasonal changes in large herbivore foraging behavior.  
889 Moreover, the time since last burn in watersheds with different burn histories is a critical link  
890 between fire and grazing and is an important driver behind variation in feeding measures at this  
891 fine scale. Our results indicate that bison feeding responses to forage availability and quality at  
892 the feeding station are influenced by fire-induced transient maxima dynamics.

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

909 McArt et al. 2009), or allocate more time for raising young, regulating thermal balance or  
910 maintaining social status. If true, the time saved by selecting a diet that maximizes short-term  
911 intake should also improve fitness (Fortin et al. 2002).

912 *Response to transient maxima resource availability*

913 The TMH complements the FMH by providing a useful mechanistic framework for  
914 understanding grazing herbivores in nutritionally heterogeneous, mesic grasslands; the pulse in  
915 forage quantity and quality made available by periodic burning corresponds to patterns of large  
916 herbivore use during the early growing season (Archibald and Bond 2004). Periodic fire is  
917 essential for the development and maintenance of tallgrass prairie ecosystems and has strong  
918 effects on productivity (Briggs and Knapp 1995, Blair 1997) and nutrient cycling rates (Seastedt  
919 and Ramundo 1990, Ojima et al. 1994). Throughout the study period, standing crop of grass  
920 biomass was generally lower in infrequently-burned watersheds that burned in the spring of that  
921 year (late March), followed by intermediate levels of grass biomass in frequently-burned  
922 watersheds also burned in the spring of that year, with the highest grass biomass observed in  
923 watersheds not burned the previous spring (Fig. 2a). This observation is consistent with the FMH  
924 that posits grasslands are maintained by aggregations of large herbivores in a state of low to  
925 intermediate quantity (Fryxell 1991, Hebblewhite et al. 2008). Furthermore, bison in tallgrass  
926 prairie are sometimes known to use recent burns even after they are virtually devoid of  
927 vegetation (Mitchell et al. 1996, Schuler et al. 2006). Foraging at locations offering low to  
928 intermediate levels of vegetation, where foragers tradeoff food digestibility and availability  
929 corresponds to expectations where herbivores maximize energy and nutrient intake rate (Fryxell  
930 1991, Bergman et al. 2001,). Fine-scale foraging behavior by the KPBS bison herd can be  
931 viewed as a tradeoff between forage quality and quantity where fire attracts aggregations of large



932 herbivores, especially to periodically-burned watersheds, and subsequent prevention of forage  
933 maturation by grazing in burned watersheds guides the spatio-temporal distribution of grazers as  
934 long as regrowth is possible. Although the generality of these results to other grasslands remains  
935 to be tested we anticipate this interaction between non-equilibrial forage resources and ungulate  
936 foraging behavior is a key driver for ungulate distributions in fire-prone systems generally.

937 *Bison nutrient acquisition in the tallgrass prairie*

938 Ungulates increase forage intake following periods of low food availability to regain body  
939 condition in both arctic and alpine systems and to compensate for a decline in food quality  
940 during the dry season (Van der Wal et al. 2000, Hamel and Côté 2008). In arid systems, equids  
941 reduce intake rate during the dormant season when plant greenness is lowest (St-Louis and Côté  
942 2012) although the behavioral mechanism behind reduced intake rate is poorly understood and  
943 has not been addressed in temperate systems with an intact fire-grazer interaction. In the  
944 Serengeti, Thomson's gazelles (*Gazella thomsoni thomsoni*) compensate for unfavorable  
945 temporal variation in resource availability (e.g. due to depletion of quality resources) at small  
946 spatial scales (Fryxell et al. 2005). In bison, we found that bite quality during the growing season  
947 was positively associated with plant nutrients and bite mass was negatively associated with plant  
948 structural properties. Late summer bite quality and bite mass were positively associated with  
949 plant digestibility and plant structural properties, respectively. The inverse relationship between  
950 bite mass and plant structural properties observed in the growing season differed from feeding  
951 station behavior during late summer when both average short-term forage intake and nutrient  
952 intake rate were minimal. This suggests bison were compensating for low foliar nutrient  
953 availability by increasing bite mass which concomitantly reduced mean intake rate in the  
954 dormant season. This pattern was most pronounced during 2013 when forage quality did not

955 increase in late summer with increased precipitation as was observed in 2012 when precipitation  
956 was markedly reduced.

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

### 973 *Synthesis*

974 The interplay between fire-induced nutritional enhancement of forage and temporal variation in  
975 feeding behavior suggests that fine-scale foraging is an integral component of understanding the  
976 role of fire on bison distribution and foraging activity in this nutritional landscape. The observed  
977 increase in bite mass and instantaneous intake rate of individual bison during the growing season

978 in periodically burned grassland indicates the “pulse” of N availability and ANPP driven by fire  
979 in previously light-limited, unburned grassland modulated ungulate foraging behavior. Thus, the  
980 importance of fire in controlling grazer behavior at the feeding station scale was temporally  
981 contingent upon fire frequency, the elapsed time since the last burn, and the timing of plant  
982 productivity pulses. Whether such behavioral responses occur in grasslands where burning  
983 occurs at other times of the year remain unclear.

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

990         Our investigation of fine-scale foraging behavior in mesic grasslands when fire results in  
991 markedly different nutritional value also provides baseline information for forecasting animal  
992 foraging behavior in other fire-prone ecosystems. While grassland fires are influential in  
993 generating large herbivore distributions in and of themselves (Sensenig et al. 2010, Allred et al.  
994 2011*a,b*), we conclude that the fine-scale behavioral mechanism associated with foraging at the  
995 feeding station is also responsible for herbivore affinity to recently-burned grassland. Our data  
996 suggest that fire-induced heterogeneity in vegetation quality may be an important landscape scale  
997 process that helps promote nutrient attainment in a historically important native grazer and  
998 illustrates the utility of linking optimal foraging theory with insights from consumer resource and  
999 fire ecology.

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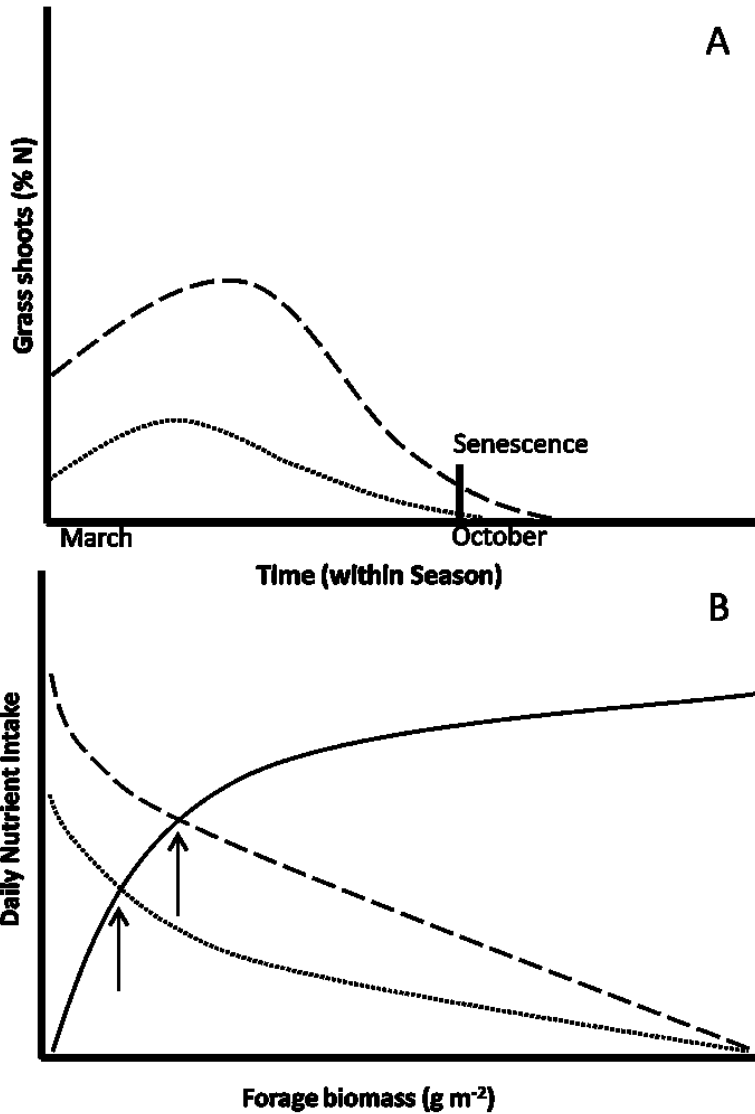
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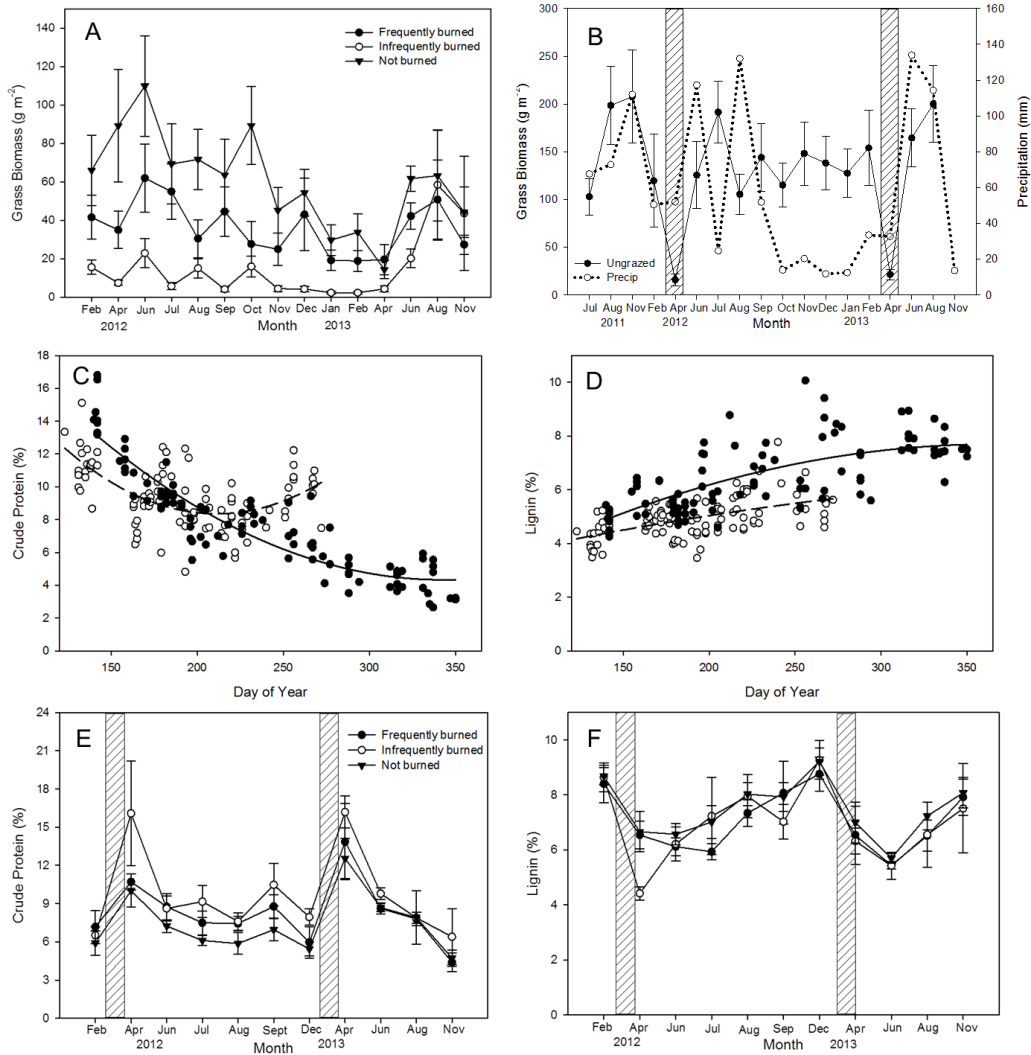


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1207 **Figure 2-1. (A) Graphical illustration of the transient maxima hypothesis, which predicts**  
1208 **transient “pulses” of plant N availability (solid line) that are greater than the average N**  
1209 **availability in tallgrass prairie that is annually-burned (fine-dotted line) sites as a result of**  
1210 **increased light availability and gradually declining N availability as plants senesce. Note**  
1211 **that the figure illustrates patterns of change over a post-spring burn period in a year. (B)**  
1212 **Schematic showing general mechanisms of the forage maturation hypothesis (FMH)**  
1213 **complemented by the transient maxima hypothesis (TMH). Foraging constraints of daily**

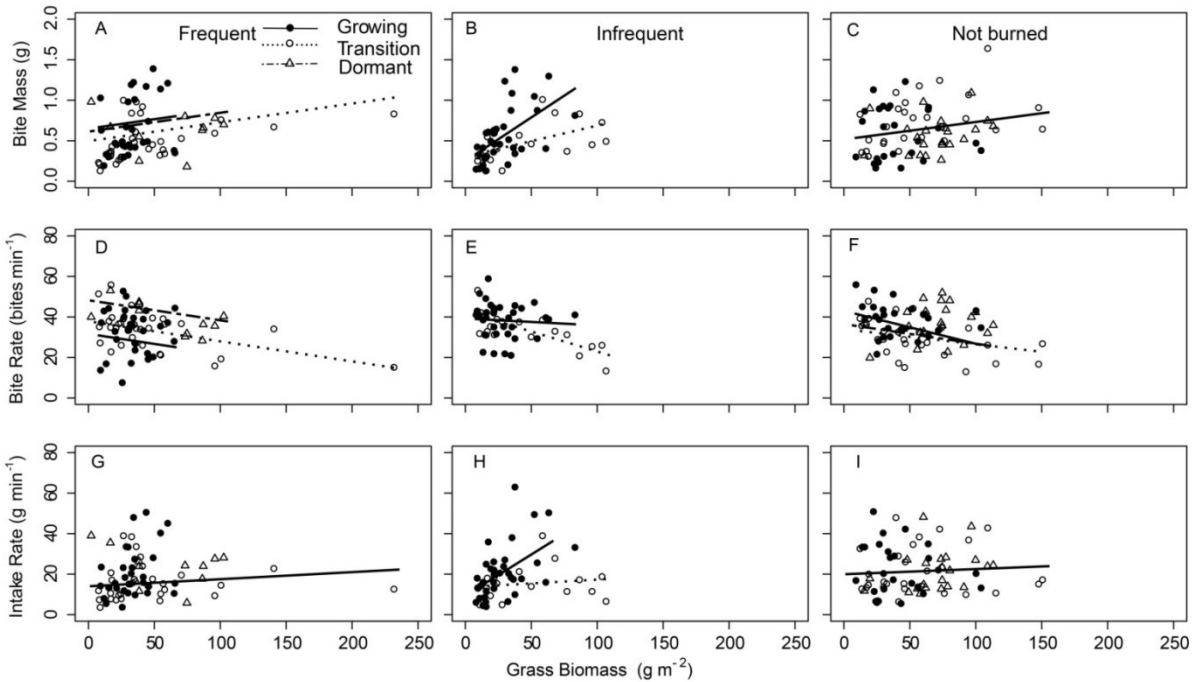
1214 cropping (solid line) and digestion in frequently-burned (fine-dotted line) and infrequently-  
 1215 burned (dashed line) grassland that result in a foraging optima (arrows) at low-to-  
 1216 intermediate biomass. (Modified from Fryxell 1991).  
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 1220 **Figure 2-2. Seasonal variation in forage properties at Konza Prairie, Manhattan, KS,**  
 1221 **U.S.A. (A) Variation ( $\pm 95\%$  CI) in the availability of standing grass biomass recorded**  
 1222 **along a 6m transect and averaged for upland and lowland areas in the three burn**  
 1223 **treatments used by bison. (B) Variation in grass biomass in frequently burned, ungrazed**  
 1224 **grasslands recorded along a 6m transect and averaged for upland and lowland**  
 1225 **topographical areas, 2011-2013. Data are shown with the monthly rainfall pattern; shaded**  
 1226 **bars indicate when burning occurred. (C) Percentage of crude protein in grass leaf tissue at**  
 1227 **feeding stations. (D) Percentage of lignin in grass leaf tissue at feeding stations. (E)**  
 1228 **Seasonal variation in the crude protein content of grass in the three grassland types**  
 1229 **available to bison recorded along a 6m transect and averaged for upland and lowland**

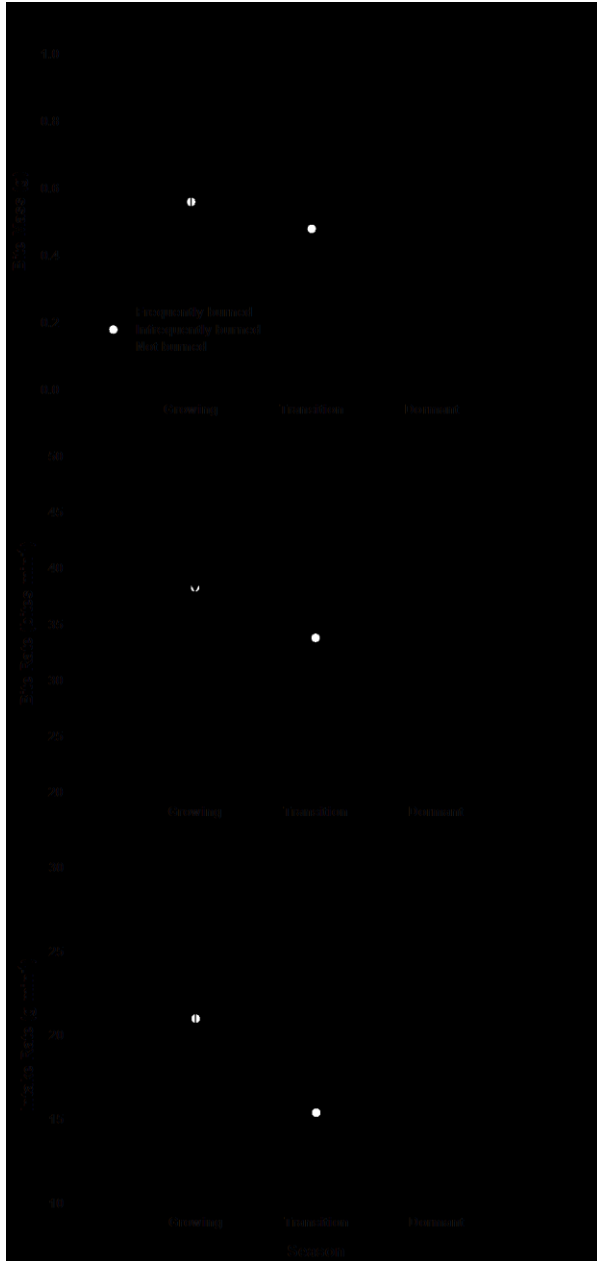
1230 **topographical areas. (F) Seasonal variation in the lignin content of grass in the three**  
1231 **grassland types.**

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1238 **Figure 2-3. Functional relationship of bite mass in relation to grass biomass at feeding**  
1239 **stations. (A) Frequently-burned, (B) infrequently-burned, and (C) not-burned grasslands**  
1240 **in the different seasons. Similar bite mass was obtained in (C) not-burned grasslands**  
1241 **throughout the three seasonal periods, so a single line was fitted to these data. Functional**  
1242 **relationship of bite rate in relation to grass biomass at feeding stations of (D) frequently-**  
1243 **burned, (E) infrequently-burned, and (F) not-burned grasslands in the different seasons.**  
1244 **Functional relationship of intake rate in relation to grass biomass at feeding stations of (G)**  
1245 **frequently-burned, (H) infrequently-burned, (I) not-burned grasslands in the different**  
1246 **seasons. Similar intake rate were obtained in (G) frequently-burned and (I) not-burned**  
1247 **grasslands lands throughout the three seasonal periods, so a single line was fitted to these**  
1248 **data.**

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1256 **Figure 2-4. Seasonal changes ( $\pm$ SE) in (a) mean bite mass; (b) mean bite rate; (c) mean**  
 1257 **intake rate across burn treatments by plains bison pooled across 2012-2013.**

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1261 **APPENDIX A**

1262 *Temporal Variation in Grassland-type Biomass*

1263 Permanent sampling stations were established in the lowland and upland areas of all bison-  
1264 grazed watersheds as well as two ungrazed watersheds (1D and K1B) located adjacent to the  
1265 bison unit to measure variation in monthly vegetation biomass and height over the course of this  
1266 two year study. The two ungrazed, annually burned watersheds were sampled to estimate  
1267 differences in forage complexity between grazed and non-grazed units. Six swaths of 0.1 x 1 m  
1268 of vegetation were clipped in both upland and lowland topographical areas. To avoid resampling  
1269 recent plots, each new sample was located randomly approximately 5 m from samples taken the  
1270 previous month. Twenty grass canopy height measurements were made along a 30 m transect  
1271 running parallel to the clipped vegetation swath. Clipped samples were sorted into graminoids,  
1272 forbs, and litter and each fraction dried and weighed. Vegetation biomass and grass height  
1273 measurements were collected every two months during the non-growing season. For grazed  
1274 watersheds, two of the six 0.1 x 1 m graminoid samples were randomly selected for nutrient  
1275 analysis.

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1285 **Table A.1. 1. Results from a mixed linear model ANOVA for the effects of seasonal period, burn frequency, and year on total**  
 1286 **grass biomass as well crude protein content of grass shoots at Konza Prairie Biological Station, 2012-2013.**

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			Grass		Crude Protein	1289
Effect	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Season	2, 7.5	7.54	0.02	2, 6.7	0.44	0.65
Burn Frequency	2, 22.7	8.11	0.002	2, 21.1	3.43	0.05
Season*Burn Frequency	4, 22.6	0.83	0.52	4, 21.2	0.18	0.94
Year	1, 22.2	0.07	0.78	1, 9.8	0.16	0.70
Season*Year	2, 25.0	4.25	0.02	2, 12.1	3.67	0.06
Burn Frequency*Year	2, 22.7	3.41	0.05	2, 21.1	0.64	0.53
Season*Burn Frequency*Year	4, 22.6	0.30	0.87	4, 21.2	0.23	0.91

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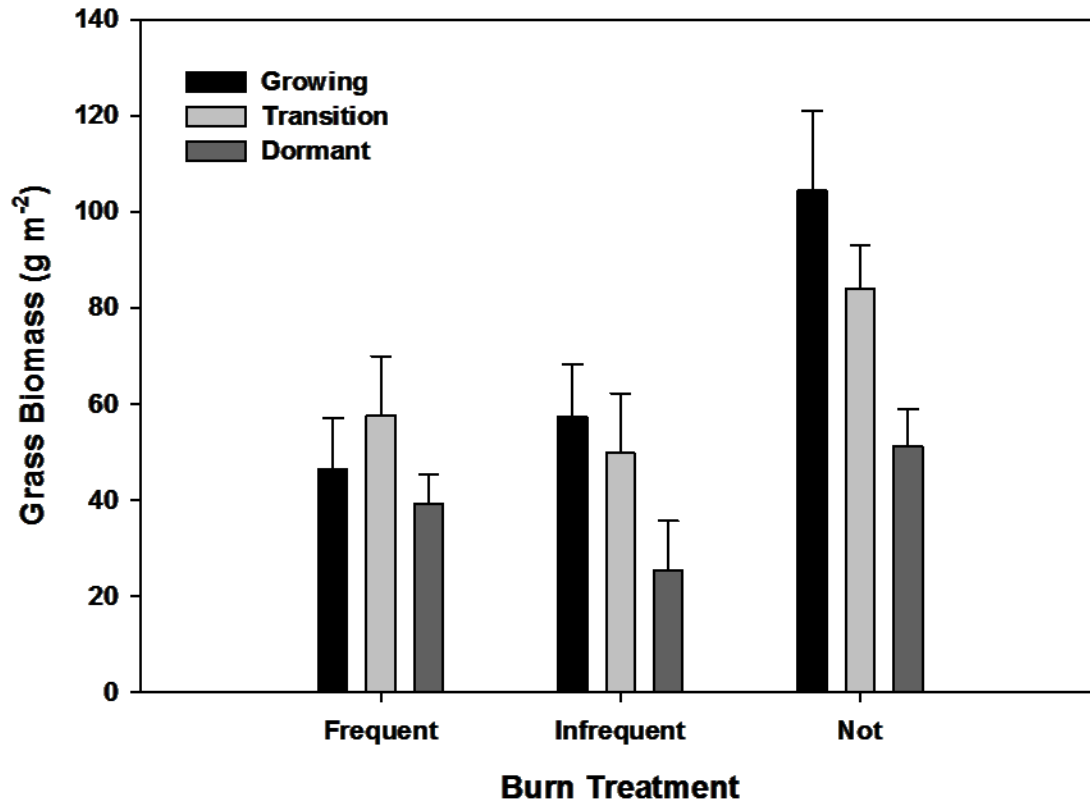
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1307 **Figure A.1 1. Total grass biomass from permanent sampling stations pooled across 2012-**  
1308 **2013 for each for each burn treatment by seasonal period at Konza Prairie Biological**  
1309 **Station, Manhattan, KS, U.S.A.**

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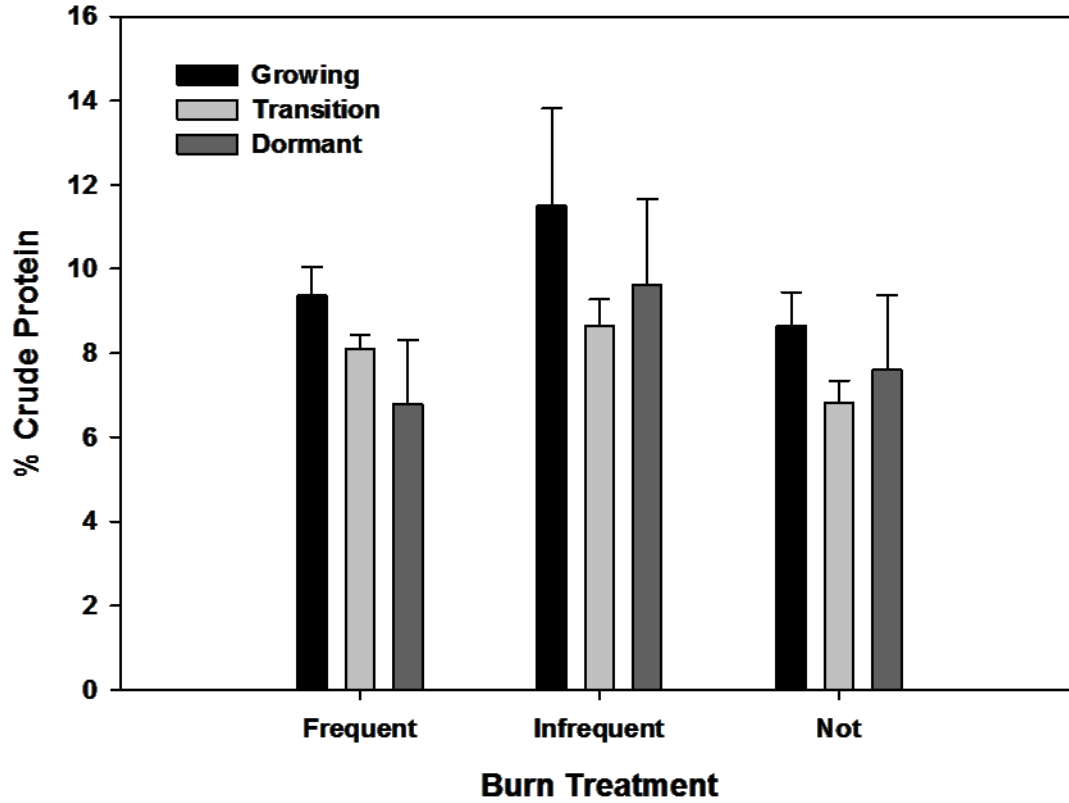
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1325 **Figure A.1 2. Crude protein content of grass leaf tissue from permanent sampling stations**  
1326 **pooled across 2012-2013 for each for each burn treatment by seasonal period at Konza**  
1327 **Prairie Biological Station, Manhattan, KS, U.S.A.**

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1338 **APPENDIX B**

1339 *Functional Responses to Feeding Station Live Biomass*

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1341 *Bite mass*

1342 To test whether this trend between bite mass and available forage was observed in relation to live  
1343 tissue availability by seasonal period we conducted ANCOVA with live grass mass. In all three  
1344 treatments, a significant interaction between season and live grass mass did not occur in the bite  
1345 mass ANCOVA ( $P>0.1$ ); therefore we did not test whether the slope of bite mass with increasing  
1346 live grass mass differed between seasons.

1347 *Bite rate*

1348 In frequently- and not-burned watersheds, a significant interaction between season and live grass  
1349 mass did not occur in the bite rate ANCOVA ( $P>0.1$ ); therefore we did not test whether the slope  
1350 of bite rate with increasing live grass mass differed between seasons in these treatment types. A  
1351 marginally significant interaction between season and live grass mass did occur for bite rate  
1352 (slope,  $F_{1,50} = 3.48$ ,  $P=0.07$ , intercept,  $F_{1,50}=3.92$ ,  $P=0.05$ ) in infrequently-burned watersheds  
1353 with transitional season bite rate decreasing at a greater rate than the growing season.

1354 *Intake rate*

1355 In frequently- and not-burned watersheds, a significant interaction between season and live grass  
1356 mass did not occur in the intake rate ANCOVA ( $P>0.1$ ); therefore we did not test whether the  
1357 slope of intake rate with increasing live grass mass differed between seasons in these treatment  
1358 types. A significant interaction between season and live grass mass did occur for bite rate (slope,  
1359  $F_{1,50} = 5.5$ ,  $P=0.02$ , intercept,  $F_{1,50}=1.2$ ,  $P=0.28$ ) in infrequently-burned watersheds with  
1360 transitional season intake rate decreasing at a greater rate than the growing season.

1361 Overall, we found significant differences in slopes of seasonal bite rate and intake rate  
1362 with increasing total grass mass and live grass mass with transitional season rates decreasing at a  
1363 greater rate than the growing season only in infrequently-burned watersheds.

1364 *Seasonal Trends in Feeding Measures*

1365 Mean bite mass increased with increasing grass biomass during spring in both years with an  
1366 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  
1367 (Fig. B1a). Thereafter, mean bite mass decreased to 0.45 g in 2012, whereas in 2013 it rose to  
1368 0.71 g until October. Mean bite rate remained between 33 and 38 bites  $\text{min}^{-1}$  from April to July  
1369 in both years (Fig. B1b). Thereafter, mean bite rate remained at  $\sim 35$  bites  $\text{min}^{-1}$  in 2012, whereas  
1370 in 2013 it decreased to 22 bites  $\text{min}^{-1}$  in August then rose to  $\sim 38$  bites  $\text{min}^{-1}$ .

1371 The mean grass intake averaged across burn types increased during spring in both years  
1372 from 12 g  $\text{min}^{-1}$  to 27 g  $\text{min}^{-1}$  in 2012 and from 8 to 11 g  $\text{min}^{-1}$  in 2013. Thereafter, grass intake  
1373 rate decreased to 15 g  $\text{min}^{-1}$  in 2012, whereas in 2013 it rose to 26 g  $\text{min}^{-1}$  during the transitional  
1374 months of September and October (Fig. B1c). In 2013, the larger mean bite mass made possible  
1375 by the generally more productive growing season led to an increase in the mean grass intake rate  
1376 to over 19 g  $\text{min}^{-1}$  from September to November. Overall grass intake rate increased with grass  
1377 biomass toward an asymptote of 31.4, 21.9, and 22.4 g  $\text{min}^{-1}$  during the growing ( $F_{1,90}=9.2$ ,  
1378  $P=0.003$ ), transitional ( $F_{1,77}=5.93$ ,  $P=0.017$ ), and dormant seasons, respectively ( $F_{1,35}=4.9$ ,  
1379  $P=0.03$ ) (Fig. B2).

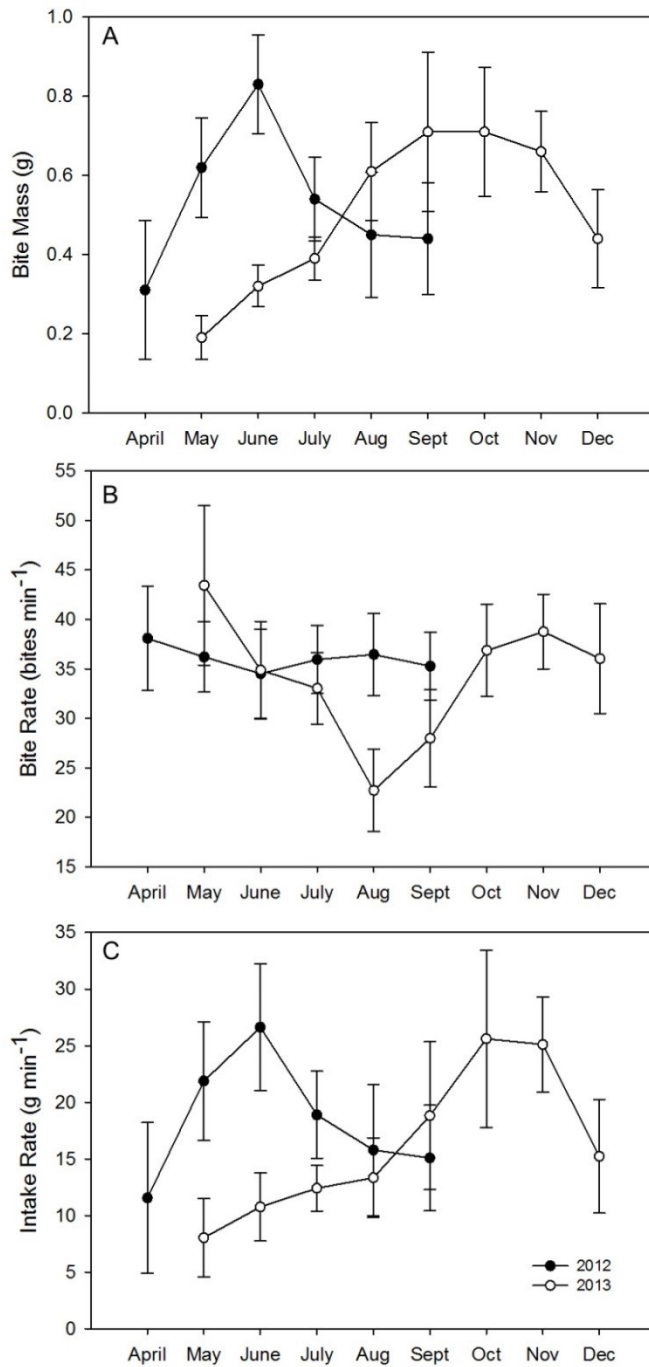
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1386 **Figure B.1. 1. Monthly changes ( $\pm$ SE) in (a) mean bite mass; (b) mean bite rate; (c) mean**  
 1387 **intake rate by plains bison in 2012-2013 at Konza Prairie Biological Station, Manhattan,**  
 1388 **KS, U.S.A.**

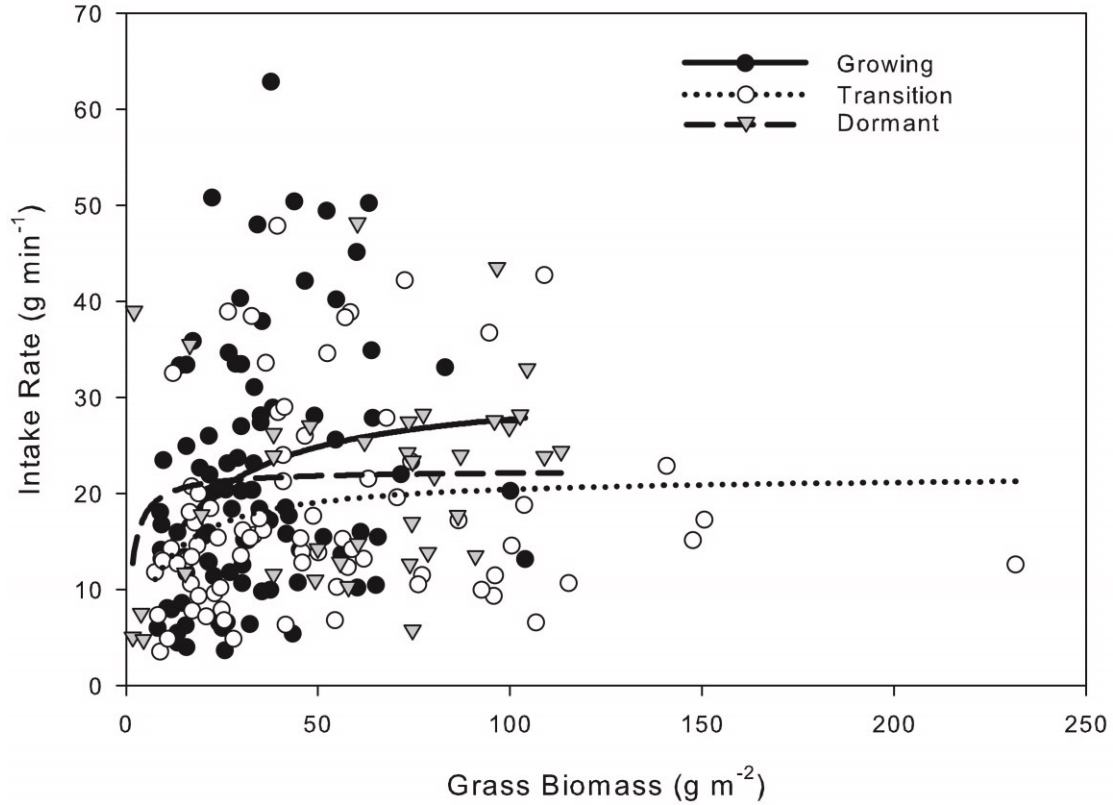
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1395 **Figure B.1. 2. Non-linear relation between overall bison intake rate and feeding station**  
1396 **biomass during the growing (April to mid-July), transitional (mid-July to early October),**  
1397 **and dormant (mid-October to late March) seasons at Konza Prairie Biological Station,**  
1398 **Manhattan, KS, U.S.A.**

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1408 *Multivariate Methods*

1409 Redundancy Analysis (RDA) was used to represent vegetation characteristics as a linear  
1410 function of foraging behavior during the early growing season(April-June) and late summer (15  
1411 Aug-Oct); these periods reflect grass developmental and early-senescence periods when variation  
1412 in grass quality is most pronounced. Values of the vegetation characteristic dataset were  
1413 centered and standardized using z-transformation. Permutation tests were used to test the  
1414 significance of the relationships between vegetation characteristics and foraging behavior  
1415 variables (Ter Braak 1995). Canonical ordination analyses were performed using function *rda* in  
1416 the *labdsv* package for Program R (v2.15).

1417 Associations between vegetation characteristics and the foraging behavior variables were  
1418 deduced from the RDA biplot. In RDA, response and explanatory variables are represented as  
1419 vectors in a multidimensional space and the relative positions of these vectors indicate  
1420 correlations (Makarenkov and Legendre 2002, Borcard et al. 2011). The ordination biplot  
1421 reduced the multi-dimensional space to the two most differentiating dimensions. When the angle  
1422 between the vectors of vegetation characteristics and foraging behavior variables in the  
1423 horizontal plane was  $<45^\circ$  and  $>135^\circ$ , we inferred that variables were positively and negatively  
1424 correlated, respectively. No correlation between variables was inferred when the enclosed angle  
1425 lay between  $45^\circ$  and  $135^\circ$ . Significant factors were identified by a stepwise forward selection  
1426 procedure.

1427 Results

1428 In spring, bite mass and bite quality averaged across years were associated with grass structure  
1429 and grass chemistry, respectively (RDA, Fig. B3a). Bite mass was negatively associated with

1430 grass structure, while bite quality was positively associated with grass nutrient content. Bite mass  
1431 ( $P=0.01$ ) and bite quality ( $P=0.01$ ) were significantly correlated with forage nutrient  
1432 concentrations and physical structure (Monte Carlo Permutation test), but bite rate was not  
1433 significant ( $P=0.46$ ) nor was it associated with bite mass or bite quality (Table B1). In late  
1434 summer, bite mass, bite quality, and bite rate were associated with various measures of  
1435 vegetation structure and grass foliar chemistry (RDA, Fig. B3b). The vectors representing bite  
1436 mass and bite rate pointed to opposite quadrants of the RDA biplot, suggesting an inverse  
1437 relationship between these variables and vegetation structure (Table B1). Bite quality was  
1438 positively associated with grass nutrient contents. Bite mass ( $P=0.01$ ), bite quality ( $P=0.01$ ), and  
1439 bite rate ( $P=0.01$ ) were significantly correlated with vegetation nutrients and structure (Monte  
1440 Carlo permutation test).

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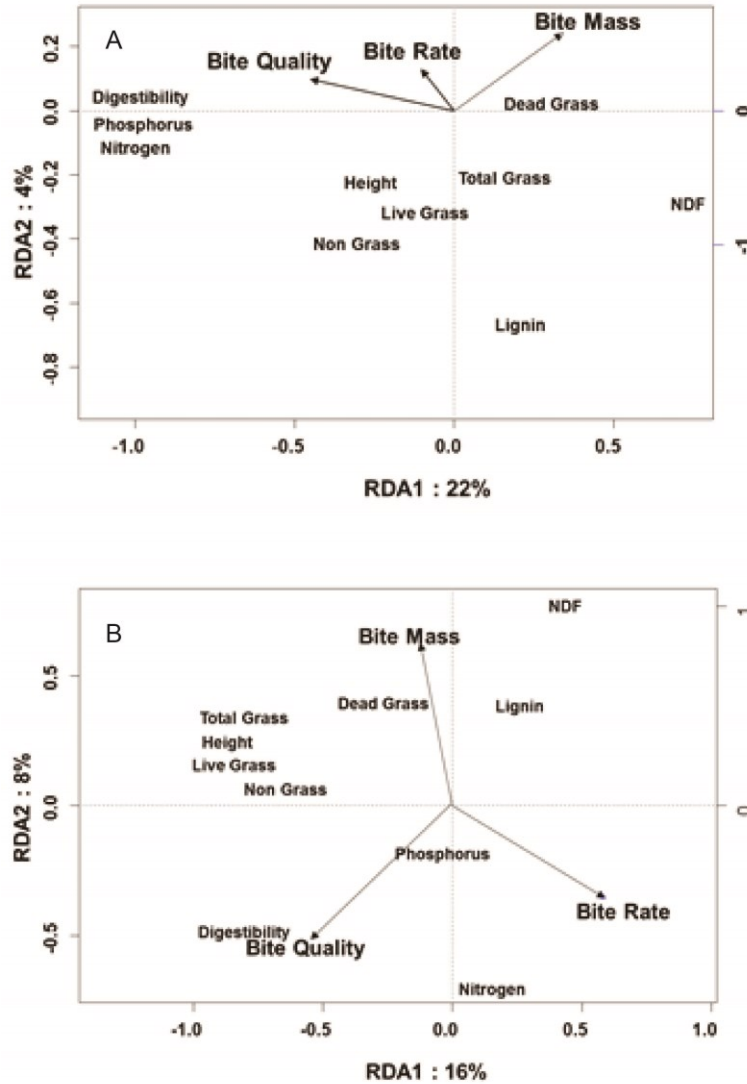
1453

1454 **Table B.1 1. List of vegetation characteristics likely to be correlated with bite size and with**  
 1455 **bite quality as indicated by the spring and late summer RDA biplots (Fig.B1, B2) and the**  
 1456 **directions of the indicated correlation at Konza Prairie Biological Station, Manhattan, KS,**  
 1457 **U.S.A.**

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Bite Mass			Bite Quality			Bite Rate		
	Spring	Late Summer		Spring	Late Summer		Spring	Late Summer
Vegetation characteristic	Direction of correlation		Vegetation characteristic	Direction of correlation		Vegetation characteristic	Direction of correlation	
Total grass mass	-	+	Grass digestibility	+	+	Total grass mass	-	-
Live grass	-	+	%N	+	+	Live grass	-	-
Dead grass	+	+	%P	+	+	Dead grass	-	-
Height	-	+	%NDF	-	-	Height	-	-
No-grass mass	-	+	Lignin	-	-	No-grass mass	-	-
%NDF		+	Total grass mass	-		%N		+
Lignin		+				%NDF	-	

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 1462 **Figure B.1. 3. (A) RDA biplot showing the relationship between foraging behavior**  
 1463 **variables and vegetation characteristics for bison grazing at Konza Prairie during the**  
 1464 **spring season (1 April to 20 June). Of the total variance in vegetation characteristics, 26%**  
 1465 **could be explained by foraging behavior variables. Of this variance, 22% is explained by**  
 1466 **the horizontal axis (axis 1 of the RDA), and another 4% by the vertical axis (axis 2). (B)**  
 1467 **RDA biplot showing the relationship between foraging behavior variables and vegetation**  
 1468 **characteristics for bison grazing during the late summer season, 1 August to 7 October. Of**  
 1469 **the total variance in vegetation characteristics, 24% could be explained by foraging**  
 1470 **behavior variables of which 16% is explained by axis 1 and another 8% by axis 2. Arrows**  
 1471 **indicate positions of foraging behavior variables.**

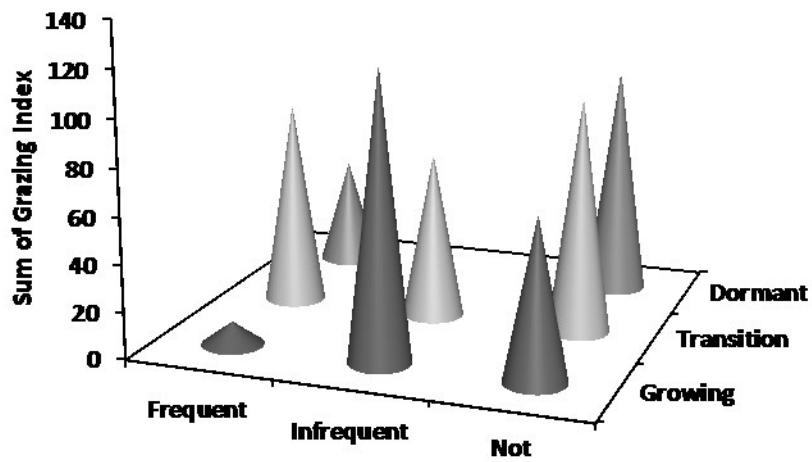
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1476 Grazing Index  
1477 *Grazing Activity Methods*  
1478 An index of recent grazing activity established by Joern (2005) was used at forage sampling sites  
1479 to estimate recent bison grazing. Joern (2005) classified an index of recent grazing activity based  
1480 on an ordinal scale: 0 (ungrazed sites; no evidence of recent grazing because bison never  
1481 present); 1 (no recent grazing but site located in grazed area); 2 (small amount of grazing  
1482 evident, probably by one or two animals); 3 (moderate grazing from many animals; many grazed  
1483 patches interspersed in ungrazed matrix, and evidence of relatively fresh dung); 4 (extensive  
1484 grazing, but grazing lawn not yet developed; evidence of large herd grazing activity, including  
1485 recent dung); and 5 (extensive grazing with much return grazing leaving a closely cropped site  
1486 and little vertical structure).

#### 1487 Results

1488 Mean grazing index for burn treatments were not different ( $p=0.53$ ), while mean grazing index  
1489 differed between seasons ( $p=0.001$ ) with growing season having a lower index than the dormant  
1490 season but not transitional period. A significant interaction ( $p=0.01$ ) between burn frequency and  
1491 season revealed unburned watersheds in the growing season had a lower index than in the  
1492 dormant season. Sum of grazing index per sampling event indicate feeding stations in  
1493 infrequently burned watersheds had the greatest grazing activity during the growing season (Fig.  
1494 B4).

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1497 **Figure B.1. 4. Sum of grazing index across season and burn treatments pooled from all**  
 1498 **feeding station sampling events at Konza Prairie Biological Station, Manhattan, KS, U.S.A.**

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1521        **Chapter 3 - Foraging decisions at the feeding-site and landscape**  
1522                    **scale in nutritionally heterogeneous grassland**

1523        **ABSTRACT**

1524        When foraging in seasonal environments, herbivores select among plant patches that vary in  
1525        standing crop and nutritional quality at several spatial and temporal scales. Although ruminants  
1526        can maintain basic metabolic activity at marginal levels of forage quality, foraging tactics may  
1527        shift to meet maintenance requirements during periods of plant dormancy. We investigated fine-  
1528        and coarse-temporal scale foraging tactics of plains bison (*Bison bison bison*) throughout two  
1529        growing seasons, hypothesizing that (a) forage quality will influence feeding-site selection at the  
1530        fine, patch-scale, and (b) at the coarse, landscape-scale, avoidance of mature forage will decay as  
1531        the growing season progresses. We investigated foraging behavior at two temporal scales  
1532        throughout the growing season in a fire-dependent landscape – short-term foraging decisions in  
1533        terms of feeding-site selection and coarse-scale foraging decisions in terms of time spent feeding  
1534        over the growing season. In burned watersheds, bison feeding sites had higher a grass:forb ratio  
1535        and forage quality, and lower forage quantity than measured at nearby random sites in the same  
1536        habitat, especially in burned watersheds. Over the growing season, bison spent more time  
1537        feeding in burned watersheds, and the diurnal time spent feeding increased from spring to fall as  
1538        forage quality declined. An isotopic record of seasonal diet change from bison hair corroborated  
1539        our fine-and coarse-scale findings that bison were moving into primarily unburned areas of high  
1540        vegetation structure with C<sub>3</sub>, cool-season graminoids later in the season after C<sub>4</sub> plants senesced.  
1541        Our detailed foraging observations and stable carbon isotope records indicate that bison  
1542        minimize time spent foraging by grazing in high-nutrient, burned grassland during the growing



1543 season and shift foraging tactics by grazing in unburned grassland to meet nutrient requirements  
1544 during periods of plant dormancy.

1545 Keywords: *Bison bison*, Feeding-site Selection, Foraging, Mesic grassland, Scale, Stable Isotope

## 1546 **INTRODUCTION**

1547 For large mammalian herbivores, the spatial distribution of vegetation standing stock (stock or  
1548 biomass) and nutritional quality are fundamental components affecting foraging behavior and  
1549 resource-selection tactics (Wilmshurst et al. 1999a, b). Patterns of resource use reflect a  
1550 hierarchy of scale-dependent limiting factors by foraging mammalian herbivores (Rettie and  
1551 Messier 2000, St-Louis and Côté 2014). As plant cellulosic content increases over a growing  
1552 season, plant nutritional quality in guiding foraging decisions can vary in a spatially dependent  
1553 manner (Spalinger and Hobbs 1992, Fortin et al. 2002, Wallace and Crosthwaite 2005). In  
1554 grassland ecosystems, forage abundance and quality are often inversely related because plant  
1555 maturation increases fiber content in stems and leaves, thus lowering forage digestibility  
1556 (McNaughton 1985, Van Soest 1994). Consequently, plants in low-stature vegetation patches  
1557 such as in the early growing season may be more digestible than plants in patches with high  
1558 vegetation stature (Miller et al 1965). On the other hand, a mosaic of heterogeneous vegetation  
1559 patches may be created with burning in response to simultaneous increased soil nutrient  
1560 availability and release from light limitation, which can combine to increase both forage quantity  
1561 and quality (Seastedt and Knapp 1993) especially in mesic grasslands. Herbivores thus face  
1562 choices when foraging in a variable landscape of forage quantity and quality across several  
1563 spatio-temporal scales, potentially leading to scale-dependent resource use patterns (Drescher et  
1564 al. 2006, Hebblewhite et al 2008, St-Louis and Côté 2013).

1565           Bovids can maintain metabolic function and cellulosic digestion at marginal levels of  
1566 forage quality because nutrients from plants are extracted efficiently, in part due to the generally  
1567 slow passage rate of plant materials in their digestive tract (Gilchrist and Clark 1957, Peden et al.  
1568 1974). In seasonal environments, forage resources are generally abundant, yet dependent on  
1569 annual rainfall patterns. Therefore, resource selection tactics by foraging herbivores should  
1570 reflect a strategy to maximize nutrient intake and minimize digestion constraints (Van der Wal et  
1571 al. 2000). We expect grassland herbivores to forage in areas with high accessibility to young  
1572 forage tissue to minimize foraging and digestion constraints (Fryxell 1991). Investigating  
1573 patterns of patch selection will provide insight regarding the relative importance of forage  
1574 availability and quality to modulate landscape-level distributions of ungulates throughout a year  
1575 as patch selection drives choice of landscape features and foraging tactics may shift in response  
1576 to availability of resources in the landscape.

1577           Recently, quantitative information regarding bison grazing patterns in response to  
1578 recently-burned grasslands has been primarily studied in tallgrass prairies, which are productive  
1579 mesic grasslands in the North American continent (Vinton et al. 1993, Coppedge and Shaw  
1580 1998, Knapp et al. 1999, Allred et al. 2011a, b; 2013, Chapter Four, this thesis). In these studies,  
1581 bison affinity for nutrient-rich, post-fire plant regrowth has been shown to drive their distribution  
1582 across the landscape in space and time. However, little is known about how the increased forage  
1583 quality and quantity associated with burned grassland will affect the behavioral mechanisms  
1584 underlying bison attraction to recently-burned grassland. Finding and handling food normally  
1585 dominates the activity budgets of ruminants (Beier and McCullough 1990), so an understanding  
1586 of feeding-site selection and activity budgets of a wild bovid in fire-dependent, productive mesic

1587 grasslands (e.g. tallgrass prairie) should shed light on how availability of forage resources of  
1588 varying quality modulate the fire-grazer interaction at multiple spatiotemporal scales.

1589         In this study, we investigated factors influencing foraging behavior by plains bison in  
1590 tallgrass prairie that is managed with spring-season prescribed-burning. Our main objectives  
1591 were twofold: (1) to assess the effects of vegetation abundance and quality on feeding-site  
1592 selection in bison, and (2) to determine if coarse-scale foraging behavior differs among burn  
1593 treatments in response to whether they were burned or not early in the growing season. We  
1594 evaluated how forage quality and quantity influenced the foraging behavior of bison at three  
1595 temporal scales: (a) feeding site selection patterns at the patch-level, the intermediate level  
1596 between the feeding-station and landscape levels in the ecological hierarchy of foraging in large  
1597 herbivores (fine scale; Senft et al. 1987), (b) the percentage of time spent feeding per week by  
1598 bison groups relative to total activity budgets (intermediate scale), and (c) shifts in diet selection  
1599 based on isotopic record of C<sub>3</sub>-C<sub>4</sub> plant composition over a year (coarse scale).

1600         At the fine, temporal scale to assess the effect of vegetation abundance and forage quality  
1601 on patterns of feeding site selection, we assessed selection among three vegetation groups (i.e.  
1602 graminoids, forbs, and litter). Crude protein content of forage at feeding sites was used to index  
1603 plant quality. Observations were made during summer and fall to assess seasonal variability in  
1604 forage biomass and quality as they affect fine-scale, short-term foraging decisions. In a previous  
1605 study, we showed that bison intake of forage increased at a greater rate in the early growing  
1606 season than during the transitional mid-summer season only in recently-burned, highly-nutritious  
1607 and digestible grassland (Chapter 2; Raynor et al. 2015). We therefore hypothesized that low-to-  
1608 intermediate forage abundance would be a main factor driving forage selection at the feeding  
1609 site. Accordingly, we hypothesized that (a) patches with low-to-intermediate vegetation biomass

1610 should be used in greater proportion than their relative availability within the study area,  
1611 especially when plants are capable of regrowth, and (b) active feeding sites should contain forage  
1612 with higher crude protein content than that measured in forage from nearby, randomly selected  
1613 sites that were not grazed during short-term, group foraging bouts. Moreover, (c) as overall plant  
1614 biomass increases but quality declines throughout summer and fall, patterns of feeding-site  
1615 selection should be mostly driven by forage quality early during the growing season, and then  
1616 shift toward increased standing stock of vegetation as summer and fall progress.

1617         At the intermediate, temporal scale, we considered the effect of the time of the day in our  
1618 analysis of weekly time spent-feeding in the daytime, since foraging may also be dependent on  
1619 daily patterns of temperature or daily movements (Berger and Cunningham 1994). In mesic  
1620 grasslands, large herbivores shift coarse-scale resource selection patterns with increasing  
1621 ambient temperatures (Maichek et al. 2004, Allred et al. 2013). Here, we hypothesized that (a) in  
1622 the growing season when temperatures are warmer, bison may spend more time feeding during  
1623 the morning and late afternoon than during the middle of the day. In addition, (b) the proportion  
1624 of time spent feeding should be negatively related to forage quality, and bison foraging activity  
1625 should track seasonal shifts in plant quality and spend a smaller proportion of their daily activity  
1626 budget feeding early in the summer when plants are most nutritious compared with later in  
1627 growing season when forage is less nutritious; thus more time feeding is required to meet  
1628 metabolic demands.

## 1629         **METHODS**

### 1630         **Study Area**

1631         We conducted this study in spring-summer 2012 (April to September) and summer-fall 2013  
1632         (May to December) in a 1,040 ha enclosure at Konza Prairie Biological Station (KPBS), near

1633 Manhattan, KS (USA). KPBS is a mesic tallgrass prairie landscape that experiences a variable,  
1634 continental climate with warm, wet springs, hot summers and dry, cold winters. Mean annual  
1635 precipitation is 826 mm with ~75% falling during the April-September growing season, which is  
1636 characterized by increasing biomass and fiber content in graminoids. Moreover, seasonal  
1637 precipitation and landscape features also contribute to the mosaic of vegetation patches that vary  
1638 in abundance and quality throughout the growing season. The bison area at KPBS is managed  
1639 using spring controlled-burning with a fully-replicated watershed level experimental design,  
1640 where watersheds are burned at varying frequencies (1, 2, 4 and 20 years). This variable fire  
1641 frequency affects forage availability and quality, which in turn strongly influences bison  
1642 resource-selection strategies and foraging behavior over time. The current bison herd was  
1643 established in 1987, and is currently maintained at a stocking rate of ~260 adult individuals, with  
1644 ~90 calves born in each spring. This stocking rate of ~14.5g bison m<sup>2</sup> (~ 0.3 animals ha<sup>-1</sup>) results  
1645 in a target density that removes ~25% of the standing vegetation biomass annually (Knapp et al.  
1646 1999).

1647 *Fine Temporal-scale Foraging Behavior: Feeding-site Selection*

1648 To evaluate feeding-site selection at the fine temporal scale, we measured vegetation attributes at  
1649 active feeding sites that we compared with nearby, randomly located sites located within the  
1650 same watershed at least 50 m away. A group feeding site was defined as an approximately  
1651 circular area where >50% of the bison in a group were observed feeding together for a minimum  
1652 of 30 min). Bison observations were taken throughout the entire daylight period. Bison were  
1653 approached on foot and observed at distances between 100 and 500 m. On those rare occasions  
1654 when bison were disturbed, observations were started after they resumed their foraging activities.  
1655 Vegetation characteristics at feeding-sites were sampled using three 1 m<sup>2</sup> plots, placed randomly

1656 within a 25 m<sup>2</sup> radius circle adjacent to the feeding-site location (Schaefer and Messier 1995). In  
1657 every plot, the percentage of graminoids, forbs and litter was estimated visually for each  
1658 vegetation group in 10% classes. We repeated the same sampling design at sites not grazed  
1659 during feeding observations in a random direction from each feeding site at a distance of 50-75  
1660 m for comparison with feeding sites.

1661 To estimate plant biomass, we clipped individual plants 2 cm above the ground in each of  
1662 the three plots next to each feeding site and in nearby, random locations. Plant samples were  
1663 dried in the field in paper bags, and then oven-dried for 48 h at 60 °C and weighed using a 0.1 g  
1664 precision scale. Because graminoids comprise 98% of the year-round diet of bison in tallgrass  
1665 prairie (Coppedge et al. 1998), all graminoids, irrespective of photosynthetic pathway, were  
1666 separated from clipped vegetation samples and then analyzed for nitrogen content. For each  
1667 foraging observation sample and nearby, random location, two of the three clipped graminoid  
1668 samples were randomly selected for nutrient analysis. Samples were dried, ground to a 1mm  
1669 particle size in a ball mill, and analyzed by Dairyland Laboratories Inc. (Arcadia, WI) on a Foss  
1670 model 5000 NIR instrument. Graminoid crude protein was determined using NIRS (Near  
1671 Infrared Spectroscopy) analysis. Crude protein was estimated as “%-N in plant tissue \* 6.25” for  
1672 2-3 samples at each feeding site and the nearby, random location. Observations were delineated  
1673 to three seasonal periods: growing (April 15-June 30), mid-to-late summer transition (July 1-  
1674 October 14), and dormant (October 15 – December 31); periods of generally young,  
1675 transitioning, and senesced plant tissue in order to understand shifts in foraging tactics as overall  
1676 plant quality declined over the growing season.

1677 *Intermediate Temporal scale Foraging Behavior: Scan Sampling*

1678 To monitor the proportion of time spent feeding by bison during daylight, we conducted repeated  
1679 scan sampling of bison groups of at least two individuals (Altmann 1974), performed every 15  
1680 min. Bison observations spanned the entire daylight period (0600–2000 h). Each observation  
1681 period lasted between 1 and 12 h. Bison activity was divided into four categories: (1) feeding, (2)  
1682 standing, (3) lying, and (4) walking. Scan observations yielded the proportion of time a group  
1683 spent feeding, which corresponds to the coarse temporal scale of foraging behavior. Records  
1684 without full information on group composition and when behavior of every individual's behavior  
1685 could not be accounted for were not included in analysis. We followed 283 groups between 1  
1686 and 12 h, for a total of 577 h of observation throughout the study.

#### 1687 *Data Analyses*

##### 1688 *Feeding-site selection*

1689 We compared feeding sites to paired random sites using conditional (i.e., case-controlled)  
1690 logistic regression, using the LOGISTIC procedure and the STRATA statement in SAS version  
1691 9.1 (SAS Institute Inc. 2003). Because we hypothesized that plant quality and composition could  
1692 both influence the selection of feeding sites, we considered the following covariates to explain  
1693 the use of feeding sites relative to random sites: (i) percentage of green foliage, (ii) grasses, (iii)  
1694 litter, and (iv) forbs. Because we had no *a priori* information on how these factors would  
1695 influence the selection of feeding sites, alternate candidate models were built to include the  
1696 following: a full model, a null model (without covariate), a model for every single covariate, and  
1697 a set of models comprising multiple combinations of two covariates. Models were ranked based  
1698 on Akaike's information criterion corrected for small sample size (AICc; Burnham and Anderson  
1699 2002). For each candidate model *i*, we calculated the difference between the AICc of model *i* and  
1700 the AICc of the best model (AICc), Akaike weight ( $\omega_i$ ), and the evidence ratio, expressed as the

1701 ratio between the  $\omega_i$  of the best model and the  $\omega_i$  of model  $i$ . This ratio indicates how the first  
1702 model (i.e., with the lowest AICc value) is likely to be the best model compared with model  $i$ .  
1703 For the best model, we calculated the McFadden's adjusted  $r^2$  (Compton et al. 2002):  
1704 McFadden's adjusted  $r^2 = 1 - [(LL_{\text{covariate}} - k) / LL_{\text{without covariate}}]$ , where LL is the log-likelihood  
1705 and  $k$  is the number of parameters. Models with  $\Delta\text{AICc}$  less than 2 were considered to have  
1706 substantial empirical support,  $\Delta\text{AICc}$  4-7 considerably less, and  $\Delta\text{AICc} > 10$  essentially no  
1707 support (Burnham and Anderson 2002).

1708 *Intermediate Temporal-scale Foraging Behavior: Weekly Time Spent Feeding*

1709 The percentage of time that bison groups spent feeding was calculated as the proportion of scans  
1710 where more than 50% of the individuals were observed feeding relative to the total number of  
1711 scans completed on a specific group. To account for potential diurnal patterns in activity budgets,  
1712 we first divided our observations into three periods: 0600 to 1000 (morning), 1000 to 1500 (mid-  
1713 day), and 1500 to 2000 (evening). Since there was a difference in the time spent feeding between  
1714 morning and mid-day ( $t_{1,134} = -2.34$ ,  $P = 0.02$ ,  $N = 266$ ) and mid-day and evening ( $t_{1,157} = 7.44$ ,  
1715  $P < 0.0001$ ), we performed our analyses using the three daily periods. To take into account the  
1716 potential influence of group size on foraging behavior, we analyzed the influence of group size  
1717 on time spent feeding using a GLM, which was not significant ( $z_{1,264} = -1.59$ ,  $P = 0.11$ ,  $N = 266$ ).  
1718 Therefore, we did not include group size in subsequent analyses. We used logistic regression to  
1719 assess the influence of burn type, date (number of days after 1 May), and period of the day on the  
1720 proportion of scans where bison were feeding. We first tested the effect of year on time spent  
1721 foraging for summers 2012 and 2013. Because there was no difference between the two summer  
1722 seasons ( $t_{1,186} = -0.68$ ,  $P = 0.50$ ,  $N = 187$ ), we pooled the data for these 2 years. Moreover,  
1723 because the dates of observations in fall did not overlap with the dates of observations during



1724 summers 2012–2013, the date was used as a surrogate for season, and the factor year was  
1725 removed from the analyses (St-Louis and Côté 2012). We assembled candidate models to  
1726 include combinations of all covariates and interactions between covariates that were biologically  
1727 relevant to our initial hypotheses. Means are presented  $\pm$ SE. Significance level was set at 0.05  
1728 for all statistical analyses.

1729 *Coarse Temporal-scale Foraging Behavior: Seasonal shifts in diet using  $\delta^{13}\text{C}$  stable isotopes*  
1730 During annual bison roundup activities in late October, a tail hair was collected from each of the  
1731 same four matriarchal female bison that were fitted with GPS-collars throughout 2010-2013  
1732 (Chapter 4). In the laboratory, hair samples were wiped with acetone to remove dirt, grit, and  
1733 oils. Hair samples were serially sampled, with 1 sample collected from each 5-mm interval for  
1734  $\delta^{13}\text{C}$  analysis (Cerling et al. 2009).

1735 We measured the stable carbon isotope ratios in the Stable Isotope Mass Spectrometry  
1736 Laboratory (SIMSL) at Kansas State University. Samples were combusted with a CE1110  
1737 elemental analyzer (Carlo Erba Instruments, Milan, Italy) and coupled to a Delta Plus mass  
1738 spectrometer (Thermo Electron Corporation, Bremen, Germany) for isotope analysis using a  
1739 ConFlo II Universal Interface (Thermo Electron Corporation, Bremen, Germany). The isotopic  
1740 ratio of samples was calculated using delta notation as:

1741 
$$\delta = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) * 1000 \right] \quad \text{(Equation 1)}$$

1742 where  $R$  is the ratio of the heavy to light isotope for the sample and standard, respectively. The  
1743 within-run variability estimated as the standard deviation of working standards was always  
1744 0.05%, and the between run variability, estimated as the difference between the measured value  
1745 of a working standard and its calibrated value, was always 0.05%.

1746 Strongly delineated isotopic signals occur in the  $\delta^{13}\text{C}$  ratios of plants, reflecting use of  
1747 plants with  $\text{C}_3$  and  $\text{C}_4$  photosynthetic pathways. Most  $\text{C}_4$  plants have  $\delta^{13}\text{C}$  values between -11  
1748 and -14‰, whereas most  $\text{C}_3$  plants have  $\delta^{13}\text{C}$  values between -25 and -29‰ (Cerling et al. 2009).  
1749 Therefore, we classify primarily  $\text{C}_4$  plant diets as those represented by hair follicle  $\delta^{13}\text{C}$  values  
1750 above -14‰ and a value below -14‰ representing a mixed  $\text{C}_4$ - $\text{C}_3$  plant diet unless -25‰ was  
1751 reached. Regression (linear, polynomial) was performed to assess the  $\delta^{13}\text{C}$  distribution across the  
1752 tail hair length. Non-linear patterns in  $\delta^{13}\text{C}$  signatures throughout a year indicate a diet shift of  
1753 plants from one photosynthetic pathway towards another. Log-likelihood estimates were  
1754 compared for the linear or polynomial distributions for each tail hair. The distribution with the  
1755 lowest AICc value was retained for interpretation. Because our annual average tail hair length  
1756 was  $11.72 \pm 0.16$  cm and cattle hair growth rate is  $\sim 2$  cm per month (Schwertl et al. 2003), we  
1757 presume our data encapsulate isotopic history spanning from late winter through summer for all  
1758 four years in each animal.

## 1759 **RESULTS**

### 1760 *Fine temporal-scale Foraging Behavior: Feeding-site Selection*

#### 1761 *Feeding-site grass:forb ratio*

1762 Sites grazed by bison showed a higher grass:forb ratio (9.4:1) than ungrazed sites (6.1:1;  $t_{1,238} =$   
1763 2.3,  $P=0.02$ ), while grass:forb ratios at sites that were burned (7.4:1) and not-burned (8.3:1) were  
1764 not significantly different ( $t_{1,179} = 0.55$ ,  $P=0.59$ ; Fig.1).

#### 1765 *Growing season feeding-site selection*

1766 The percentage of forb and grass cover were the main variables explaining the selection of  
1767 feeding sites during the growing season since they were the only variables common to the

1768 models with  $\Delta_i < 2$  (model-averaged estimate for forb and grass cover:  $-26.15 \pm 6.19$  and -  
1769  $8.09 \pm 2.26$ ; Table 1). These results suggest that bison generally avoid areas containing both high  
1770 forb and grass cover. The top model (forbs+grass+litter) explained 41% (McFadden's adjusted  
1771  $r^2$ ) of the observations.

1772 *Transition season feeding-site selection*

1773 The percentage of forb and grass cover were the main variable explaining the selection of  
1774 feeding sites during the transitional season since they were the only variables common to the  
1775 models with  $\Delta_i < 2$  (model-averaged estimate for grass and cover:  $-12.23 \pm 2.75$  and  $-3.95 \pm 1.28$ ;  
1776 Table 2). These results suggest bison are less likely to use areas containing high forb and grass  
1777 cover during the transition season than during the early growing season. The best model  
1778 (forbs+grass) explained 18% (McFadden's adjusted  $r^2$ ) of the observations.

1779 *Dormant season feeding-site selection*

1780 The top model explaining feeding site selection during the dormant season was the null model.  
1781 However, the model-averaged estimates for the models with  $\Delta_i < 4$ , which contain some empirical  
1782 model support (Burnham and Anderson 2002), were  $-1.76 \pm 2.86$  and  $-0.08 \pm 1.98$  for forb and  
1783 grass cover, respectively (Table 3). These results suggest that bison are less likely to avoid areas  
1784 containing high forb and grass cover during the dormant season than was observed during the  
1785 early growing or transitional seasons.

1786 *Factors associated with forage quality and quantity*

1787 Higher crude protein content was found in graminoids during the growing season than was  
1788 observed for either the transition or dormant season ( $F_{2,244} = 39.0$ ,  $P < 0.0001$ ; Fig. 2). A significant  
1789 interaction between season and burn status revealed that graminoid crude protein content was  
1790 greater in burned watersheds compared to not-burned watersheds during the growing (27%

1791 higher) and transition (14%) seasons, but not during the dormant season (8%;  $F_{2, 244}=5.01$ ,  
1792  $P=0.007$ ). Across seasons, graminoid crude protein at sites selected for grazing was higher than  
1793 protein content at sites not selected for grazing ( $F_{1,132}=24.9$ ,  $P<0.001$ ). Selected areas were 15,  
1794 11, and 23% higher in crude protein content than sites not selected for grazing during the  
1795 growing, transition, and dormant season, respectively. Interactions between feeding-site selection  
1796 and season ( $F_{2,132}=1.9$ ,  $P=0.16$ ) or burn status ( $F_{1,132}=0.10$ ,  $P=0.76$ ) were not significant.

1797 Overall, standing crop biomass was lower in the dormant season than the growing and  
1798 transition seasons ( $F_{2,254}=3.9$ ,  $P=0.02$ ; Fig. 3). Standing crop biomass was also lower in burned  
1799 watersheds than unburned watersheds ( $F_{1,254}=8.6$ ,  $P=0.003$ ). Across seasons, biomass at feeding  
1800 sites was lower than that observed at nearby random locations ( $F_{1,132}=11.0$ ,  $P<0.0001$ ), probably  
1801 reflecting effects of recent bison foraging.

## 1802 *Intermediate temporal-scale Foraging Behavior*

### 1803 *Time spent grazing*

1804 The proportion of time spent feeding over the entire activity budget was explained primarily by  
1805 whether the watershed used by grazers was burned or not ( $\chi^2=6.6$ ,  $df=1$ ,  $P=0.01$ ,  $N=266$ ), the  
1806 period of the day ( $\chi^2=15.0$ ,  $df=2$ ,  $P=0.0005$ ,  $N=266$ ), and the date after 1 May ( $\chi^2=36.3$ ,  $df=1$ ,  
1807  $P<0.0001$ ,  $N=266$ ). This model had an Akaike weight of 0.74 and explained 23% of the variation  
1808 in observations (McFadden's adjusted  $r^2$ ) (Table 4). The odds that bison were feeding in burned  
1809 grassland were 2.5 times greater than the odds of bison feeding in unburned grasslands. The  
1810 proportion of time spent feeding by bison was about 30% in early summer, increased to  
1811 approximately 50% in late summer, and further increased to about 65% very late in the summer  
1812 and during autumn (Fig. 4). Bison feeding during daytime and at the end of the afternoon were

1813 about half the odds of feeding during morning (morning:  $60 \pm 1\%$ ; daytime:  $28 \pm 0.3\%$ ; late  
1814 afternoon:  $34 \pm 0.4\%$ ).

### 1815 *Coarse Temporal-scale Foraging Behavior*

#### 1816 *Isotopic record of $\delta^{13}C$*

1817 The  $\delta^{13}C$  isotopic signature of tail hair indicated that the diet shifted from a strictly  $C_4$  diet during  
1818 the growing and transitional seasons to a mixed diet of  $C_3$  and  $C_4$  plants in the dormant season  
1819 (Fig. 5). For three of four bison with tail hairs ranging from 6-14 cm in length the relationship  
1820 between  $\delta^{13}C$  signature and hair follicle length was best fit by a second-order polynomial  
1821 regression for 8 of the 12 tail hair samples. Bison #Y139 had tail hair lengths ranging from 14.5  
1822 to 21.5 cm during each collection time that were best fit by third-order polynomial regression in  
1823 2010 and 2012 and fourth-order polynomial regression in 2011 and 2013. Because cattle hair  
1824 grows at a length of  $\sim 2.5$  cm a month (Schwertl et al. 2003), we assumed hairs from bison  
1825 #Y139 provide isotopic history spanning across an annual cycle or encapsulating two dormant  
1826 seasons.

## 1827 **DISCUSSION**

1828 Integrating more than one temporal scale in ecological studies allows a better understanding of  
1829 patterns, processes, and limiting factors determining resource use (Senft et al. 1987, Rettie and  
1830 Messier 2000). To our knowledge, this is the first study to simultaneously evaluate feeding-site  
1831 selection at the patch-scale and the activity budgets of bison at the landscape-scale across the  
1832 growing season in the tallgrass prairie of North America. Previous studies documented that  
1833 components of resource use in plains bison may be driven by both forage availability and quality  
1834 (Vinton et al. 1993, Coppedge and Shaw 1998), but none considered a multi-scale approach. Our  
1835 results support our hypothesis that resource use varies across seasons and temporal scales. At the

1836 intermediate, weekly temporal scale, bison increased time spent feeding as plant quality declined  
1837 with the approaching dormant season. At the fine, temporal scale, feeding-site selection in bison  
1838 is dependent on plant regrowth during the growing season, then shifting towards areas of higher  
1839 plant abundance as plant quality declines. At this fine scale, forage quality measured through  
1840 crude protein content did not explain resource use in the dormant season, but its effect was  
1841 higher throughout the growing season. We suggest that patterns of resource use by bison may  
1842 reflect foraging tactics aimed at increasing nutrient intake while minimizing foraging effort in  
1843 productive mesic grassland.

#### 1844 *Feeding-site Selection*

1845 As seen in previous surveys of bison foraging at KPBS, bison grazed watersheds in a nonrandom  
1846 fashion (Vinton et al. 1993). In the growing season, bison preferentially grazed recently burned  
1847 watersheds, whereas their grazing was more evenly distributed among watersheds in the dormant  
1848 season. Burning modifies the grazing habits of bison and other large herbivores (Allred et al.  
1849 2011a, Sensenig et al. 2010) by enhancing growth and accessibility to desired forage. Spring  
1850 burning in tallgrass prairie increases productivity of dominant C<sub>4</sub> grasses, in part by eliminating  
1851 detrital accumulation on plant growth (Knapp and Seastedt 1986), which likely aids grazers'  
1852 ability to find high quality food. In 1988, the year after bison were re-introduced to KPBS,  
1853 feeding-site surveys of plant composition conducted in June revealed bison selected feeding sites  
1854 with low forb cover (Vinton et al. 1993), a finding consistent with our result of selection for sites  
1855 of lower forb cover than nearby available areas throughout the growing and transition season.  
1856 Since their reintroduction to KPBS, significantly increased forb cover is found in the bison  
1857 enclosure (Hartnett et al. 1996), yet our study demonstrates feeding-site selection is driven by

1858 availability of low-to-intermediate cover of graminoids which suggests bison continue to avoid  
1859 high-forb cover in their enclosure.

1860 High densities of large herbivores can maintain patches of grassland in a state of low-to-  
1861 intermediate forage quantity with increased production of young forage tissue (grazing lawns:  
1862 McNaughton 1979). Thus avoidance of areas of high forage biomass can reflect feeding-site  
1863 utilization and spatial distribution of grazers when forage regrowth is possible (Fryxell 1991,  
1864 Wilmshurst et al. 1999b). In our study of a mesic grassland, bison grazed areas of lower biomass  
1865 compared to sites available nearby. However, their avoidance of areas with high grass and forb  
1866 cover seen early in the growing season diminished as the growing season progressed, eventually  
1867 showing random selection during the dormant season. This suggests the availability of profitable  
1868 areas of low-to-intermediate biomass decreased as plants senesced, which may explain the more  
1869 random use of the landscape in the dormant season as observed by Vinton and others (1993).  
1870 Moreover, bison selected feeding sites based on forage quality (crude protein content) in all  
1871 seasons in both burned and unburned watersheds at a fine spatial resolution (50 m scale). This  
1872 suggests that they responded to local variations in forage quality within habitat types, potentially  
1873 increasing their nutrient intake by selecting food patches with a high availability of protein  
1874 (Spalinger and Hobbs 1992). At the landscape-scale, similar levels of forage protein content  
1875 between burned and unburned watersheds during the dormant season may further explain a more  
1876 random spatial distribution of grazing habits in colder months at KPBS (Chapters 2 and 4).

#### 1877 *Intermediate, temporal-scale Foraging Behavior*

1878 Because post-fire regrowth in tallgrass prairie results in greater availability of high quality food  
1879 patches, we hypothesized that bison would spend less time feeding early in summer after spring  
1880 burns. In our study, bison spent a higher proportion of their time feeding in watersheds that

1881 burned during the spring prior to the observation than in unburned watersheds, and the total time  
1882 spent feeding throughout the growing season was at its minimum during the early spring. These  
1883 results support our hypothesis that time spent foraging is inversely related to forage quality.  
1884 Coppock and others (1983) conclude that increased graminoid production and higher live:dead  
1885 tissue ratios resulting from spring burning are two important determinants of bison foraging  
1886 habits. Preferential grazing of recently-burned watersheds on tallgrass prairie during the  
1887 growing season likely reflects increased forage availability and accessibility. However, we posit  
1888 that high quality forage content is a critical factor driving preferential grazing in burned  
1889 grassland. Increased forage crude protein content and digestibility during the early growing  
1890 season likely allow bison to maintain short-term nutrient intake while incurring reduced time  
1891 spent feeding (Chapter 2; Raynor et al. 2015). High availability of highly digestible, protein-rich  
1892 forage likely allows bison to allocate time to activities related to reproduction (e.g. milking  
1893 calves and increased vigilance of lactating females). Therefore, our findings shed light on the  
1894 underlying behavioral mechanisms responsible for large herbivore resource use that drives their  
1895 attraction to recently-burned grasslands.

1896         Our hypothesis that time spent feeding would be highest in the morning and late  
1897 afternoon was partly supported. To reduce thermoregulatory stress from high ambient  
1898 temperature and heat production from rumination (Galbraith et al. 1998), bison reduce overall  
1899 daily activity (Belovsky and Slade 1986) and decrease daily foraging and intake (McHugh 1958).  
1900 Bison are known to seek woody cover at extreme temperatures ( $>35^{\circ}\text{C}$ ; Allred et al. 2013) and  
1901 increase foraging activity as daytime temperatures decrease (Collins and Smith 1989, Rutley and  
1902 Hudson 2001). Thus, we expected bison to begin feeding in the late afternoon. Because bison  
1903 increase nocturnal foraging in periods of increased ambient temperature (Hudson and Frank



1904 1987, Hein and Preston 1998, Maichek et al. 2004), we presume that increased nocturnal feeding  
1905 occurred during our study as ambient temperature was well above the study area's mean (KNZ  
1906 LTER). Several nocturnal surveys indicated bison were feeding at night although our restricted  
1907 ability to observe foraging activity and small sample size limited our ability to draw inferences.  
1908 Future studies of direct effects of ambient temperature on large herbivore behavior and  
1909 physiological adaptations and responses are warranted as temperatures increase globally  
1910 (Maichek et al. 2004, Allred et al. 2013).

1911         Seasonal fluctuations in diets of large herbivores can arise from variation in temporal and  
1912 spatial resource quality and abundance (Stearns 1992). At KPBS, the most infrequently burned  
1913 watersheds support a high proportion of cool-season C<sub>3</sub> grasses (Gibson and Hulbert 1987,  
1914 Vinton et al. 1993). During the dormant season, observational studies and distribution of GPS-  
1915 collared bison show bison prefer watersheds that are not burned in the spring (Vinton et al. 1993,  
1916 Chapter 4, this thesis). Our limited stable isotope record of  $\delta^{13}\text{C}$  using tail hairs of GPS-collared  
1917 matriarchal female bison indicates their attraction to not-burned watersheds in the dormant  
1918 season is driven by the availability of cool-season C<sub>3</sub> grasses. Moreover, watersheds not-burned  
1919 the previous spring contain high vegetation structure during the colder months (Chapter 2;  
1920 Raynor et al. 2015) that may reduce the foraging efficiency of bison that occurs in highly  
1921 accessible and nutrient-rich patches in the growing season. Cool-season C<sub>3</sub> graminoids tend to  
1922 occur in unburned tallgrass prairie with high vegetation structure (Coppedge and Shaw 1998,  
1923 Stueter and Hidingier 1999, Rosas et al. 2005), which likely decreases the accessibility of these  
1924 forage resources and reduces foraging efficiency. During this period, we surmise that bison were  
1925 compensating for low protein availability in forage by consuming higher amounts of low-quality

1926 forage although this strategy may reduce short-term nutrient intake as observed in other studies  
1927 (Laca et al. 1994, Laca et al. 2001).

1928 *Implications*

1929 Plant phenology and environmental conditions strongly influence physiological balance and the  
1930 foraging behavior of herbivores living in seasonal environments (Moen et al. 2006, Shrader et al.  
1931 2006). The observation that bison closely adjust their foraging behavior to the seasonal patterns  
1932 of plant phenology and select patches with respect to foliar-N concentrations suggests that plant  
1933 quality is an important driver of their foraging ecology. Unlike tropical systems, where plant  
1934 regrowth after grazing occurs almost year round (Fryxell 1991), availability of high quality  
1935 forage is seasonal in temperate grasslands. At KPBS, bison selected feeding sites of low  
1936 vegetation stature during the early growing season when regrowth was possible and then shifted  
1937 to high vegetation stature patches in the dormant season where more effort is likely expended to  
1938 reach nutrient requirements. Thus, large herbivores in seasonal environments select food  
1939 resources on the basis of both forage quantity and quality using different tactics to increase  
1940 nutrient intake at several temporal scales as predicted by the forage maturation hypothesis  
1941 (Fryxell 1991). In particular, bison experience a shifting mosaic of habitat quality within and  
1942 among seasons and years, and can track such variability in resource availability at multiple  
1943 spatiotemporal scales.

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- 2078



2079 **Table 3-1. Candidate models and parameter estimates for feeding-site selection of bison at Konza Prairie, Manhattan, Kansas**  
 2080 **in spring 2012-2013, where selection for feeding sites were compared with random sites located in a random direction 50 m**  
 2081 **away.**

2082

2083

Model	Intercept	Forbs	Grass	Litter	Green	df	AICc	$\Delta$ AICc	$\omega_i$	Evidence Ratio
I + Forb + Grass + Litter	7.60	-25.70	-7.87	-11.96		4	73.00	0.00	0.31	1.00
I + Forb + Grass + Green	4.84	-27.16	-8.49		3.60	4	73.20	0.18	0.29	1.09
I + Forb + Grass + Litter + Green	5.65	-26.72	-8.24	-9.44	2.73	5	73.70	0.63	0.23	1.37
I + Forb + Grass	6.94	-24.53	-7.64			3	74.20	1.18	0.17	1.80
I + Forb + Litter	2.45	-18.19		-9.39		3	88.40	15.40	0.00	2208.35
I + Forb + Grass	2.04	-17.27				2	89.00	16.01	0.00	2995.90
I + Forb + Litter + Green	1.43	-18.81		-8.77	1.34	4	90.00	16.97	0.00	4841.60
I + Forb + Green	0.79	-18.22			1.70	3	90.10	17.09	0.00	5140.99
I + Grass	1.30		-2.54			2	111.50	38.45	0.00	223517439.93
I + Grass + Litter	1.50		-2.59	-5.62		3	112.30	39.27	0.00	336800053.78
I (null)	0.00					1	113.00	39.92	0.00	466141595.99
I + Grass + Green	1.72		-2.52		-0.53	3	113.50	40.48	0.00	616765842.43
I + Litter	0.16			-5.37		2	113.80	40.75	0.00	705911193.99
I + Grass + Litter + Green	2.14		-2.56	-5.97	-0.78	4	114.20	41.20	0.00	884028623.85
I + Green	0.48				-0.59	2	114.90	41.84	0.00	1217420362.37
I + Litter + Green	0.86			-5.83	-0.85	3	115.60	42.56	0.00	1744964415.27

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2086 **Table 3-2. Candidate models and parameter estimates for feeding-site selection of bison at Konza Prairie, Manhattan, Kansas**  
 2087 **in summer 2012-2013, where selection for feeding sites were compared with random sites located in a random direction 50 m**  
 2088 **away.**

Model	Intercept	Forbs	Grass	Litter	Green	df	AICc	$\Delta$ AICc	$\omega_i$	Evidence ratio
I + Forb + Grass	3.91	-12.47	-4.08			3	156.80	0.00	0.45	1.00
I + Forb + Grass + Green	4.45	-11.82	-3.71		-1.38	4	157.90	1.10	0.26	1.73
I + Forb + Grass + Litter	3.93	-12.38	-4.03	-1.94		4	158.70	1.85	0.18	2.52
I + Forb + Grass + Litter + Green	4.50	-11.70	-3.64	-2.23	-1.45	5	159.70	2.89	0.11	4.24
I + Forb + Green	2.76	-8.44			-2.50	3	164.90	8.12	0.01	57.97
I + Forb + Litter + Green	2.87	-8.40		-3.27	-2.54	4	166.20	9.43	0.00	111.61
I + Forb	1.36	-8.96				2	167.00	10.20	0.00	164.02
I + Forb + Litter	1.44	-8.90		-3.14		3	168.40	11.56	0.00	323.76
I + Green	1.71				-2.92	2	180.30	23.48	0.00	125492.34
I + Litter + Green	1.81			-3.37	-2.92	3	181.30	24.53	0.00	212139.64
I + Grass + Green	2.01		-0.91		-2.69	3	181.50	24.73	0.00	234450.56
I + Grass + Litter + Green	2.10		-0.85	-3.18	-2.71	4	182.70	25.94	0.00	429338.10
I + Grass	0.68		-1.40			2	184.90	28.09	0.00	1257957.59
I (null)	0.00					1	185.00	28.21	0.00	1335745.34
I + Litter	0.10			-3.38		2	186.00	29.21	0.00	2202271.75

I + Grass + Litter	0.75		-1.35	-3.06		3	186.10	29.31	0.00	2315184.64
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2089 **Table 3-3. Candidate models and parameter estimates for feeding-site selection of bison at Konza Prairie, Manhattan, Kansas**  
 2090 **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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Model	Intercept	Forbs	Grass	Litter	Green	df	AICc	$\Delta$ AICc	$\omega_i$	Evidence ratio
I(null)	0.00					1	76.90	0.00	0.27	1.00
I + Litter	0.09			-2.00		2	78.50	1.61	0.12	2.24
I + Forb	0.23	-1.44				2	78.80	1.87	0.11	2.55
I + Green	-0.08				0.64	2	79.00	2.05	0.10	2.79
I + Grass	-0.08		0.14			2	79.10	2.15	0.09	2.93
I + Forb + Litter	0.37	-1.69		-2.18		3	80.40	3.46	0.05	5.64
I + Forb + Green	0.21	-2.60			1.61	3	80.60	3.62	0.04	6.11
I + Grass + Litter	0.44		-0.56	-2.30		3	80.70	3.78	0.04	6.62
I + Litter + Green	0.03			-1.95	0.51	3	80.70	3.79	0.04	6.65
I + Forb + Grass	0.56	-1.77	-0.47			3	81.00	4.07	0.04	7.65
I + Grass + Green	-0.18		0.17		0.65	3	81.20	4.29	0.03	8.54
I + Forb + Grass + Litter	2.07	-3.52	-2.28	-3.60		4	82.00	5.10	0.02	12.81
I + Forb + Litter + Green	0.35	-2.79		-2.14	1.55	4	82.30	5.34	0.02	14.44
I + Forb + Grass + Green	0.90	-3.52	-1.00		1.92	4	82.70	5.76	0.02	17.81
I + Grass + Litter + Green	0.35		-0.51	-2.22	0.47	4	83.00	6.06	0.01	20.70
I + Forb + Grass + Litter + Green	2.77	-6.08	-3.27	-4.15	2.48	5	83.50	6.52	0.01	26.05

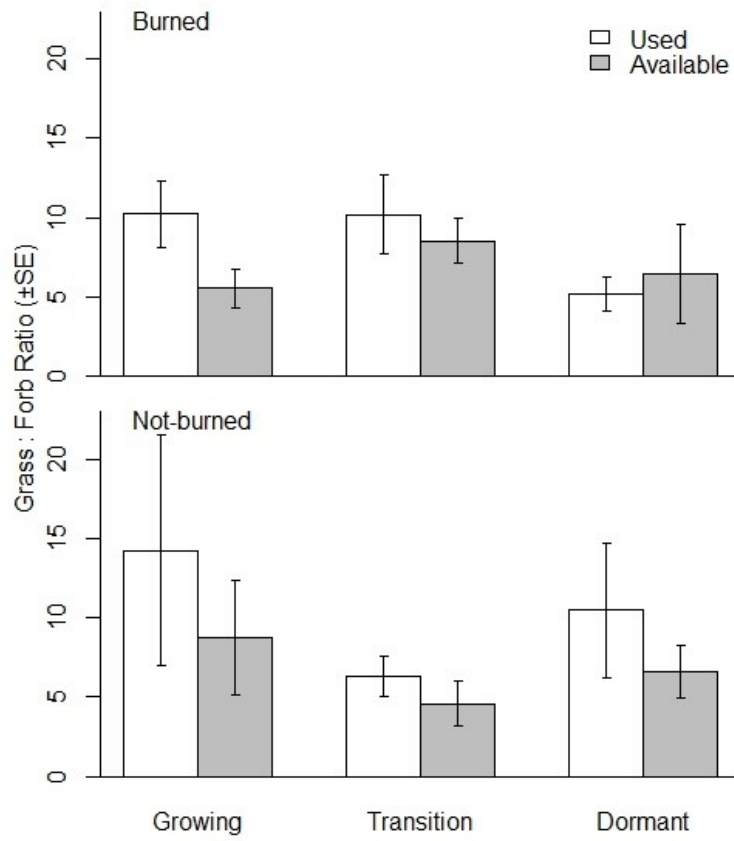
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**Table 3-4. Models explaining the proportion of time spent feeding by bison groups during scans at Konza Prairie, Manhattan, Kansas (2012–2013, N = 282). The models are ranked according to their AICc values.**

Model	df	AICc	$\Delta$ AICc	$\omega_i$	Evidence ratio
I + Burn + Period + Date	5	267.7	0	0.741	1.00
I + Burn + Period + Period*Burn + Date	7	270.4	2.68	0.194	3.82
I + Period + Date	4	272.6	4.87	0.065	11.42
I + Burn + Date	3	292.4	24.65	0	225257.62
I + Date	2	300.4	32.65	0	12298649.28
I + Period	3	314.7	46.95	0	15669782293.28
I + Burn + Period	4	316.6	48.91	0	41751449241.00
I + Burn + Period + Period*Burn	6	318.9	51.16	0	128603517418.86
I (null)	1	336.8	69.09	0	1006243011958810.00
I + Burn	2	338.3	70.61	0	2151625504512620.00

2098 I: intercept; burn types: burned that year, not-burned that year; period of the day: morning, daytime, evening; date: number of days  
2099 since 1 May.

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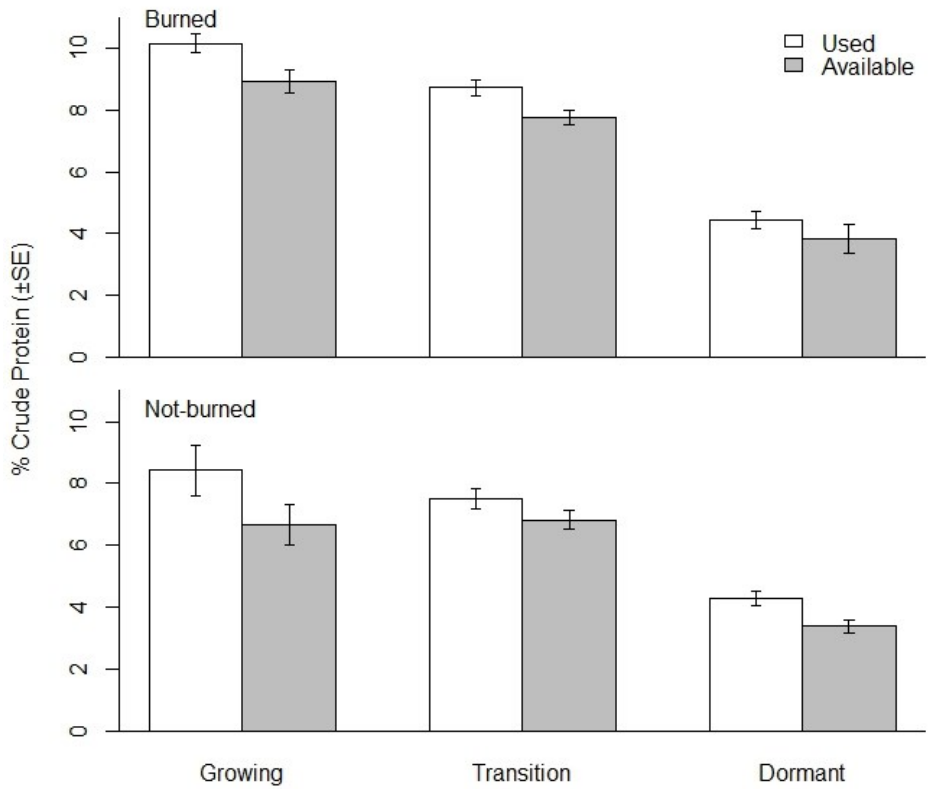
2105 **Figure 3-1. Mean grass:forb ratio (±SE) at feeding sites and nearby, available sites located**  
 2106 **50 m away in watersheds that burned that year and watersheds that did not burn that year**  
 2107 **from 2012-2013 at Konza Prairie Biological Station, Manhattan, Kansas.**

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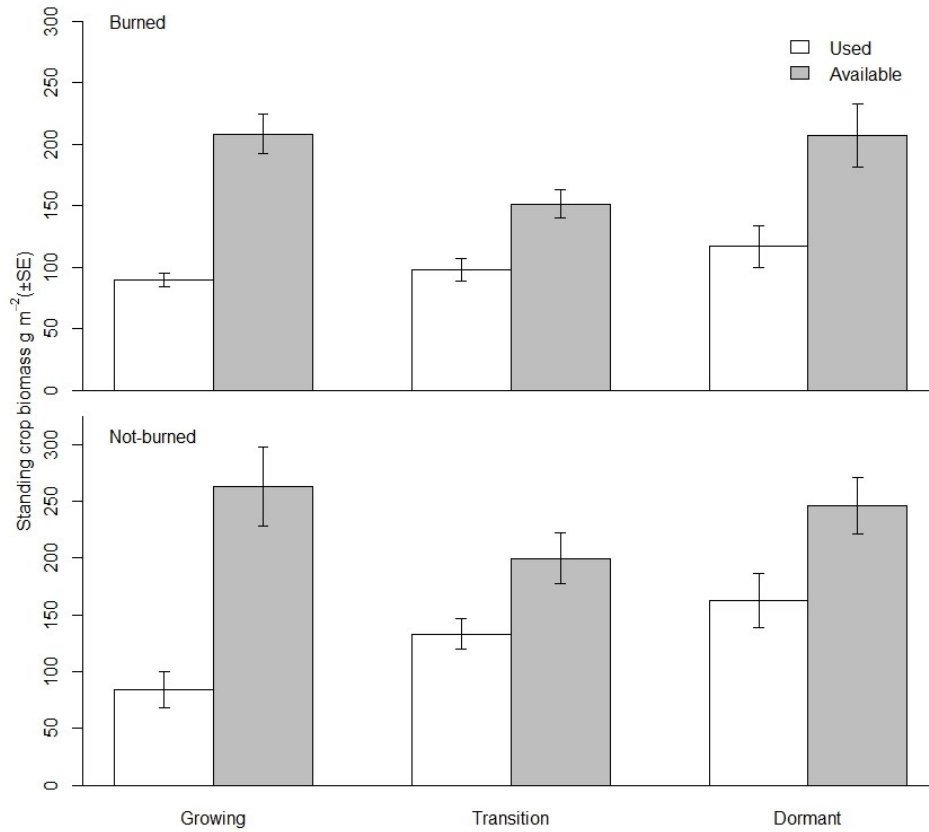
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2113 **Figure 3-2. Mean graminoid crude protein content ( $\pm$ SE) at feeding sites and nearby,**  
 2114 **available sites located 50 m away in watersheds that burned that year and watersheds that**  
 2115 **did not burn that year from 2012-2013 at Konza Prairie Biological Station, Manhattan,**  
 2116 **Kansas.**

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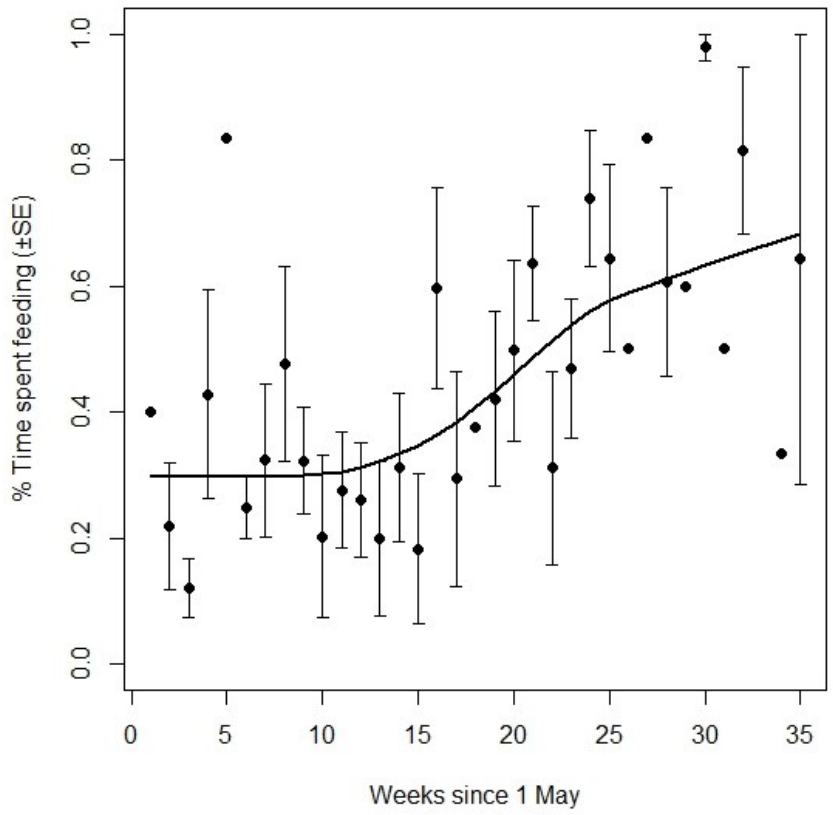
2119 **Figure 3-3. Mean standing crop biomass ( $\pm$ SE) at feeding sites and nearby, available sites**  
 2120 **located 50 m away in watersheds that burned that year and watersheds that did not burn**  
 2121 **that year from 2012-2013 at Konza Prairie Biological Station, Manhattan, Kansas.**

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2126 **Figure 3-4. Mean percentage of time spent feeding ( $\pm$ SE) per week by bison in relation to**  
 2127 **date from 2012-2013 (pooled) at Konza Prairie Biological Station, Manhattan, Kansas.**

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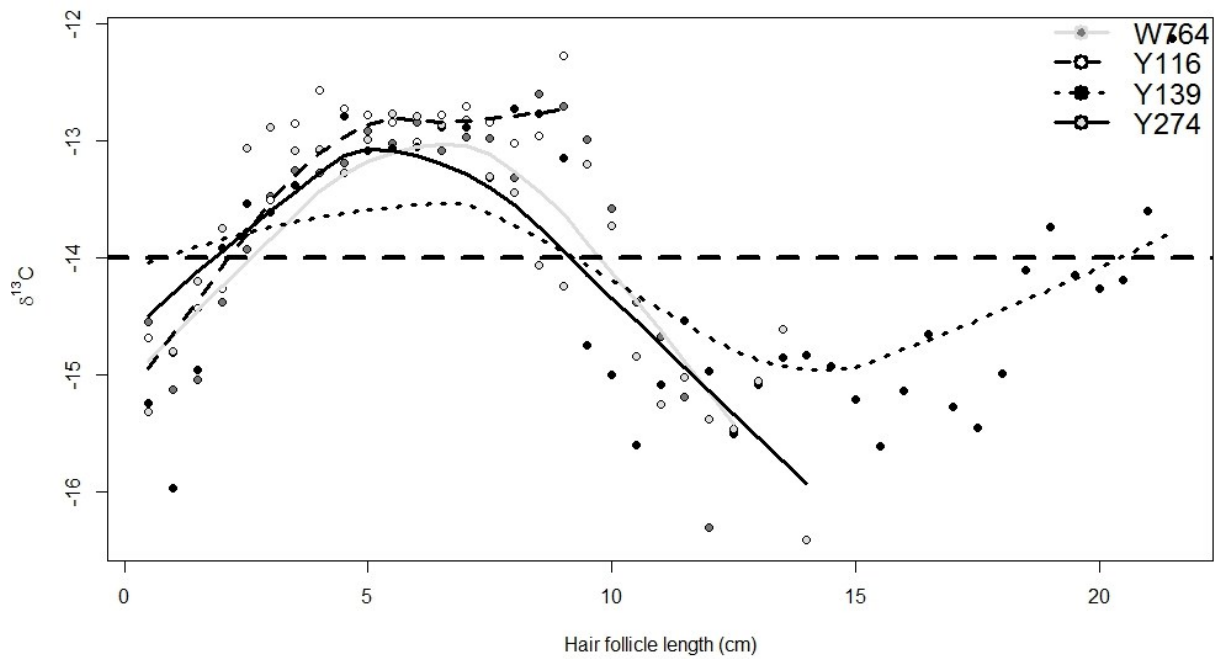
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2136 **Figure 3-5.  $\delta^{13}\text{C}$  ‰ of composite hair profile in relation to hair follicle length (cm)**  
 2137 **averaged over 2010-2013 for four matriarchal female bison fitted with GPS-collars.**  
 2138 **Beginning of hair follicle is when hair was plucked from bison tail during management**  
 2139 **activities in late October of each year. Dashed line indicates separation of mostly  $\text{C}_4$  plant**  
 2140 **diet and mixed  $\text{C}_3\text{-C}_4$  diet.**

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2183 **Chapter 4 - Extending the transient maxima hypothesis to grazing:**  
2184 **bison preferentially select infrequently burned watersheds in fire-**  
2185 **managed mesic grassland**

2186 **ABSTRACT**

2187 Consideration of fire-grazer interactions is critical for understanding grassland structure and  
2188 function globally. In turn, grassland structure and function determines ungulate distributions and  
2189 forage selection. We compared the preferential use of watersheds by bison in a tallgrass prairie  
2190 landscape managed with different burn frequency treatments to understand the contribution of  
2191 recent fire and burn history. Based on the Transient Maxima Hypothesis, one expects an  
2192 increase in plant productivity and forage quality with increased time since the last burn.  
2193 Accordingly, one expects bison to preferentially select infrequently burned watersheds in the  
2194 year of burn over watersheds that were frequently burned or watersheds that were not burned that  
2195 year. Using GPS collars, individual bison were tracked among experimental watersheds managed  
2196 with four burn treatments (1-, 2-, 4-, and 20-year burn intervals), over a 7-year period at Konza  
2197 Prairie Biological Station, Manhattan, KS (USA). Bison preferred recently burned watersheds  
2198 during the growing season and unburned watersheds during winter periods. In accordance with  
2199 predictions of the transient maxima hypothesis, the strength of selection by bison in the year a  
2200 watershed burned increased as the time since a watershed last burned increased. Space use had a  
2201 positive relationship with the availability of recently burned watersheds that had not burned in  
2202 four years, where the strength of attraction attenuated with time and disappeared by the end of  
2203 the growing season. Moreover, the availability of watersheds that did not burn the previous  
2204 spring was the strongest predictor of space use during the non-growing, dormant season. Our  
2205 study applies resource utilization function methodology to a large herbivore population in

2206 response to the availability of grassland burned at varying frequencies, and our results provide  
2207 new quantitative insights into the spatial ecology of the consumer processes behind the fire-  
2208 grazer interaction in a mesic grassland ecosystem.

2209 Keywords: GIS, GPS collars, resource ecology, transient maxima hypothesis, resource utilization  
2210 functions (RUF), ungulate space use, utilization distributions (UD)

## 2211 **INTRODUCTION**

2212 Understanding the grazer-plant interaction as affected by fire in a tallgrass prairie ecosystem is  
2213 central for understanding mesic, grassland ecosystems. Along with climate, fire and especially  
2214 the fire-grazer interaction are key drivers of grassland ecosystem function and structure  
2215 (Archibald et al. 2005, Anderson et al. 2007, Fuhlendorf et al. 2009, Allred et al. 2011a, Allred et  
2216 al. 2014). Effects of the fire-grazer interaction include altered vegetation quality and primary  
2217 productivity (Bond and Keeley 2005, Anderson et al. 2007), increased plant, arthropod, and  
2218 vertebrate species richness (Collins et al. 1998, Joern 2005, Fuhlendorf et al. 2012), and  
2219 increased woody encroachment in response to long burn intervals where grasslands could  
2220 become increasingly woody and ultimately no longer grasslands in its absence (Ratajczak et al.  
2221 2014). In this context, it is important to understand how fire affects landscape-level distributions  
2222 of ruminant grazers, in time and space, in their quest to track and use food resources of the  
2223 highest available quality (Archibald and Bond 2004, Archibald et al. 2005, Anderson et al. 2007,  
2224 Prins and van Langevelde 2008). This becomes a bigger challenge for ungulates foraging in  
2225 heterogeneous landscapes as food often can be of substandard quality and the best quality food is  
2226 distributed spatially in a patchy configuration that varies over time as a shifting mosaic  
2227 (Augustine and McNaughton 1998, Augustine and Frank 2001, Augustine and Derner 2014). In  
2228 turn, the spatial and temporal heterogeneity of forage quality dictates the spatial distribution and  
2229 movement kinetics of large herbivores at the landscape level, although predation risk or physical

2230 features of the environment can also affect habitat use (Fryxell 1991, Fryxell et al. 2005,  
2231 Anderson et al. 2010). Moreover, large herbivores can themselves alter the spatial heterogeneity  
2232 of forage resources through their significant levels of forage consumption and effects on  
2233 subsequent fuel loads, because of their relative large individual and population sizes. Accurate  
2234 spatial memory allows large ungulates to anticipate the heterogeneous distribution of food  
2235 resources that coupled with their high mobility increases the likelihood they will select sites with  
2236 high forage quality (Prins and van Langevelde 2008, Augustine and Derner 2014, Merkle et al.  
2237 2014). Although the study of foraging and distribution of grazers in time and space requires an  
2238 understanding of herbivore-plant interactions at multiple scales (Senft et al. 1987), other aspects  
2239 of the landscape may also contribute to ungulate distributions, including topography, availability  
2240 of soil mineral nutrients (Tracy and McNaughton 1995), distance to water, risk of predation, and  
2241 physical factors (e.g., temperature, soil water) (Anderson et al. 2010, Allred et al. 2013).

2242         As critical ecological drivers, fire and grazing influence habitat heterogeneity and  
2243 vegetation community composition, productivity, and physical structure especially in mesic  
2244 grassland ecosystems. Consumer diversity and abundance also respond accordingly (Hobbs  
2245 1996, Adler et al. 2001, Fuhlendorf and Engle 2004, Derner et al. 2009). As is seen for grazing  
2246 systems elsewhere, plains bison (*Bison bison*) in North American grasslands both respond to and  
2247 contribute to the creation of spatial heterogeneity in forage quality and standing crop (Fuhlendorf  
2248 and Engle 2001). Vegetation regrowth after fire is very nutritious and highly sought by large  
2249 grazers (Archibald and Bond 2004, Archibald et al. 2005, Murphy and Bowman 2007, Allred et  
2250 al. 2011a,b, Eby et al. 2014). In turn, recent grazing decreases the likelihood that a patch will  
2251 burn again for a period of time, leading to relatively decreased forage quality during the inter-  
2252 burn intervals, increased low-quality biomass, and reduced foraging activity until there is enough

2253 regrowth to carry the next fire (Archibald et al. 2005, Fuhlendorf and Engle 2001, Raynor et al.  
2254 2015). Ultimately, this fire-grazing interaction leads to the establishment of spatially  
2255 heterogeneous patches of forage quality that exhibit shifting-mosaic dynamics over time, where  
2256 patches representing different times since the last burn co-mingle in space.

2257        Like ungulate grazers worldwide, bison preferentially select recently burned over unburned  
2258 habitats during the growing season (Coppock and Detling 1986, Shaw and Carter 1990, Nellis  
2259 and Briggs 1997, Coppedge and Shaw 1998, Biondini et al. 1999, Wallace and Crosthwaite  
2260 2005, Schuler et al. 2006, Allred et al. 2011a). Fire significantly alters nutrient concentrations in  
2261 post-fire regrowth, resulting in increased concentrations of leaf nutrients (Blair 1997, van de  
2262 Vijver et al. 1999, Oliveras et al. 2012) and removal of older, non-palatable tissues (Knapp 1985,  
2263 Pfeiffer and Hartnett 1995). Unanswered at this time is whether variable time since the last burn  
2264 differentially alters resource quality, and if so, what is the significance to an ungulate consumer?  
2265 The non-equilibrial “transient maxima hypothesis” (TMH) (Seastedt and Knapp 1993) posits  
2266 that vegetation responses (e.g. ANPP and foliar quality) in tallgrass prairie are co-limited by  
2267 multiple factors (light, energy and soil nutrients) that vary with time since the last fire. After  
2268 periods without fire and the accumulation of litter, vegetation becomes light-limited and soil  
2269 nutrients accumulate to relatively high levels (Blair 1997). With frequent fire, soil nutrients  
2270 become limiting to plant growth, even while sufficient light exists to promote growth. Enhanced  
2271 ANPP is seen immediately following infrequent fires (e.g. 4 years) that lasts over a relatively  
2272 short non-equilibria transition stage (e.g., one growing season) in response to the relatively high  
2273 availability of both light and soil nutrients in areas burned at intermediate frequencies compared  
2274 with sites burned annually or left unburned for long periods. Here, the ecosystem switches from  
2275 primary light limitation to one of soil-nutrient limitation. High levels of ANPP of high nutritional

2276 quality result only during this transient period when neither light or soil nutrients are limiting  
2277 (Blair 1997, Chapter 2; in bison unit).

2278         Most available studies of the responses to fire by ungulate grazers are usually represented  
2279 in a simple binary fashion – i.e., burned vs. not-burned sites. However, the time since the last  
2280 burn potentially can increase the expected strength of ungulate responses to vegetation in  
2281 accordance with TMH (Seastedt and Knapp 1993, Blair 1997). With time, soil-N availability  
2282 following fire will decline to intermediate levels with plant growth, and continue to decline with  
2283 successive annual burns (Blair 1997), leading to lower quality forage overall for grazers in  
2284 annually burned vs. infrequently burned sites in the year of the burn. Moreover, net N-  
2285 mineralization rates and plant-tissue-N content both decline with successive annual burning,  
2286 which ultimately reduces foliar nutritional quality available to grazers. Unburned sites provide  
2287 less palatable forage as well (Vinton et al. 1993, Pfeiffer and Hartnett 1995, Knapp et al. 1999).

2288         Our overarching goal in this paper is to understand changes in bison distribution and  
2289 movement patterns with respect to effects of fire-frequency in the context of the transient  
2290 maxima hypothesis. We examine the relative distribution and movement of bison in a  
2291 continental tallgrass prairie in response to controlled spring fires at different burn frequencies.  
2292 Our study takes advantage of the experimental design at Konza Prairie Biological Station  
2293 (hereafter, KPBS) (Kansas, USA) that allows us to track bison preferences among watersheds  
2294 with different burn-interval treatments as they change from year to year. At KPBS, bison can  
2295 move freely among watersheds that are burned at 1-, 2-, 4-, and 20-year intervals, a process that  
2296 sets up fire-grazing interactions that underlie the development of highly variable grassland  
2297 structure and resource distribution. From 2007-2013, we tracked the movements of selected  
2298 female bison fitted with GPS collars to determine how bison used the habitat in response to



2299 spring prescribed burning treatments. The TMH predicts spatially-explicit differences in resource  
2300 quality in response to fire that should influence the distribution of grazers if plant quality is a key  
2301 factor underlying space use by bison. Key questions and predictions include: (1) Bison will  
2302 prefer recently burned watersheds to unburned watersheds during the growing season, where the  
2303 spatial pattern shifts in space following different sequences of controlled burning at the  
2304 watershed level. (2) Because of seasonal drops in foliage quality, bison preferences for recently  
2305 burned watersheds will decay as the season progresses, and no difference in use is expected  
2306 between burned and unburned watersheds during the non-growing season. And, (3) the TMH  
2307 predicts that bison will prefer recently burned watersheds with longer burn intervals compared to  
2308 recently burned watersheds with short burn intervals (e.g., annual burns) during the growing  
2309 season in years that watersheds are burned.

## 2310 **METHODS**

### 2311 *Study system*

2312 Our study was conducted at Konza Prairie Biological Station (KPBS) (Knapp et al. 1998), a  
2313 3,487-ha native tallgrass prairie preserve located in the Flint Hills grassland near Manhattan,  
2314 Kansas (39°05'N, 96°35'W; Fig.1). Vegetation is mostly tallgrass prairie dominated by C<sub>4</sub>  
2315 grasses (*Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Panicum*  
2316 *virgatum*) along with a diverse mixture of warm- and cool-season graminoids. Forbs constitute  
2317 ~75% of species richness (575 species) and vegetation biomass is >75% from grasses (Towne  
2318 2002, Collins and Calabrese 2012). Average monthly temperatures range from -2.7° C (January)  
2319 to 26.6° C (July). Average annual precipitation is ~835 mm, with 75% falling during the growing  
2320 season. A drought occurred from mid-summer of 2011 to the beginning of the growing season in

2321 2013, and ANPP in an ungrazed watershed, 1D, was 19% lower than the long-term average at  
2322 KPBS (Chapter 2, Fig 2).

2323 KPBS is divided into replicated, watershed-level experimental treatments that cross bison  
2324 grazing with fire frequency; ungrazed sites are not considered further. Bison at KPBS have free  
2325 access to 10 experimental watersheds over approximately 1040 ha (Fig.1) subjected to 1-, 2-, 4-,  
2326 and 20-year burn-interval treatments. All prescribed management burns in the bison-grazed  
2327 watersheds are conducted in the spring (mid-March to end of-April in the year of burning).  
2328 Watersheds are labeled according to fire frequency (1, 2, 4, 20 years between burns); all  
2329 watersheds included here are part of the bison unit (labeled as N, native grazer). A watershed  
2330 label indicates replicate number (A–D). For example, N04D is replicate-D of a bison grazed  
2331 watershed (N) burned every 4 years. Individual replicate watersheds with the same fire frequency  
2332 are burned in different years (additional information regarding watershed treatments found at  
2333 [kpbs.konza.ksu.edu](http://kpbs.konza.ksu.edu)). Watersheds in the bison unit studied here were burned in the spring  
2334 according to the schedule shown in Knapp et al. (1998, pp.9-11). We refer to watersheds that  
2335 were burned in the spring in the year in question as “recently burned”.

2336 The current bison herd was established in 1987, and is currently maintained at a stocking rate  
2337 of ~260 adult individuals, with ~100 calves born in each spring. This stocking rate of ~14.5g  
2338 bison/m<sup>2</sup> (~ 0.3 animals ha<sup>-1</sup>) results in a target density that removes ~25% of the standing  
2339 vegetation biomass annually (Knapp et al. 1999); the actual %-loss rate depends on precipitation  
2340 and forage quality. Individuals are weighed and general health assessed at an annual round-up of  
2341 all animals in late October/ early November; some individuals are culled at this time to maintain  
2342 prescribed stocking densities. Young animals (>1y of age), old animals, and excess males are  
2343 removed from the herd to maintain the stocking rate stated above, resulting in a sex ratio of

2344 mature females to mature males of approximately 4:1. All males are removed from the herd at  
2345 age 8, while females may remain until the age of 15 or older (Ungerer et al. 2013).

2346 Natural mineral soil licks and artificial mineral supplements are available in the enclosure and  
2347 the corral, respectively, throughout the year (Tracy and McNaughton 1995).

2348 *Data collection*

2349 Individual bison were tracked using Telonics TGW-3700 GPS collars during 2007-2013. Four  
2350 individuals were tracked in 2007, 7 in 2008-2009, 11 in 2010, 13 in 2011, 12 in 2012, and 11 in  
2351 2013. All individuals fitted with collars were older, matriarchal females; no males were collared.  
2352 Collars were fitted or replaced annually at the bison roundup, using the same individuals in  
2353 consecutive years when possible. Collars in the early part of the study (2007-2009, 5 individuals  
2354 in 2010) collected location data at intervals of two hours, while later collars (6 individuals in  
2355 2010, all individuals in 2011-2013) collected data at one-hour intervals during the dormant  
2356 season and at thirty-minute intervals during the growing season. Only 3D fixes with a DOP of  
2357 less than 3.5 were used for the analyses; ~98% of fixes met these criteria. Two-hour collar fixes  
2358 were used for all individuals in analyses described here. Data from twice-yearly periods during  
2359 which bison movement was restricted for herd management activities (October-November) and  
2360 other scientific work taking place on the site (March)) were excluded from analyses to avoid  
2361 distortion of behavioral analyses. Estimates indicate that collared animals are often accompanied  
2362 by about 30-40 individuals (Raynor, personal observations).

2363 Landscape attributes for use in the analysis were generated using ArcMap v10.1 with shape  
2364 files that included polygons of each watershed-type. A 30 x 30 m grid was overlain over the  
2365 bison enclosure to investigate how space use by bison changed with landscape characteristics.

2366 We obtained topographic information (elevation and slope) from a digital elevation model (2m<sup>2</sup>  
2367 resolution) for each grid cell.

2368 *Utilization distributions (UD) and resource utilization functions (RUF)*

2369 Separate utilization distributions (UD) were calculated for monthly distributions of each  
2370 individual bison using the biased-random bridge (BRB) method (Benhamou and Cornélis 2010;  
2371 Behamou 2011). All individuals for each month met the minimum number of 200 locations  
2372 recommended for UD analysis (Millspaugh et al. 2006; Benhamou and Cornélis 2010). The  
2373 diffusion coefficient was calculated using the function BRB.D (Benhamou 2011) in the package  
2374 ‘adehabitatHR’ for Program R (Calenge 2006). The shapefile containing the UD for each  
2375 individual was loaded into ArcMap together with landscape attributes for the enclosure. Any  
2376 points with a UD>99 were excluded so that only grid squares with a 99% probability of use are  
2377 analyzed. Landscape attributes for each 30 x 30 m grid cell was extracted using the Spatial  
2378 Analyst Extraction tool for ArcGIS v10.1 to create spatially explicit data files for the package  
2379 ‘ruf’ for Program R (Kertson and Marzluff 2010). The package ruf, version 1.5.2 (Handcock  
2380 2012), was used to analyze the UD. Resource utilization functions (RUF) were calculated for  
2381 each female bison to investigate the relationship between space use and landscape attributes on a  
2382 cell-by-cell basis (Marzluff et al. 2004). RUFs use a multiple regression approach to relate  
2383 multiple landscape variables of watershed-type, elevation, and slope, to a continuous measure of  
2384 the UD height. The resulting RUF coefficients indicate the contribution of each landscape  
2385 variable to the variation in the UD. To account for the spatial autocorrelation generated by  
2386 natural environmental autocorrelation (Schiegg 2003), the RUF uses a maximum likelihood  
2387 procedure with a Matern correlation function (Marzluff et al. 2004). Because we were interested  
2388 in how space use may change from month-to-month between burn periods, our analyses are

2389 based on each individual’s monthly UDs for each burn period from April (post-burn) to February  
 2390 (pre-burn). Indicator categories were created for the three watershed-types that burned that  
 2391 spring. For each year, watersheds that did not burn that spring were combined into one class  
 2392 (not-burned) and were used as a reference category against which two annually burned, one  
 2393 biannually burned, and one watershed burned every four years were compared. Because a  
 2394 twenty-year watershed was burned in 2012, the additional indicator variable “20y burned  
 2395 watershed” was incorporated into analyses for April 2012 to February 2013 only. The continuous  
 2396 landscape characteristics, elevation and slope, were not transformed. Log (100-UD) was used as  
 2397 the response variable to give a normal distribution (Kertson and Marzluff 2010; Papworth et al.  
 2398 2012). We estimated RUFs with standardized and unstandardized  $\beta$  coefficients to investigate the  
 2399 influence of landscape attributes on bison space use within the enclosed experimental landscape  
 2400 at KPBS and the potential for interactions with prescribed fire management activities (Marzluff  
 2401 et al. 2004; Kertson et al. 2011).

2402 To develop population level inferences, we calculated mean standardized  $\beta$  coefficients ( $\bar{\beta}$ )  
 2403 and variance for each landscape attribute by monthly period (Marzluff et al. 2004). Standardized  
 2404  $\beta$  coefficients were used to compare the relative importance of landscape factors on the  
 2405 concentration of use by each bison:

2406

$$\widehat{\beta}_j = \hat{\beta}_j^* \frac{S_{xj}}{S_{RUF}} \quad , \quad \text{(Equation 1)}$$

2407

2408

2409 where  $\hat{\beta}_j^*$  is the maximum likelihood estimate of the partial regression coefficient from the  
 2410 multiple regression estimate (unstandardized  $\beta$ ), and  $S_{xj}$  is the standard deviation of the UD  
 2411 values (Marzluff et al. 2004). Standardized  $\beta$  coefficients allow comparisons between the relative

2412 importances of landscape characteristics despite differences in quantifying scales. For both  
2413 individual and population level inferences, standardized coefficients with 95% confidence  
2414 intervals that did not overlap zero were significant predictors of space use (Marzluff et al. 2004).  
2415 If a resource coefficient was significantly different from zero, we inferred that resource use was  
2416 greater than (+) or less than (-) that expected based on the availability of the resource within the  
2417 enclosure (Marzluff et al. 2004). We ranked the relative importance of significant landscape  
2418 attributes using the absolute value of their mean standardized  $\beta$  coefficients. To assess  
2419 heterogeneity among individuals, we used individual standardized  $\beta$  coefficients and associated  
2420 95% confidence intervals to quantify the number of female bison with significant positive or  
2421 negative relationships with each of the landscape attributes. Relative use of watersheds (sum UD  
2422 values within the watershed divided by the area ( $m^2$ ) of that watershed) was tested for  
2423 significance using an analysis of variance (ANOVA), with post hoc Tukey's HSD tests when  
2424 appropriate (Marzluff et al. 2004). All means are given  $\pm$ SE. Significance level was set at 0.05  
2425 for all statistical analyses. SAS version 9.2 (SAS Institute Inc. 2011) was used for the ANOVA.

## 2426 **RESULTS**

### 2427 *Landscape-scale resource use*

2428 In the growing season, bison used recently-burned watersheds more frequently than watersheds  
2429 not-burned that year (ANOVA of sum UD by watershed type area;  $F_{3,1586}=177.3$ ,  $P<0.0001$ ; Fig.  
2430 3a). Watersheds that burned during spring and that had not burned for two or four years  
2431 previously experienced higher relative use by bison than annually-burned watersheds (Tukey  
2432 mean difference=0.01,  $P<0.0001$ ). The relative use of biannually-burned watersheds in the year  
2433 of a spring burn did not differ from use of watersheds burned after four years of not-burning  
2434 (Tukey mean difference=-0.005,  $P=0.18$ ). We had one opportunity to examine responses to

2435 burning after 20 years of not burning in N20A, which burned in 2012. In 2012, bison used  
2436 recently-burned watersheds more frequently than watersheds not-burned the previous spring  
2437 ( $F_{4,355}=125.9$ ,  $P<0.0001$ ). The four-year watershed burned in spring 2012 had higher use than all  
2438 other watersheds burned that spring (Tukey mean difference=0.035,  $P<0.0001$ ). In 2012, the sum  
2439 UD m<sup>2</sup> averaged across the early growing season was 0.045, 0.045, 0.081, and 0.046 for annual,  
2440 biannual, four, and twenty-year watersheds burned that spring, respectively.

2441 During the transitional mid-summer season when plant growth slows and begins to senesce,  
2442 all burn-type comparisons met our predictions that bison used recently-burned watersheds more  
2443 frequently higher use than watersheds not burned in the current year, and use of recently-burned  
2444 watersheds use was highest in watersheds with the longest elapsed time (4 y) since they were last  
2445 burned ( $F_{3,1526}=384.8$ ,  $P<0.0001$ ; Fig.3b). In 2012, use of all recently-burned watersheds was  
2446 greater than watersheds not-burned the previous spring. However, unlike responses seen in other  
2447 years, use of biannually-burned (sum UD m<sup>2</sup> = 0.055) and four-year (0.055) watersheds did not  
2448 differ from bison use of annually-burned (0.047) watersheds in 2012. *Post-hoc* comparisons  
2449 showed that bison use of N20A (0.06), the watershed that burned after twenty years of no  
2450 burning, was greater than that observed in the annually-burned watersheds (Tukey mean  
2451 difference=0.01,  $P=0.012$ ). Bison use of N20A did not differ from biannually-burned and four-  
2452 year watersheds ( $P=0.91$ ), nor did the biannually-burned and four-year watersheds differ in  
2453 relative use during the transitional season of 2012 ( $P=0.99$ ).

2454 In the dormant season, overall differences in relative use among burn-types were significant  
2455 ( $F_{3,1476}=25.5$ ,  $P<0.0001$ ; Fig.3c), and differed from those seen during the growing season.  
2456 Watersheds not burned the previous spring had higher use by bison in the dormant season than  
2457 did annually-burned and biannually-burned watersheds that were burned the pervious spring

2458 (Tukey mean difference=0.01,  $P<0.0001$ ). The use of watersheds that burned after four years of  
2459 no burning did not differ from use of not-burned watersheds in the dormant season (Tukey mean  
2460 difference=0.002,  $P=0.49$ ), although bison used four-year watersheds more often in the dormant  
2461 season than their use of recently burned annually- and biannually-burned watersheds (Tukey  
2462 mean difference=0.006,  $P<0.01$ ). Use of recently-burned biannually- and annually-burned  
2463 watersheds was not different ( $P=0.99$ ). In 2012, overall differences in relative use among burn-  
2464 types were significant in the dormant season ( $F_{4,345}=14.8$ ,  $P<0.0001$ ). Use of watersheds not-  
2465 burned the previous spring was higher than all recently-burned watersheds (Tukey mean  
2466 difference= -0.01,  $P<0.001$ ), except the biannually-burned watershed (Tukey mean  
2467 difference=0.001,  $P=0.99$ ). The biannually-burned watershed that burned the previous spring had  
2468 higher use than all recently burned watersheds during the dormant season (Tukey mean  
2469 difference=-0.01,  $P\leq 0.049$ ).

#### 2470 *Drivers of space use*

2471 Areas highly utilized by bison were associated with a greater availability of grassland burned in  
2472 the spring after two and four years without burning as compared to habitat not burned throughout  
2473 the growing season, while areas highly utilized in the dormant season were associated with  
2474 greater availability of unburned grassland as compared to all watershed types burned the  
2475 previous spring (Table 1). Throughout the dormant season, frequently-burned (annual and  
2476 biannual burns) watersheds were avoided to greater extent than watersheds that burned after four  
2477 years without burning, whereas the watershed that burned in 2012 after twenty years of no  
2478 burning had the highest level of avoidance as compared to unburned watersheds.

2479 We used standardized  $\beta$  coefficients to compare the relative importance of landscape factors  
2480 on the concentration of use by individual bison in each month of the study. Areas that were



2481 highly used by collared bison were associated with a greater proportion of recently-burned  
2482 grassland compared to not-burned grassland from May to September. During the dormant  
2483 season, bison preferentially used watersheds that did not burn the previous spring. Relative use  
2484 of recently-burned watersheds that burned at varying frequencies decayed as time since burn  
2485 increased (Fig 4). Bison showed higher use of burned watersheds than of watersheds not-burned  
2486 the previous spring in the growing and transitional seasons, but not during the dormant season.

2487       The most frequent, significant predictor of space use during the early growing season by  
2488 bison was the proportional availability of watersheds burned after 4 years without burning  
2489 compared to not burned watersheds ( $\bar{\beta} = 0.27$ ; ranging from -0.22 to 0.71; Fig. 5, Table 2). Space  
2490 use was significantly positively related to watersheds burned after four years compared to all not-  
2491 burned watersheds in 77% (149 of 195) of individuals in all growing season months (Table 2).  
2492 During the mid-summer transitional period, the most frequent significant predictor of space use  
2493 by female bison was the availability of watersheds burned after 4 years without burning  
2494 compared to all not-burned watersheds ( $\bar{\beta} = 0.29$ ; ranging from 0.07 to 0.53). Space use was  
2495 significantly positively related to watersheds burned after four years compared to all not-burned  
2496 watersheds in 91% (172 of 189) of individuals in all transitional season months. In contrast, the  
2497 most frequent significant predictor of space use during the dormant season was the proportional  
2498 availability of watersheds not-burned the previous spring compared to annually-burned  
2499 watersheds ( $\bar{\beta}$  ranging from -0.31 to 0.08). Space use was significantly negatively related to  
2500 watersheds burned annually compared to all not-burned watersheds in 69% (125 of 181) of  
2501 individuals in all dormant season months. Elevation was the strongest topographical predictor of  
2502 space use during the transitional season months ( $\bar{\beta} = 0.26$ ; ranging from -0.35 to 0.62), while  
2503 elevation was less important as a predictor during the growing ( $\bar{\beta} = 0.16$ ; ranging from -0.15 to

2504 0.47) and dormant season months ( $\bar{\beta} = 0.07$ ; ranging from -0.18 to 0.38; Table 2). Slope was  
2505 most frequently a significant topographical predictor of space use during the dormant season  
2506 months when behavioral avoidance was evident ( $\bar{\beta} = -0.02$ ; ranging from -0.05 to 0.006; Table  
2507 2). Space use was significantly negatively related to slope in 16% (29 of 181) of individuals in  
2508 all dormant season months, while a positive relationship between space use and slope for  
2509 individual female bison occurred during the growing season (5%[9 of 195]) and transitional  
2510 season months(1%[1 of 189]).

## 2511 **DISCUSSION**

2512 In this study, we focused primarily on how fire modulates the spatial and temporal dynamics of  
2513 bison distribution in response to forage quality affected through soil-plant interactions. Bison at  
2514 KPBS are not subject to predation, the physical features of the site have only a small impact on  
2515 their distribution (this study, Vinton et al. 1993), and a range of fire frequencies are manipulated  
2516 experimentally at the watershed level; therefore, this site provides a unique opportunity to tease  
2517 apart their landscape-level distribution in response to fire-induced variation in forage quality and  
2518 quantity.

2519 To test our primary hypotheses, we quantified space use by bison in response to fire  
2520 frequency using the probabilistic utilization distribution (UD) and its correlation with landscape  
2521 characteristics (Resource Utilization Function, RUF; Marzluff et al. 2004). UDs quantify an  
2522 animal's relative use of space in terms of a probabilistic density function (Van Winkle 1975),  
2523 removing pseudoreplication without presuming equal usage across the entire available habitat.  
2524 This approach accommodates statistical issues that arise from the repeated collection of GPS  
2525 collar relocation points from the same animal. UDs were used to quantify space use in relation  
2526 to categorical and continuous resource variables using resource utilization functions. The

2527 significance of regression coefficients was calculated for each animal and across individuals to  
2528 test key individual-and population-level hypotheses.

2529         Bison track recently burned watersheds, a response that has been observed repeatedly.  
2530 During the growing season, bison preferentially use watersheds burned in the spring of that year  
2531 over unburned ones, a finding consistent with other studies of bison habitat use in response to  
2532 fire (Coppock and Detling 1986, Shaw and Carter 1990, Vinton et al. 1993, Nellis and Briggs  
2533 1997, Coppedge and Shaw 1998, Biondini et al. 1999, Wallace and Crosthwaite 2005, Schuler et  
2534 al. 2006, Allred et al. 2011a). Different burn schedules at different sites lead to the same  
2535 qualitative conclusions, indicating the generality of the pattern. For example, at the Tallgrass  
2536 Prairie Preserve (TPP) in Oklahoma (Coppedge and Shaw 1998, Wallace and Crosthwaite 2005,  
2537 Schuler et al. 2006, Allred et al. 2011a), bison preferentially selected burned patches distributed  
2538 randomly on the landscape that differ in size and season burned (Allred et al. 2011a). While  
2539 bison-grazed watersheds at KPBS are only burned in the spring at set burn frequency treatments,  
2540 both schedules yielded similar outcomes. Our study builds on such fire-driven responses and  
2541 assesses the effect of different fire frequencies at the watershed-level to bison responses. We link  
2542 differential responses to prescribed burning at different frequencies to a possible ecosystem level  
2543 mechanism – the transient maxima hypothesis and the creation of spatially-explicit, shifting  
2544 mosaics of forage suitability.

2545         *Bison distribution and the Transient Maxima Hypothesis*

2546 Clear distinctions in bison habitat use were affected by watershed burn intervals. Among  
2547 recently burned watersheds, bison preferentially used watersheds with higher burn intervals (2, 4  
2548 or 20 years) compared to annually burned watersheds; space use was graded among 1, 2 and 4-  
2549 year intervals with the highest use observed for watersheds burned at 4 year intervals. At KPBS,

2550 soil nitrogen is more limiting to vegetation growth in annually burned watersheds, while light  
2551 limitation becomes more important in unburned watersheds with litter buildup (Blair 1997).  
2552 Infrequently burned watersheds at KPBS typically show increased aboveground net primary  
2553 productivity (ANPP) and foliar-N concentrations compared with annually burned watersheds in  
2554 the growing season following a burn (Seastedt et al. 1991, Seastedt and Knapp 1993, Blair 1997,  
2555 Raynor et al. 2015). This increase in ANPP for infrequently-burned watersheds during a burn  
2556 year when light is no longer limiting is linked to the transient high availability of soil-N after  
2557 several years without fire and the accumulation of litter (leading to light limitation) relative to  
2558 annually burned watersheds (Blair 1997). Furthermore, because annually burned sites are more  
2559 likely to be N-limited than are infrequently burned sites in the year of burn, foliar-N is higher in  
2560 plants in the recently burned sites subjected to longer burn interval watersheds (Blair 1997). The  
2561 high ANPP in recently burned plots with longer burn intervals combined with higher, foliar  
2562 nitrogen content likely explains why bison select these watersheds (Coppock et al. 1983, Allred  
2563 et al. 2011a).

2564 Mechanisms underlying how non-equilibrium forage resources should direct grazer  
2565 resource utilization largely reflect the importance of forage quality. The TMH was originally  
2566 proposed as a soil-plant-light interaction, with an emphasis on explaining vegetation responses  
2567 (Seastedt and Knapp 1993, Blair 1997). Increased ANPP and foliar-N was observed in the year  
2568 of burn compared to unburned sites, with the magnitude of the response increasing with elapsed  
2569 time since the watershed's last burn (Blair 1997). Because bison and other ungulate grazers  
2570 routinely respond positively to forage with higher protein content (Allred et al. 2011a,b), and  
2571 actively select the highest quality patches (Archibald and Bond 2004, Ranglack and du Toit  
2572 2015, Raynor Chapter 4, this thesis) as long as sufficient vegetation standing stock exists, one

2573 expects that the strength of behavioral selection for watersheds should track vegetation recently  
2574 released from light- and soil-N limitation. Our results indicate this occurs during the growing  
2575 season in the year of burn as bison preferentially select infrequently burned watersheds over  
2576 frequently burned watersheds, and select burned watersheds over unburned ones. Moreover, the  
2577 KPBS management plans for prescribed burning results in a shifting mosaic of recently burned  
2578 watersheds among years, changing the spatial relationships of where the most profitable,  
2579 nutrient-laden watersheds are each year. Bison reliably track the shifting mosaic of watershed  
2580 forage quality as expected.

2581         In all cases, effects of elevated forage quality on bison foraging as predicted by the  
2582 transient maxima hypothesis last about one growing season for all burn histories. However, the  
2583 effects of recent burning on elevated space use of watersheds reflected burn histories that  
2584 extended into September in 4-y burned watersheds, but ended in August for those that were  
2585 annually or biannually burned. We presume the 20-year watershed, N20A, that burned in  
2586 spring 2012 was not the strongest predictor of space use during that growing season because  
2587 almost half of this watershed was ungrazable due to woody vegetation cover (J. Briggs, personal  
2588 communication). The effect of woody encroachment on ungulate space use remains mostly  
2589 unexplored in mesic grasslands (but see Allred et al. 2013), which is cause for concern as this  
2590 biome is facing a major risk of conversion to woodland (Ratajczak et al. 2014 and references  
2591 therein). Moreover, campaigns in the Great Plains to limit woody encroachment using altered  
2592 fire regimes and implementation of prescribed-burning programs (Twidwell et al. 2013), such  
2593 efforts may benefit from our record of native grazer space use in mesic grassland managed with  
2594 prescribed-burning under varying temporal frequencies.

2595 Previous work elsewhere has shown that large grazer responses to burning can be short-  
2596 lived (i.e. ~1 month; Augustine and Derner 2014). In this study, we found use of burned areas  
2597 compared to not-burned areas lasted an entire growing season (May to September). We surmise  
2598 that the plant productivity of this tallgrass prairie interacted with soil-N availability in recently-  
2599 burned watersheds to maintain the availability of high quality forage well into mid-summer. In  
2600 infrequently-burned watersheds, the availability of high quality forage has been shown to last  
2601 through the transitional season (Raynor et al. 2015), thus we expected bison to respond to the  
2602 resources throughout the summer. Furthermore, recent studies have demonstrated that grazers  
2603 track the availability of high forage quality in efforts to ensure reproductive success (Bischof et  
2604 al. 2012, Si et al. 2015).

2605 *Seasonal space use in response to fire*

2606 In recently unburned watersheds, bison exhibit a pattern of very low use (avoidance) during the  
2607 growing season and relatively higher use during the dormant season. This pattern was evident in  
2608 the 20-year burns during our study, with relatively high dormant season use in N20B in  
2609 particular. Bison may be attracted to low burn frequency watersheds because these plots tend to  
2610 have higher concentrations of cool season, C<sub>3</sub> grasses, which have higher digestibility during the  
2611 dormant season (Vinton et al. 1993, Steuter and Hiding 1999, Post et al. 2001). Moreover, as  
2612 the dominant C<sub>4</sub> forage matures at KPBS, bison may shift foraging strategies to locate C<sub>3</sub> grasses  
2613 in unburned watersheds (Vinton et al. 1993, Raynor Chapter two).

2614 In semi-arid rangeland, however, cattle actively select recently burned areas during the  
2615 period of rapid vegetation growth, but to a lesser degree than that observed in highly, productive  
2616 mesic grasslands such as KPBS; topography becomes important after greening periods end  
2617 (Augustine and Derner 2014). Furthermore, Augustine and Derner (2014) also quantified the

2618 amount of time cattle were grazing in burned areas, the only way a behavioral response to fire  
2619 could be detected unlike other studies in mesic grasslands that did not account for foraging-  
2620 specific resource selection (Allred et al. 2011a, Augustine and Derner 2014).

2621 Differences in woody vegetation cover are possible explanations for the higher use of  
2622 individual watersheds with similar burn histories, and ways of factoring these into analysis need  
2623 to be developed further. In the growing season, cattle and bison seek thermal refugia in wooded  
2624 areas as air temperature increases, which may be compounded by predicted warming in the Great  
2625 Plains (Allred et al. 2013). Understanding how grazer space use differs in grasslands with  
2626 varying woody vegetation cover is critical because their affinity for thermal refugia in periods of  
2627 extreme air temperature may drive reductions in riparian vegetation productivity and increases of  
2628 nonpoint source pollution (Belsky et al. 1999, Bailey 2005, Allred et al. 2013).

2629 Our study only utilized adult female bison, but space use and movement patterns may vary  
2630 by sex and developmental stage (Ruckstuhl and Neuhaus 2000). For example, work by  
2631 Coppedge and Shaw (1998) show that bulls do not prefer spring burned areas during the growing  
2632 season, but mixed-sex herds do. Thus, we posit that male bison groups may not need to track  
2633 high quality forage because they are not nursing offspring. KPBS bulls are known to have lower  
2634 quality diets than calves, cows, and juveniles (Post et al. 2001).

### 2635 *Management implications*

2636 Managing for habitat heterogeneity is a conservation strategy that can increase taxonomic  
2637 diversity in grassland systems (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006, Engle et al.  
2638 2008). Managing grasslands by allowing large herbivores to choose among patches of varying  
2639 burn frequency in the landscape, thus interactively influences vegetation heterogeneity through  
2640 grazing of burned and unburned patches, is a means to sustain grassland heterogeneity, form, and

2641 function (Fuhlendorf et al. 2006, 2012). Many grassland bird populations are generally declining,  
2642 and increasing habitat heterogeneity may be an especially important conservation practice for  
2643 maintaining grassland bird populations (Fuhlendorf et al. 2006). For example, insectivorous  
2644 Upland Sandpiper (*Bartramia longicauda*) select grazed watersheds at KPBS (Sandercock et al.  
2645 2015), which offer higher densities of grasshoppers than ungrazed watersheds (Joern 2004).  
2646 Understanding how bison use habitats in response to fire frequency and distribution will be key  
2647 for implementing management regimes that conserve grassland systems and lead to increased  
2648 diversity. Although the generality of these results to other grasslands remains to be tested, we  
2649 anticipate that this interaction between nonequilibrium forage resources and ungulate foraging  
2650 behavior is a key driver for ungulate distributions in fire-prone systems generally. Because  
2651 grazing can modulate plant species diversity while concomitantly enhancing invertebrate  
2652 abundance and diversity when interacting with fire (Collins et al. 1998, Joern 2004; 2005,  
2653 Collins and Calabrese 2012), our findings may improve land-use practices dedicated to  
2654 maintaining landscape heterogeneity.

### 2655 *Conclusions*

2656 Our project is the first quantitative examination of the spatial ecology of native grazer herd in  
2657 response to varying burn frequencies in tallgrass prairie, one that provides a direct link to the  
2658 transient maxima hypothesis for consumers. We found that the mean space use of watersheds  
2659 burned at different yearly intervals followed a graded pattern of low to high use across a  
2660 spectrum of watersheds burned annually to every four years. Although use of a watershed that  
2661 burned after twenty years of no burning was greater than annually-burned watersheds, its lack of  
2662 grazable area due to woody encroachment likely kept it from being used more than a watershed  
2663 burned after four years without burning. We observed that the strongest predictor of space use



2664 throughout the growing season was the availability of grassland burned after four years of no  
2665 burning over unburned watersheds, whereas the availability of grassland not-burned the previous  
2666 spring over annually-burned was the best predictor during the dormant period. Moreover,  
2667 preference for four-year burns compared to not-burned watersheds lasted longer into the growing  
2668 period than frequently-burned watersheds; thus suggesting soil-N availability for grazing-  
2669 induced graminoid regrowth in infrequently-burned grassland may indirectly sustain grazer use  
2670 in the year that watershed-type burns at a higher level than frequently-burned grassland. Our new  
2671 understanding of bison space use could be used to inform management of grassland with intact  
2672 fire-grazer interactions. The resource utilization function approach was developed to allow  
2673 researchers to investigate why animals use resources and space disproportionately within their  
2674 available landscape (Marzluff et al. 2001). Our use of this approach provides insight into spatial  
2675 and temporal dynamics of bison behavioral ecology in relation to landscape characteristics and  
2676 management-induced variation in resource availability that can be targeted in management and  
2677 assessment of large herbivore land use dynamics (Boyce et al. 2002, Millspaugh et al. 2006).

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2846 **Table 4-1. Mean unstandardized coefficients ( $\bar{\beta} \pm SE$ ) for resource utilization functions (RUFs) calculated for female Plains**  
 2847 **Bison (*Bison bison bison*) from 2007-2013 at Konza Prairie Biological Station. Burn-types (annual, biannual, four, twenty)**  
 2848 **modeled in response to not-burned grassland availability, showing how space use by bison differs between months in the study**  
 2849 **area. Positive coefficients indicate that use increases with increasing availability of the resource.**  
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Month	n	Intercept	Annual	Biannual	Four	Twenty*	Elevation	Slope
April	65	0.675 (0.657)	0.02 (0.145)	-0.204 (0.237)	-0.122 (0.241)	0.058 (0.073)	0.006 (0.002)	0.003 (0.001)
May	59	0.366 (0.398)	1.029 (0.089)	1.32 (0.191)	1.306 (0.229)	1.206 (0.051)	0.005 (0.001)	0.002 (0.001)
June	62	-0.914 (1.145)	0.849 (0.14)	1.325 (0.255)	1.448 (0.217)	1.391 (0.017)	0.009 (0.003)	0.002 (0.001)
July	61	-1.886 (1.932)	0.677 (0.157)	1.125 (0.244)	1.245 (0.168)	0.959 (0.035)	0.012 (0.005)	0.001 (0.001)
August	65	-3.743 (1.532)	0.427 (0.196)	0.907 (0.255)	1.0 (0.161)	0.623 (0.047)	0.017 (0.004)	0.002 (0.001)
September	60	1.412 (1.061)	0.21 (0.131)	0.474 (0.233)	0.672 (0.143)	0.122 (0.096)	0.004 (0.003)	-0.001 (0.001)
December	65	2.436 (0.978)	-0.543 (0.066)	-0.503 (0.099)	-0.246 (0.162)	-0.449 (0.168)	0.001 (0.002)	-0.004 (0.001)
January	64	0.817 (1.013)	-0.252 (0.112)	-0.398 (0.143)	-0.26 (0.235)	-0.789 (0.183)	0.005 (0.003)	-0.003 (0.001)
February	64	1.708 (0.974)	-0.286 (0.091)	-0.499 (0.242)	-0.178 (0.177)	-1.425 (0.124)	0.003 (0.002)	-0.004 (0.001)

2851 \*N20a was burned only in 2012; number of collared bison per month: 12,12,12,12, 12,12,13,10, and 11.

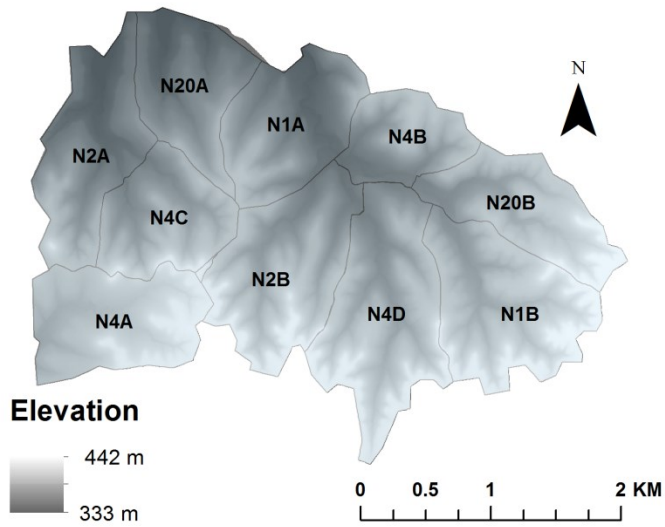
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2854 **Table 4-2. Standardized  $\beta$  RUF coefficients for female bison for each month. The table illustrates the standardized coefficient**  
 2855 **averaged across the study period and the number of significant coefficients (where the 5-95% confidence intervals did not**  
 2856 **include 0) for each RUF variable in each month. The highest standardized  $\beta$  coefficient for each bison is the best predictor of**  
 2857 **space use. Boldface indicates variable with the greatest number of times individual bison had significant selection coefficients**  
 2858 **per month in that season.**

Month	Annual	+	-	Best	Biannual	+	-	Best	Four	+	-	Best	Twenty	+	-	Best	Elevation	+	-	Best
April	0.01	13	36	1	-0.06	21	27	1	-0.04	25	29	3	0.01	3	1	0	0.15	42	11	2
May	0.44	60	0	1	0.44	58	0	3	0.41	60	3	3	0.33	12	0	0	0.11	36	6	0
June	0.36	61	1	0	0.43	58	1	3	0.44	64	0	3	0.41	12	0	0	0.21	50	10	1
Growing	0.27	134	37	2	0.27	137	28	7	0.27	<b>149</b>	32	9	0.25	27	1	0	0.16	128	27	3
July	0.28	59	2	0	0.36	57	1	2	0.36	64	0	2	0.28	12	0	0	0.28	48	12	2
August	0.18	44	10	0	0.29	53	3	2	0.30	60	2	2	0.19	10	2	0	0.40	55	7	3
September	0.09	35	13	0	0.15	38	14	3	0.19	48	3	2	0.05	7	2	0	0.11	27	18	2
Transition	0.18	138	25	0	0.27	148	18	7	0.29	<b>172</b>	5	6	0.17	29	4	0	0.26	130	37	7
December	-0.21	0	52	4	-0.14	9	38	1	-0.05	11	34	0	-0.13	3	9	0	0.02	24	21	1
January	-0.10	10	39	1	-0.11	8	40	1	-0.05	11	35	2	-0.21	0	9	0	0.12	30	14	2
February	-0.11	6	34	0	-0.12	14	35	4	-0.04	20	23	0	-0.34	0	11	1	0.08	31	14	1
Dormant	-0.140	16	<b>125</b>	5	-0.120	31	113	6	-0.046	42	92	2	-0.226	3	29	1	0.073	85	49	4
Total	0.12	288	187	7	0.15	316	159	20	0.18	363	129	17	0.07	59	34	1	0.17	343	113	14

2859 Slope was not the best predictor of bison space use throughout the study; the number of individual bison with significant positive slope  
 2860 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,  
 2861 September, December, January, and February, respectively.



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2863 **Figure 4-1. Map of bison enclosure at Konza Prairie Biological Station, Manhattan, KS.**

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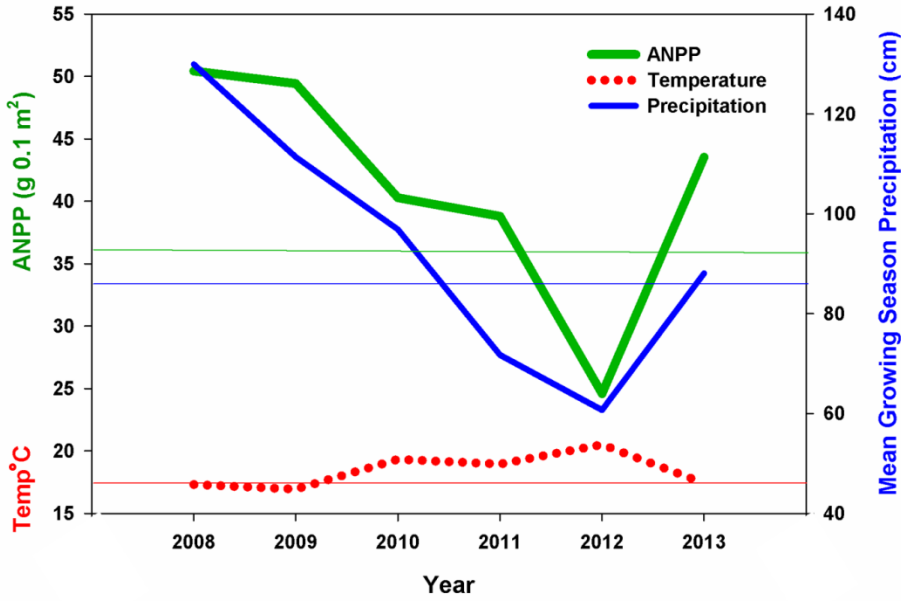
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2875 **Figure 4-2. Cumulative growing season (Mar-Oct) precipitation (blue line) with 30-year**  
 2876 **mean of cumulative growing season precipitation (dashed blue line), annual net primary**  
 2877 **productivity(ANPP) averaged across ungrazed watersheds: 04B, 1D, 20B (green line) with**  
 2878 **29-year mean (dashed green line; Konza-LTER dataset PAB01), and average growing**  
 2879 **season ambient temperature (°C; red line) with 32-year mean (dashed red line) during**  
 2880 **2008-2013 at Konza Prairie Biological Station, Manhattan, Kansas, U.S.A.**

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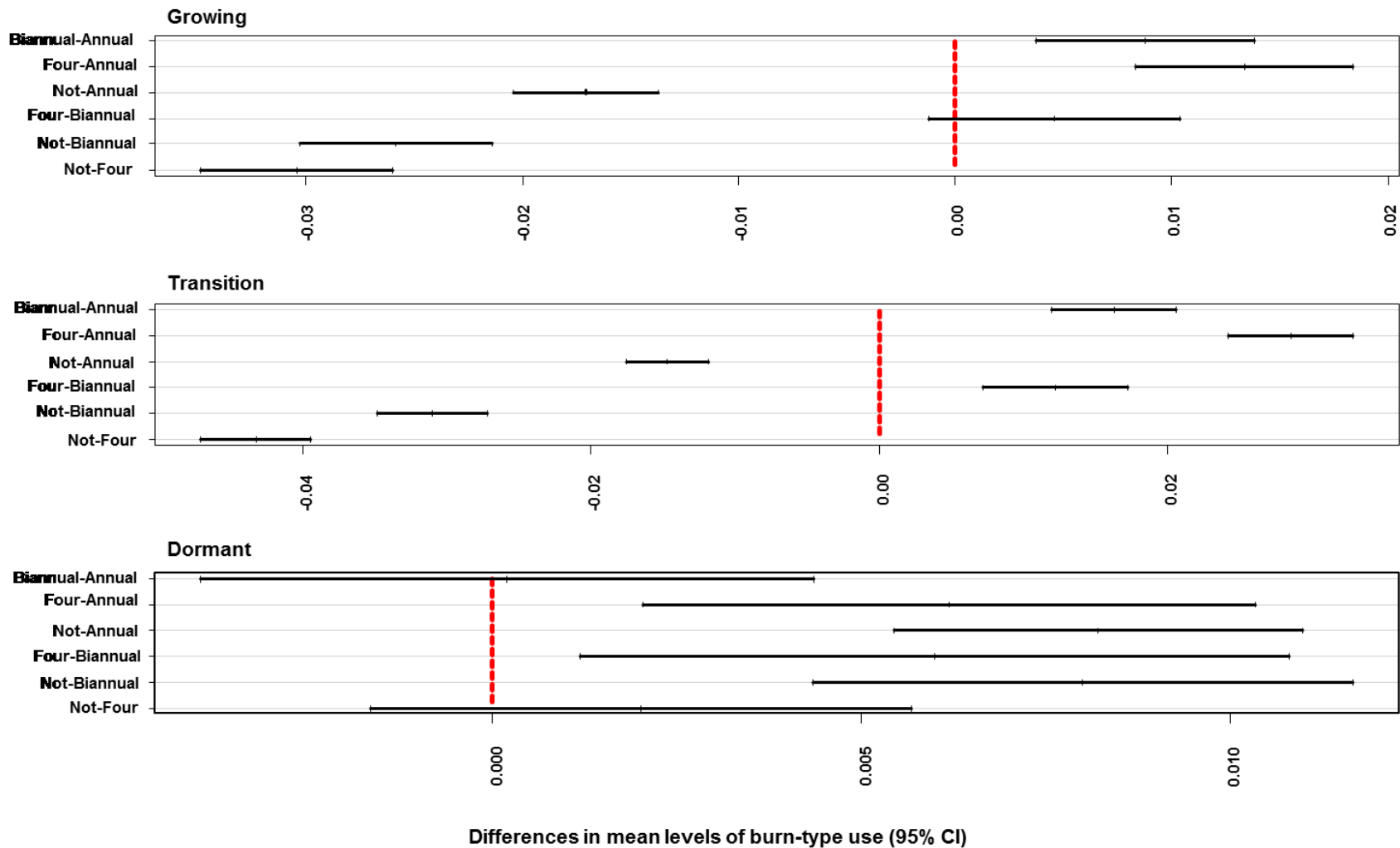
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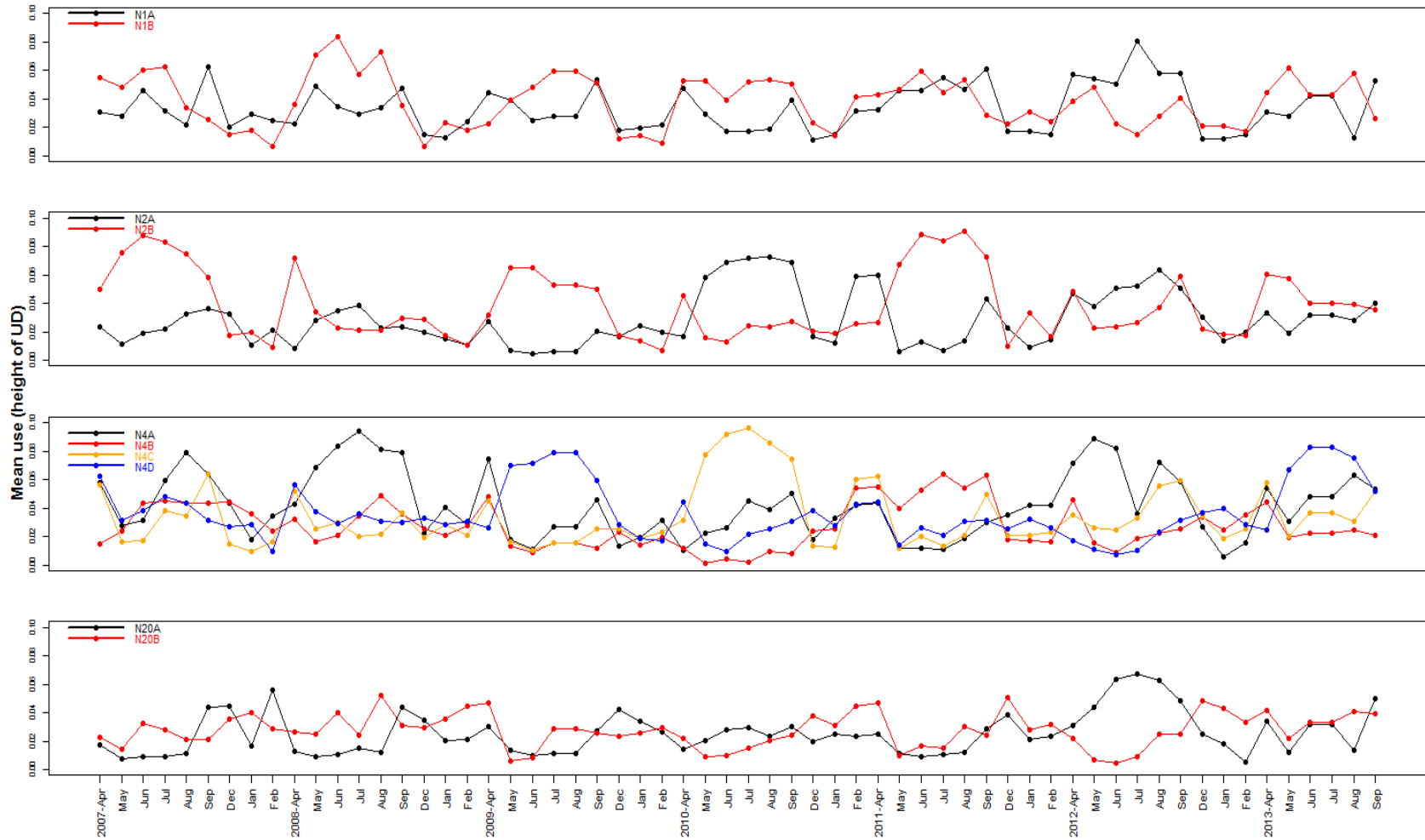
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2891 **Figure 4-3. Differences in levels of mean relative use of available burn-types from 2007-2013 at Konza Prairie Biological**  
 2892 **Station excluding 2012 when a twenty-year burn occurred. Relative use was calculated from the sum of UD values within**  
 2893 **habitat divided by area (m<sup>2</sup>) of that habitat for each month within a season.**



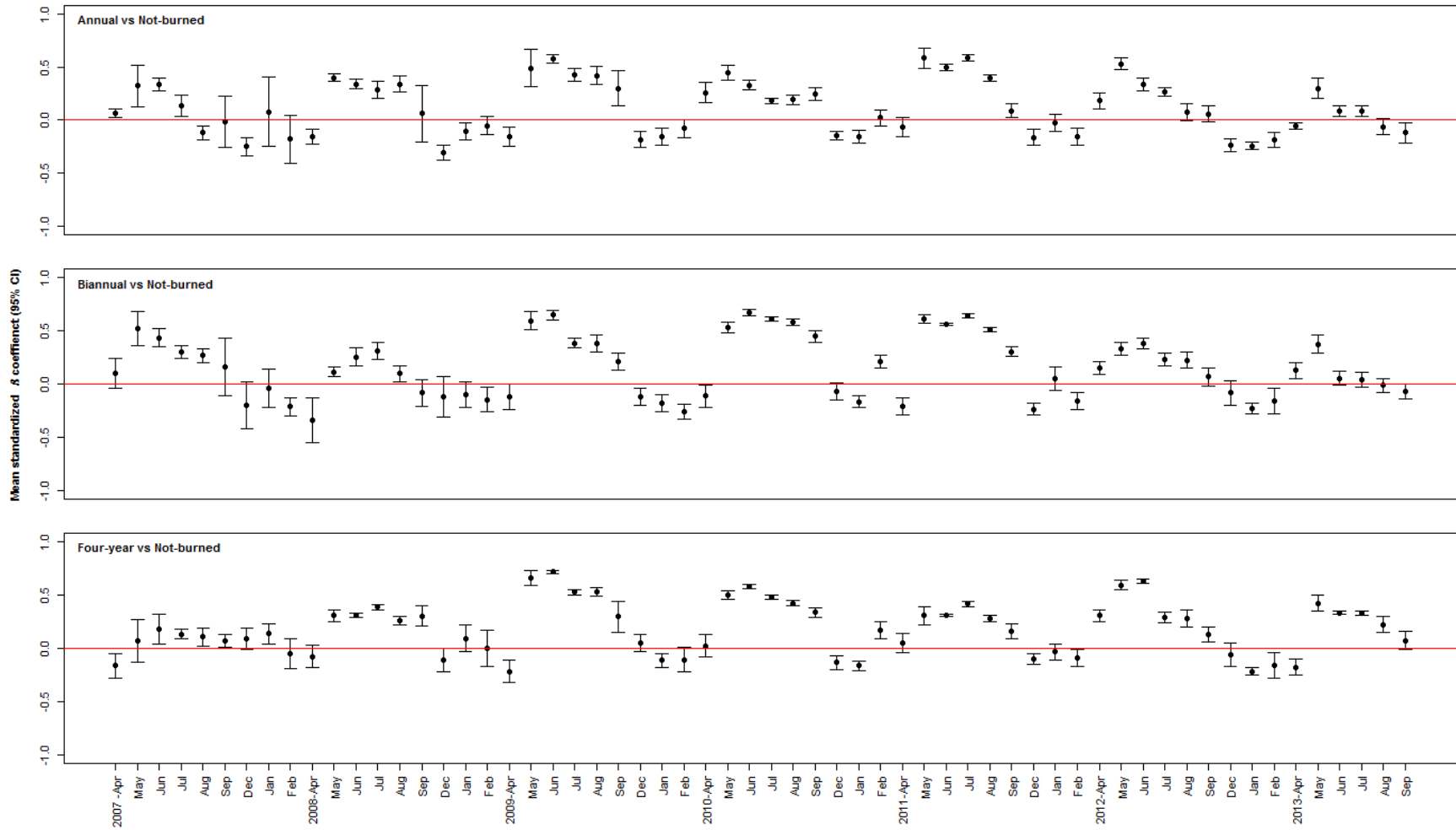
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2895 **Figure 4-4. Relative use (sum UD / m<sup>2</sup> of watershed) of each watershed over each month of study. Means are calculated by**  
 2896 **summing the heights of the UD at each grid cell comprising a specific watershed within the bison enclosure from 2007-2013 at**  
 2897 **Konza Prairie Biological Station, near Manhattan, Kansas, U.S.A.**

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**Figure 4-5. Monthly population-level standardized  $\beta$  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.**



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2907 **Chapter 5 - Resource selection by the native grazer *Bison bison* in a**  
2908 **nutritionally heterogeneous landscape**

2909 **ABSTRACT**

2910 Maintaining the fire-grazer interaction in grasslands requires a mechanistic understanding of the  
2911 effects of landscape heterogeneity on grazer movements and habitat selection. Using an analytic  
2912 framework for simultaneously quantifying the effects of habitat preference and intrinsic  
2913 movement on space use, we examined how native grazers assess the forage quantity-quality  
2914 tradeoff at the landscape-scale. We evaluated the association of dynamic, biotic forage resources  
2915 and static, abiotic landscape features with movement and habitat selection in an experimental  
2916 landscape, where forage resources vary in response to prescribed burning, grazing by a native  
2917 grazer (*Bison bison bison*), and variable weather. Our overarching goal was to determine how  
2918 biotic and abiotic factors govern habitat preference and movement of plains bison in nutritionally  
2919 heterogeneous grassland with an intact fire-grazer interaction. We integrated spatially-explicit  
2920 relocations of GPS-collared bison and vegetation surveys to link bison distribution in a landscape  
2921 with an intact fire-grazer interaction. High-quality upland habitat constrained bison movement  
2922 rates during the growing season, while selection for slope and aspect did not limit movement.  
2923 Preference for habitat with high foliar crude content and low stature forage structure was  
2924 consistent across years, although substantial variation in the magnitude of selection for high  
2925 quality forage occurred among years. In years of below-average plant productivity, the strength  
2926 of selection for high foliar crude protein content was greater than in years of normal to above  
2927 average plant productivity. Avoidance of areas with high herbaceous biomass content was  
2928 strongest during years of low plant production. The inverse relationship in selection between  
2929 forage quality and quantity varied in magnitude across years. Climatic interactions in plant

2930 quality and quantity seemingly shaped female bison distribution as they sought to maximize  
2931 nutrient gains by selecting areas containing immature plants of high nutrient value. Our results  
2932 provide experimental evidence for documenting a key behavioral mechanism that drives fine-  
2933 scale movement of a large grazer in response to fire- and local-climate-induced changes in forage  
2934 attributes. Combined, results elucidate a complex strategy that promotes nutrient acquisition and  
2935 illustrates the utility of linking foraging theory with insights from consumer resource, movement,  
2936 and fire ecology.

2937 Keywords: animal movement, habitat preference, forage quantity, local climate, protein content,  
2938 step selection

## 2939 **INTRODUCTION**

2940 Many animals respond to environmental heterogeneity by fostering selectivity in their choice of  
2941 habitats to best fulfill basic nutritional requirements. Habitat selection is the process whereby  
2942 individuals preferentially use a nonrandom set of available habitats (Morris 2003) that result  
2943 from habitat-specific variation in fitness and have important implications for population  
2944 dynamics (Fretwell and Lucas 1970, Holt 1985, Pulliam 1988). Movement is a behavioral  
2945 mechanism employed by animals to mediate trade-offs in life-history requirements arising from  
2946 heterogeneous distribution of forage resources. Therefore, understanding how animal movement  
2947 and habitat preference patterns respond to the interaction of biotic and abiotic processes as they  
2948 influence forage attributes in heterogeneous environments is paramount to evaluating ecosystem  
2949 structure and function. The interactions between various biotic and abiotic processes are complex  
2950 and dynamic over time, and initial movement patterns may not reflect long-term responses and  
2951 dynamics to biotic or abiotic drivers. Therefore, long-term data and experimental manipulations  
2952 are needed to assess how multiple drivers interact to affect animal distribution and space use  
2953 over the long term.

2954           Animal distribution is considered to be fitness-based as all animal movements incur a  
2955 cost to an individual in terms of energy/nutrient resources, time (opportunity cost), and exposure  
2956 to risk (Ricketts 2001, Baker and Rao 2004, Fahrig 2007). For example, the cost of movement to  
2957 an ungulate moving through a nutritionally heterogeneous grassland may be influenced by  
2958 topographic variation (reducing movement rate and increasing the energy cost of movement)  
2959 compared to moving in a habitat with less topographical relief, limited availability of high-  
2960 quality forage (opportunity cost relative to occupying homogeneous, low quality habitat), and  
2961 possibly an increased risk of predation arising from the increased likelihood of encountering  
2962 predators when covering more geographic space (mortality risk). Reduced movement rates  
2963 should result in areas where energetic costs are low, predation risk is minimal, and diet  
2964 optimization is likely.

2965           Because foraging goals (e.g. intake of protein and energy) dictate diet choices, an initial  
2966 step to understand food-motivated animal distribution is to identify the objective that foragers  
2967 pursue. For example, ruminants can maximize their instantaneous intake rate of digestible energy  
2968 by consuming large plants that result in rapid satiation but reduced digestibility compared to  
2969 feeding on small plants (Illius et al. 1999). Alternately, foragers can maximize their daily intake  
2970 of digestible energy by foraging on small and/or immature plants, which demand longer cropping  
2971 times and extended time to satiation, but ultimately provide more digestible energy due to their  
2972 higher digestibility than large plants (Wilmshurst et al. 1999a, Bergman et al. 2001, Shipley  
2973 2007). Few studies have assessed the dynamic forage quantity-quality tradeoff experienced by  
2974 ungulates to meet nutritional and energetic requirements. Plains bison (*B. bison bison*) in boreal  
2975 forest and meadows dominated by C<sub>3</sub> vegetation make foraging decisions that maximize their  
2976 instantaneous intake rate of digestible energy at the cost of reduced daily energy gains (Bergman

2977 et al. 2001, Fortin et al. 2002, Babin et al. 2011); these studies did not examine responses to  
2978 protein. Because nitrogen (protein) content in forage is often limiting to herbivores, diets  
2979 deficient in protein can delay growth and loss of body condition (Van Soest 1994). Animals may  
2980 adopt a foraging strategy that yields rapid nutrient assimilation and energy intake to meet daily  
2981 nutrient requirements for basic metabolic function (Owen-Smith and Novellie 1982), especially  
2982 where nutrients are limited, which can shape herbivore distribution across a landscape  
2983 (McNaughton 1988). Yet, the impact of the forage quantity-quality tradeoff on large herbivore  
2984 distribution in fire-dependent, C<sub>4</sub> forage-dominated landscapes remains to be examined.

2985         Our general goal was to determine how biotic and abiotic factors govern habitat  
2986 preference and movement of plains bison in nutritionally heterogeneous grassland dominated by  
2987 warm season (C<sub>4</sub>) graminoids subject to a variable continental climate. Our study area, Konza  
2988 Prairie Biological Station (KPBS), is a tallgrass prairie research tract where experimental  
2989 watersheds are managed with varying temporal frequencies of prescribed-fire. During the  
2990 growing season, bison are attracted to recently-burned sites over those not burned during the  
2991 spring burning period (Vinton et al. 1993, Chapter 4, this thesis), and the magnitude of this  
2992 attraction to recently-burned grassland depends on the watershed's burn history (Chapter 4; this  
2993 thesis). Here, we assess biotic and abiotic environmental variables related directly (forage  
2994 biomass and quality) or indirectly (landscape topography) to the use of a location by bison  
2995 (Beyer et al. 2010). Specifically, we investigate the effect of topography along with forage  
2996 quantity (herbaceous biomass) and quality (foliar protein) on bison habitat preference and  
2997 movement patterns. Our primary objective was to assess habitat selection patterns at the  
2998 landscape level along the forage quantity-quality resources gradient and in response to  
2999 topographical characteristics that are dynamic or static in time, respectively (Beyer et al. 2014).

3000 Protein was used to represent forage quality as this biomolecule is integral for maintenance of  
3001 intrinsic biological processes in adults and nursing offspring (Van Soest 1994). Because the  
3002 collared animals studied here were reproductive females, we predicted that grass protein content  
3003 would be an important driver of habitat selection or habitat types would be strongly preferred if  
3004 they offer optimum levels of forage and quantity.

3005         Developing tools that help predict animal distributions in the face of environmental  
3006 change is integral to understanding ecosystem function. Fundamental knowledge of resource use  
3007 decisions should provide stronger quantitative grounds for projecting future ecological scenarios  
3008 (Coreau et al. 2009). Our dynamic vegetation modelling approach incorporates vegetation  
3009 responses to prescribed burning and precipitation in the growing season so that inferences made  
3010 from movement modelling in this study reflects large herbivore responses to fire- and  
3011 precipitation induced variation in forage quantity and quality, and thus describes the fire-grazer  
3012 interaction, a critical ecological process within tallgrass prairies (Fuhlendorf and Engle 2001,  
3013 Allred et al. 2011a). The need to predict future ecosystem states has been growing in recent years  
3014 (Coreau et al. 2009), so insight gained from this long-term study can inform managers of fire-  
3015 grazer systems about large grazer response to variation in local climate as well as fire-induced  
3016 variation in forage resources.

## 3017 **METHODS**

### 3018 *Study Area and Bison Population*

3019 Our study was conducted at Konza Prairie Biological Station (KPBS) (Knapp et al. 1998), a  
3020 3,487-ha native tallgrass prairie preserve located in the Flint Hills grassland near Manhattan,  
3021 Kansas (39°05'N, 96°35'W). Because the Flint Hills are steep and rocky and largely unsuitable  
3022 for row crop farming, the region is used primarily for cattle production (Launchbaugh and

3023 Owensby 1978). Flint Hills bedrock is composed of alternating layers of shale and limestone,  
3024 leading to topography with a "stair-step" appearance including steep slopes and shallow soils  
3025 forming over limestone and shallow slopes with deep soils over shale (Schimel et al. 1991). The  
3026 most elevated areas of the "stair-step" shaped topography are flat, bench-like areas with shallow  
3027 soils, while the least elevated areas are riparian habitat with deeper soils. Topographic relief from  
3028 lowland to upland is about 100 m. Vegetation is mostly tallgrass prairie dominated by C<sub>4</sub> grasses  
3029 (*Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Panicum virgatum*)  
3030 along with a diverse mixture of warm- and cool-season graminoids. Short-statured, stoloniferous  
3031 and grazing- tolerant graminoids found in flat, upland areas include *Bouteloua dactyloides* and  
3032 *Bouteloua gracilis*, respectively. Forbs constitute ~75% of species richness (575 species) and  
3033 vegetation biomass is >75% from grasses (Towne 2002, Collins and Calabrese 2012). Average  
3034 monthly temperatures range from -2.7° C (January) to 26.6° C (July). Average annual  
3035 precipitation is ~835 mm, with 75% falling during the growing season. A drought occurred from  
3036 mid-summer of 2011 through the growing season in 2012 (Fig. 1).

3037           KPBS is divided into replicated, watershed-level experimental treatments that cross  
3038 bison grazing with fire frequency; ungrazed watersheds are not considered further here. Bison at  
3039 KPBS have free access to 10 experimental watersheds over approximately 1040 ha (Fig. 2)  
3040 subjected to 1-, 2-, 4-, and 20-year burn-interval treatments. All prescribed management burns in  
3041 the bison-grazed watersheds are conducted in the spring (mid-March to early May in the year of  
3042 burning). Watersheds are labeled according to fire frequency (1, 2, 4, 20 years between burns);  
3043 all watersheds included here are part of the bison unit (labeled as N, native grazer). A watershed  
3044 label indicates replicate number (A–D). For example, N04D is replicate-D of a bison grazed  
3045 watershed (N) burned every 4 years. Individual replicate watersheds with the same fire frequency

3046 are burned in different years (additional information regarding watershed treatments are found at  
3047 [kpbs.konza.ksu.edu](http://kpbs.konza.ksu.edu)). Watersheds in the bison unit studied here were burned in the spring  
3048 according to the schedule shown in KPBS-LTER.

3049 The KPBS bison herd was established in 1987, and is currently maintained at a stocking  
3050 rate of ~260 adult individuals, with ~80 calves born in each spring. This stocking rate of ~14.5g  
3051 bison/m<sup>2</sup> (~ 0.3 animals ha<sup>-1</sup>) results in a target density that removes ~25% of the standing  
3052 vegetation biomass annually (Knapp et al. 1999); the actual %-loss rate in a specific year  
3053 depends on precipitation and forage quality. Individual bison are weighed and their general  
3054 health assessed at an annual round-up of all animals in late October/ early November; some  
3055 individuals are culled at this time to maintain prescribed stocking densities. Young animals (>1y  
3056 of age), old animals, and excess males are removed from the herd to maintain the stocking rate  
3057 stated above, resulting in a sex ratio of mature females to mature males of approximately 4:1. All  
3058 males are removed from the herd by age 8, while females may remain until the age of 15 or older  
3059 (Ungerer et al. 2013). Natural mineral soil licks and artificial mineral supplements are available  
3060 in the enclosure and the corral, respectively, throughout the year (Tracy and McNaughton 1995).

3061 Individual bison were tracked using Telonics TGW-3700 GPS collars during 2008-  
3062 2013. Seven individuals were tracked in 2008-2009, 11 in 2010, 14 in 2011, 13 in 2012, and 11  
3063 in 2013. All individuals fitted with collars were older, matriarchal females; no males were  
3064 collared. Collars were fitted or replaced annually at the bison roundup, using the same  
3065 individuals in consecutive years when possible. Handling procedures were approved by KSU-  
3066 IACUC and in accordance with the guidelines established by American Society of  
3067 Mammologists. Only 3D fixes with a DOP of less than 3.5 were used for the analyses; ~98% of  
3068 fixes met these criteria. Two-hour collar fixes collected during 1 April to 30 September were



3069 used for all individuals in analyses described here. Estimates indicate that collared animals are  
3070 often accompanied by roughly 30-40 individuals (Raynor, unpublished data), a value that  
3071 fluctuates somewhat and depends on whether the herd has coalesced or fragmented at the time.

3072 *Forage quality*

3073 The quality of the forage was estimated from grass nitrogen measured at 1,039 locations that  
3074 were opportunistically selected between the 2011-2013 growing seasons and distributed  
3075 throughout the different watershed burn types at KPBS. The aboveground grass biomass was  
3076 clipped in 25 × 25 cm plots at each of the 1,039 locations (pooling all graminoid species) and air  
3077 dried, ground to a 1-mm particle size, and analyzed by Dairyland Laboratories (Arcadia,  
3078 Wisconsin, USA) on a Foss model 5000 Near Infra-Red (NIR) spectrophotometer (Foss,  
3079 Hillerød, Denmark). Crude protein (%) was estimated as %-N in plant tissue \* 6.25.

3080 *Forage quantity*

3081 The quantity of forage was estimated at 16,792 locations that were opportunistically selected  
3082 between the 2011-2013 growing seasons and distributed throughout different watershed burn  
3083 types at KPBS. Total dry plant biomass ( $B$ ; grams/m<sup>2</sup>) was estimated using a calibrated pasture  
3084 disk meter that measured the height (cm) to which a plastic disk of constant weight could be  
3085 supported as it settled on top of the canopy (Vartha and Matches 1977). Height was related to  
3086 total plant biomass by regressing pasture meter readings on plots that were subsequently  
3087 harvested to determine dry biomass, leading to the following regression models:

3088  $y=3.778406x+6.175267$ ,  $R^2=0.63$ ,  $P<0.0001$ ,  $n=55$  for 2012, a drought year and

3089  $y=2.398824x+3.697927$ ,  $R^2=0.85$ ,  $P<0.0001$ ,  $n=35$  for 2013, a normal year for precipitation.

3090 The calibration for 2013 was used to estimate herbaceous biomass at sites from 2011 because  
3091 2011 ANPP was similar to 2013 ANPP.

3092 *Describing vegetation dynamics*

3093 We used Random Forest regression models to estimate grass nitrogen and herbaceous  
3094 biomass in watersheds as a function of cumulative precipitation in that year, time since burn, and  
3095 site topography. The Random Forests approach is a regression tree technique in which many  
3096 regression trees are generated from random subsets of the available observations and predictor  
3097 variables (Liaw and Weiner 2012, Bohrer et al. 2014). The response variable is then predicted  
3098 from the combination of all regression trees. This approach performs well when modeling non-  
3099 linear relationships between predictors and the response and accommodates complex interactions  
3100 among predictors (Bohrer et al. 2014). These model properties are important for modeling forage  
3101 quality and quantity relationships across space because nutritive and structural values of plants  
3102 are spatially heterogeneous (e.g. along environmental gradients; Adler et al. 2001). As such,  
3103 interactions between spatial (e.g. topography) and temporal (e.g. cumulative precipitation and  
3104 time since burn) predictors can be effectively incorporated into the model (Prasad et al. 2006,  
3105 Vincenzi et al. 2011). The topographical characteristics assigned to each site sampled during the  
3106 growing seasons of 2011-2013 included: the sine and cosine of aspect (radians), slope (degree),  
3107 and scaled elevation (m) extracted from a digital elevation model (DEM, with spatial resolution  
3108 of  $2 \times 2$  m; ~333-443 m a.b.s.l) (KPBS LTER). Cumulative daily precipitation (mm) collected  
3109 from KPBS headquarters and the number of days since the sampling area burned (KPBS LTER)  
3110 was assigned to each sampling event in the training set. Accounting for topographic variation  
3111 and meteorological events are important parameters for determining aboveground herbaceous  
3112 biomass at KPBS (Briggs and Knapp 1995). The number of times the watershed had burned  
3113 since 1980 and type of burn schedule assigned to the watershed if it burned in a particular year  
3114 (Frequent [1-2 year], Infrequent [4-20], or Not-burned that Year) were additional predictors  
3115 incorporated into the Random Forest models for forage quality and quantity. We trained the

3116 model on a randomly-selected set of data comprising 33% of the sites, “the out-of-the-bag”  
3117 sample, and withheld the remaining 67% to test model performance. Performance was assessed  
3118 using the root mean squared error of log-transformed response variable. This validation  
3119 procedure was repeated 10 times and model performance was characterized using the average  
3120 root mean squared error from the 10 random validation datasets. Random Forests models were fit  
3121 using the *randomForest* library in the R statistical language (Liaw and Wiener 2015).

3122         The grass nitrogen and herbaceous biomass models described above were used to project  
3123 grass nitrogen and herbaceous biomass across a 10 m grid of points throughout the bison  
3124 enclosure, excluding points known to occur within 5 m radius of known shrub cover identified  
3125 from a 1 x 1 m resolution raster map from summer 2011 (Ling et al. 2014). For this  
3126 extrapolation, the model was trained on the entire 2011-2013 dataset (as opposed to the 33%  
3127 used for model validation described in the previous section). Year was not used as a predictive  
3128 variable in the Random Forest model. Instead, cumulative precipitation since 1 March and time  
3129 since burn variables substituted for the temporal aspect of the projection model. This allowed us  
3130 to predict spatial and temporal coverage of forage quality and quantity across the entire bison  
3131 enclosure at bi-weekly intervals from 15 April to 15 October in the 2008 to 2013 growing  
3132 seasons. Bi-weekly raster projections of grass crude protein content and herbaceous biomass  
3133 were generated across the entire enclosure using the *raster* package in Program R for use in  
3134 bison movement modelling (Fig. 3).

### 3135 *Modelling effects of environmental variables on movement*

3136 Our starting point for understanding drivers underlying movement follows the framework of  
3137 Rhodes et al. (2005) and Forester et al. (2009), which defines the probability that an animal

3138 moves from location a to location b (a ‘step’) in a given time interval and conditional on habitat  
3139 covariates, X, at location b to be:

$$3140 \quad f(b|a, X) = \frac{\phi(a,b,\Delta t;\theta)\omega(Xb;\beta)}{\int_{c \in D} \phi(a,c,\Delta t;\theta)\omega(Xc;\beta)dc} \quad , \quad \text{(Equation 1)}$$

3141 where  $\phi(a, b, \Delta t; \theta)$  is defined as a habitat-independent movement kernel (HIMK, sometimes  
3142 referred to as the resource-independent movement kernel) describing how the animal would  
3143 move over time interval  $\Delta t$  in the absence of habitat influences, and  $\omega(X)$  is the resource  
3144 selection probability function and X is a matrix of habitat covariates (including a column of  
3145 one’s representing the intercept term (Manly et al. 2002, Lele and Kiem 2006). ‘Use’ refers to  
3146 habitat that has been encountered and selected, while ‘availability’ defines the habitat that could  
3147 potentially be encountered by the animal (Lele et al. 2013). The shape of the HIMK is  
3148 determined by parameter vector  $\theta$ , while parameter vector  $\beta$  represents the habitat preferences.  
3149 The numerator is normalized by the denominator, integrated over all locations, c, with the spatial  
3150 domain, D. Each observed step (segments of the landscape; N $\approx$ 1,000) was paired with 100  
3151 random steps, and landscape characteristics of observed and random steps were contrasted using  
3152 conditional logistic regression. We simultaneously estimated the habitat-independent movement  
3153 kernel and habitat preference by fitting  $f(b|a, X)$  (eqn 1) to the location data. The model was fit  
3154 using the ‘optim’ function in R (R Development Core Team 2015). Confidence intervals for the  
3155 parameter estimates were calculated from the Hessian matrix ( $\pm 1.96$  times the square roots of the  
3156 diagonal elements of the covariance matrix (Beyer et al. 2014). Habitat covariates included  
3157 elevation (m), slope (degrees), cosine of aspect (radians), grass crude protein content (% CP),  
3158 and herbaceous biomass content, all of which were raster format data sets with a spatial  
3159 resolution of 10 x 10 m. Parameters were back-transform after fitting. The habitat selection  
3160 function was modelled as:

3161  $\omega(Xb; \beta) = \exp(\beta_1 \text{ELEV} + \beta_2 \text{SLOPE} + \beta_3 \text{Cos}(\text{ASPECT}) + \beta_4 \text{PROTEIN} + \beta_5 \text{BIOMASS} +$   
3162  $\beta_6 \text{PROTEIN} * \text{BIOMASS})$ .

3163 We used a generalized linear mixed model to test differences between years among  
3164 habitat selection and movement kernel coefficients generated from the mechanistic movement  
3165 model. We included a random effect for individual bison in the model to account for the repeated  
3166 sampling of some animals across years. We used the R-package *lme4* to analyze these data (R  
3167 Development Core Team 2015).

## 3168 **RESULTS**

### 3169 *Forage quality and quantity*

3170 The out-of-bag estimates of the error rate were used to select the optimum Random Forest  
3171 parameters (trees=1000, terminal node size=5). The root mean square error averaged across the  
3172 10 random validation datasets was 1.47 for herbaceous biomass (n=5541 samples) and 1.03  
3173 (n=343 samples). For the training dataset, the Random Forest model explained a large proportion  
3174 of the variance of the grass protein content (pseudo  $R^2=0.72$ ) and herbaceous biomass (pseudo  
3175  $R^2=0.49$ ). Figure 2 shows the ranking of predictors by their importance. Only a few of the  
3176 descriptors contributed substantially to the estimation of crude protein content, namely elevation,  
3177 slope, and days since burn. In decreasing order of importance, the other predictors included in  
3178 the RF model were: cosine of aspect, cosine of day, times watershed burned, sine of day, sine of  
3179 aspect, cumulative precipitation (mm), and watershed burn type. For herbaceous biomass,  
3180 descriptors that contributed substantially to its estimation included: cosine of day, day since  
3181 burn, sine of day, and cumulative precipitation (mm). In decreasing order of importance the  
3182 remaining predictors included: elevation, times watershed burned, watershed burn type, slope,  
3183 sine of aspect, and cosine of aspect.

3184 *Bison habitat preference*

3185 *Topography*

3186 Habitat preference for elevated habitat at KPBS was evident, where 61 of 63 bison favored  
3187 higher elevation relative to available elevation although preference differed among years  
3188 ( $F_{5,26}=35.01$ ,  $P<0.0001$ ; Fig. 4, Fig. 5a). In 2012, two individuals did not select higher elevation  
3189 relative to availability and the overall preference for high elevation was the lowest in this year  
3190 (Fig. 4, 5a). All bison avoided steeper slopes in all years, but the strength of avoidance differed  
3191 subtly among years (range 0 to -0.05),  $F_{5,26}=3.92$ ,  $P=0.009$ ; Fig. 5b, 6b). Preference for a  
3192 southerly aspect was evident in 37 of 63 individuals (58.9%; Fig. 4), while confidence intervals  
3193 were wide and overlapped 0 for the other 26 individuals (Fig. 5c). Only three individuals showed  
3194 any preference for non-southerly aspect although their selection coefficients overlapped 0 (Fig.  
3195 4, 5c). Variation in selection for southern aspect was evident across years ( $F_{5,26}=5.60$ ,  $P=0.001$ )  
3196 with selection for southerly aspect in 2011 being greater than 2012 ( $t_{26}=-2.22$ ,  $P=0.035$ ; Fig. 5c).

3197 *Forage resources*

3198 A significant interaction occurred between biomass and protein selection in 16 of 63 individuals  
3199 (25.4%; Fig. 4). Significant interactions revealed that 11 individuals selected areas of high  
3200 biomass and high protein, while 5 individuals selected areas of low biomass and low protein  
3201 (Fig. 4). Overall, selection for herbaceous biomass was negatively correlated with selection for  
3202 foliar crude protein content (linear regression,  $F_{1,61}=26.3$ ,  $P<0.0001$ , adjusted  $R^2=0.29$ ; Fig. 6d).

3203 *Graminoid crude protein content*

3204 During this study, all individuals favored habitat with high foliar protein content relative to  
3205 available habitat (Fig. 4,5d). The strength of selection for areas of high foliar protein content  
3206 varied among years ( $F_{5,26}=28.36$ ,  $P<0.0001$ ; Fig. 6e). Selection for foliar protein was not

3207 different between 2008 and 2009 ( $t_{1,26}=-0.09$ ,  $P=0.93$ ; Fig. 6e). In contrast, selection for high  
3208 foliar protein was greater in 2010 than 2009 ( $t_{1,26}=7.55$ ,  $P<0.00001$ ) and the strength of selection  
3209 declined from 2010 to 2012 with years being significantly different from one another in a  
3210 descending manner ( $P\leq 0.0001$ ), while selection was not different between 2012 and 2013 ( $t_{1,26}=-$   
3211  $0.81$ ,  $P=0.42$  ; Fig. 6e).

### 3212 *Herbaceous biomass*

3213 During the study, 54 of 63 individuals (78.3%) favored areas of lower herbaceous biomass  
3214 during the growing season (Fig. 4,5e). In 2013, eight individuals did not select areas of different  
3215 herbaceous biomass content relative to availability, whereas one individual showed high biomass  
3216 preference in 2008. The strength of avoidance for areas of high herbaceous biomass content  
3217 generally varied among years ( $F_{5,26}= 32.42$ ,  $P<0.0001$ ; Fig. 6f). Preference for areas of low  
3218 herbaceous biomass content was highest in 2010 through 2012 ( $P\leq 0.02$ ), while 2008 and 2009  
3219 marginally differed in selection for herbaceous biomass ( $t_{1,26}1.98$ ,  $P=0.06$ ; Fig. 6f).

### 3220 *Movement*

3221 A normal distribution was used to describe the habitat-independent movement kernel (HIMK; for  
3222 movements at 4 hr intervals) for all 63 individuals (Fig. 4, 5f). In 2009, movement rates were  
3223 lower than the other years in this study ( $F_{5,26}=11.3$ ,  $P<0.0001$ ; Fig. 6g). The distribution of step  
3224 lengths (movement) moderately decreased as a function of preference for elevation (linear  
3225 regression,  $F_{1,61}=11.55$ ,  $P=0.001$ , adjusted  $R^2=0.15$ ; Fig. 6h) and weakly decreased as a function  
3226 of preference for herbaceous biomass ( $F_{1,61}=2.45$ ,  $P=0.12$ , adjusted  $R^2=0.02$ ). Distribution of step  
3227 lengths was not explained by slope ( $P=0.70$ ) or aspect ( $P=0.79$ ). In contrast, step length  
3228 distribution was positively related to strong selection for grass protein content ( $F_{1,61}=5.57$ ,  
3229  $P=0.02$ , adjusted  $R^2=0.07$ ).

3230 **DISCUSSION**

3231 Our results demonstrate that resource-driven movement patterns of bison are shaped by the  
3232 forage quantity-quality tradeoff and site topography. Combined, these comprise the grazer  
3233 component of the so-called “shifting mosaic” of the fire-grazer interaction (Knapp et al. 1999).  
3234 Multiple biotic and abiotic attributes of landscape heterogeneity influenced the movements of  
3235 bison, which were not static from year-to-year and likely related to local weather in addition to  
3236 fire management on the landscape. Movement patterns reflected trade-offs between individual  
3237 goals such as the need for accessible high quality forage, and fitness-based selection for  
3238 topography with low potential for insect harassment (e.g., wind-prone southern facing areas) and  
3239 less energy-demanding locomotion (e.g., steep slopes).

3240 *Landscape attributes influencing bison habitat selection at KPBS*

3241 Fire-induced changes in plant quality modulate bison forage behavior and space use at KPBS  
3242 (Chapter 2 & 4, this thesis), yet identification of the dynamic forage and static topographical  
3243 resources driving movement patterns remain unclear. Mechanistic movement modelling  
3244 developed in this chapter identified multiple dynamic (biotic) and static (abiotic) features of the  
3245 environment influencing movements of female bison at KPBS. First, the strength of selection for  
3246 elevation was greatest in upland areas of high elevation relative to available elevations  
3247 throughout the enclosure. Also, the strength of selection for elevation actually constrained  
3248 movement by placing greater relative weight on the RSPF compared with the HIMK.  
3249 Furthermore, strength of selection for high elevation decreased with increasing growing season  
3250 temperatures, suggesting that bison were seeking water or shade in response to increased  
3251 temperatures (Allred et al. 2013 and references therein). However, bison attain substantial  
3252 amounts of water from wallows and forage after recent precipitation at KPBS (Nippert et al.



3253 2013). The presence of steep slopes decreased the probability of selection, and bison generally  
3254 avoided habitat that did not face south. Both of these behavioral responses to static  
3255 environmental features could be fitness-based. Locomotion on steep slopes increases energy  
3256 expenditure as compared to level areas in mountain ungulates (Hudson and White 1985, Dailey  
3257 and Hobbs 1989). Some slopes in the KPBS bison enclosure are fairly steep, with areas of  
3258 exposed soil and rock and high woody cover that reduces the probability that fire would carry  
3259 across them completely to affect quality (Collins and Calabrese 2012), thus possibly making  
3260 them less desirable to bison as grazing sites as the energetic demands that it would take to utilize  
3261 these areas may outweigh the benefits from the forage consumed. Moreover, selection for steep  
3262 slopes was strongest in years of low forage availability, which suggests steep slopes may prove  
3263 useful as a source for forage in periods of low food availability. Selection of non-southerly  
3264 aspects was highest during the drought year (2012), which further corroborates the view that  
3265 shifts of habitat preference in drought years maybe food driven; areas of non-southern aspect  
3266 may provide more forage than the highly utilized areas facing south. We hypothesize that the  
3267 propensity for parasitic insect avoidance is likely a result of overall preference for southerly  
3268 aspect as prevailing southern winds may reduce avoidance behavior. Macroparasites can cause  
3269 subclinical consequences to fitness that manifest when hosts experience additional energetic or  
3270 nutritional demands associated with immunological responses, reduced food intake, or increased  
3271 movement and avoidance behaviors (Lima and Dill 1990, Lochmiller and Deerenberg 2000,  
3272 Gunn and Irvine 2003, Fitze et al. 2004). However, high temperatures during the growing season  
3273 may also be driving bison to seek elevated areas for greater exposure to wind at KPBS.

3274 Movement paths of bison were influenced by the spatial distribution and variation in  
3275 forage quality and quantity. Habitat with graminoids of high crude protein content was the

3276 strongest dynamic driver of forage resource selection across all summers. Crude protein content  
3277 of graminoids is inversely related with time since fire in tallgrass prairie, while forage quantity is  
3278 positively related (Allred et al. 2011a). At KPBS, resource utilization functions based on GPS  
3279 collared-female bison confirmed the preference for infrequently-burned watersheds over  
3280 frequently-burned and not-burned watersheds from May to August (Chapter 4, this thesis). When  
3281 infrequently-burned tallgrass prairie is released from light-limitation through prescribed burning  
3282 in the presence of increased soil nutrients (transient maxima hypothesis), prolonged high quality  
3283 forage is the result (Blair 1997), and bison maintain the habitat in a state of low-to-intermediate  
3284 quantity throughout the remainder of the growing season (Chapter 2). Throughout the growing  
3285 season, fine-scale patch selection is driven by availability of low stature, easily accessible and  
3286 high quality forage (Chapter 3, this thesis). Foraging in such habitats allows ruminants to  
3287 maximize daily intake rate of digestible energy (Bergman et al 2001, Shipley 2007). Because  
3288 forage maturation stages are distributed variably in space and time, our approach of modelling  
3289 bi-weekly changes in forage quality and quantity captures spatio-temporal variation in forage  
3290 maturation in response to prescribed burning and climate.

3291         The strength of selection and relative avoidance of areas containing high grass crude  
3292 protein content and herbaceous biomass, respectively, varied from year to year. During this  
3293 study, weak avoidance for areas of high herbaceous biomass coincided with above-average  
3294 annual net primary productivity (ANPP), whereas avoidance of areas of high herbaceous  
3295 biomass was slightly stronger in years of average-to-below average ANPP. On the other hand,  
3296 the strongest selection for foliar crude protein content occurred during the less productive years  
3297 of this study. The inverse relationship between selection for foliar quality and quantity observed  
3298 in this study occurred in both climatic extremes studied that led to above and below average

3299 plant productivity at KPBS. Because foliar protein concentration in grasses often increases in  
3300 years of reduced precipitation (plant stress hypothesis; Jones and Coleman 1991, Milchunas et al.  
3301 1995, Joern and Mole 2005), daily nutrient gains could be maximized by selecting areas  
3302 containing small plants of high nutrient value as long as young forage tissue was available  
3303 through regrowth. Bison remember pertinent information about location and quality of forage  
3304 resources, and may use this information to selectively move to areas of higher profitability  
3305 (Merkle et al. 2014). A possible reason for favoring the long-term intake strategy of using areas  
3306 where satiation may take longer to achieve but more digestible nutrients may be attained is that  
3307 our study occurred in a predator-free system. Without the risk of predation, more time could be  
3308 spent foraging instead of performing antipredator behavior (Creel et al. 2014). Also, mature  
3309 group members seem to dictate bison herd movements (McHugh 1958). Therefore, because our  
3310 study animals are mature and highly fecund (~66% had offspring throughout the study), gaining  
3311 the most digestible food in the least amount of time (i.e. maximizing short-term instantaneous  
3312 intake) might not be favored by individuals that are likely group leaders. They may not be as  
3313 prone to interruptions during foraging bouts in efforts to maintain group membership as observed  
3314 in non-group leaders (Fortin and Fortin 2009, Babin et al. 2011). In a boreal forest-meadow  
3315 matrix in Saskatchewan in the presence of wolves, bison are time-spent- grazing minimizers  
3316 (Babin et al. 2011) and rely on group familiarity with the site coupled to their knowledge of local  
3317 foraging options and recently sampled resource quality when deciding to follow or leave a group  
3318 – this tactic leads to resource-rewarding movements (Merkle et al. 2015). In the predator-free  
3319 southern Great Plains, however, bison space use may be dictated by fire-enhanced forage  
3320 availability and concomitant graminoid regrowth following grazing by large herbivores although  
3321 the fission-fusion dynamics in these grazer populations remain to be evaluated.

3322 *Bison movement: mechanistic movement model*

3323 Extrinsic biases to bison movement were evaluated through a comparison between observed and  
3324 random steps through the heterogeneous landscape. The statistical approach used here is based  
3325 on conditional logistic regression analysis, and was inspired by resource selection studies based  
3326 on a case-control design (e.g. Compton et al. 2002, Boyce et al. 2003). In contrast, our approach  
3327 compares landscape segments instead of locations (Arthur et al. 1996, Boyce et al. 2003) or areas  
3328 (Johnson et al. 2002). Consequentially, we explicitly considered landscape characteristics that  
3329 animals would have been likely to encounter along their path (a step selection function design;  
3330 Fortin et al. 2005). Our procedure is novel, however, because estimating the HIMK and habitat  
3331 preference models simultaneously facilitates unbiased parameter estimation (Beyer et al. 2014),  
3332 and we apply this framework to a system with an intact fire-grazer interaction. Thus we  
3333 determined movement patterns in relation to forage resource variability driven by landscape-  
3334 level disturbance processes arising from fire frequency and local weather.

3335 Growing season movement rates (realized distribution of step lengths) were generally  
3336 consistent across our female study animals with the exception of 2009, when movement rates  
3337 were lower than that observed in other years of this study. We surmise that the combined ideal  
3338 rangeland conditions of below average temperature and above average rainfall during the 2009  
3339 growing season may be responsible (Pyke et al. 2002). Instead of spending more time seeking  
3340 shade or water (Allred et al. 2013), large herbivores can use this time to seek a more diverse diet  
3341 (Bailey et al. 2015). Because of high selection for the upper bench habitat at KPBS, the  
3342 distribution of step lengths (e.g., movements) was increasingly limited by this habitat preference  
3343 (Beyer et al. 2014). The highly profitable, infrequently-burned uplands at KPBS (Schimel et al.  
3344 1991, Blair 1997) may have provided suitable forage (e.g. *Bouteloua spp.*) to the extent that  
3345 leaving uplands was minimal during this season. Additionally, shallow, upland soils at KPBS

3346 lead to stressed plants of lower biomass, which in turn results in high protein availability in  
3347 forage (Schimel et al. 1991, Koricheva et al. 1998). This result of movements being constrained  
3348 by elevated habitat selection aids us in meeting our prediction that movement would be guided  
3349 by preference for areas of high protein availability, such as the upper bench habitat. However, as  
3350 grass regrowth likely became limited in years of low ANPP, bison distribution seemingly shifted  
3351 to alternate topography away from these upper bench habitats to attain resources.

3352 *Synthesis*

3353 This study provides the first empirical evidence for documenting the trade-off between resource  
3354 selection and realized movement distribution of a large grazer in response  
3355 to dynamic forage availability and static landscape characteristics in a landscape with an intact  
3356 multi-frequency fire-grazer interaction. Our framework brings together recent advances in  
3357 movement modeling including the development of mechanistic movement models (Rhodes et al.  
3358 2005, Moorcroft et al. 2006, Moorcroft and Burnett 2008) to quantify the effects of dynamic and  
3359 static environmental variables on movement and habitat selection. Moreover, the availability of a  
3360 long-term GPS dataset in this study allowed us to assess habitat selection in response to local  
3361 climate-driven variation in critical forage resources.

3362 Understanding how the forage quality-quantity tradeoff dictates large herbivore habitat  
3363 use when resources are plentiful or scarce in the Great Plains is critical to sustainable rangeland  
3364 management. Warming and drying are anticipated to reduce both plant production and nutritive  
3365 content in the southern Great Plains (Briske et al. 2015). These climatic changes are likely to  
3366 negatively affect rangeland economics by reducing stocking rates and total livestock production  
3367 (Polley et al. 2013). Furthermore, warmer temperatures will likely improve winter survival and  
3368 increase abundance of macroparasites that will further suppress livestock performance (Briske et

3369 al. 2015). Moreover, the impact of fire on over-wintering macroparasite populations may further  
3370 the complexity of understanding what is driving space use and movement in systems with intact  
3371 fire-grazer interactions. Our results shed light on native grazer preference for both dynamic  
3372 forage resources and static land characteristics in a period encapsulating relatively normal and  
3373 reduced plant production. Although food quality is influential in resource selection and  
3374 movement, understanding actual bison distribution and movement is multifactorial.

3375 Our investigation of fine-scale movements of a native grazer in mesic grasslands when  
3376 fire results in markedly different nutritional levels provides baseline information for forecasting  
3377 animal movement in other fire-prone ecosystems that support ungulate populations. While  
3378 grassland fires can have pronounced effects on landscape scale distributions of large herbivores  
3379 (Sensenig et al. 2010, Allred et al. 2011a, b), the underlying dynamic forage resources  
3380 responsible for these distributions have previously remained unexplored. Our data suggest that  
3381 fire induced heterogeneity coupled with climatic responses in vegetation quality are an important  
3382 landscape-scale process that helps promote nutrient attainment in large herbivores and illustrates  
3383 the utility of linking optimal foraging theory with insights from resource, movement, and fire  
3384 ecology.

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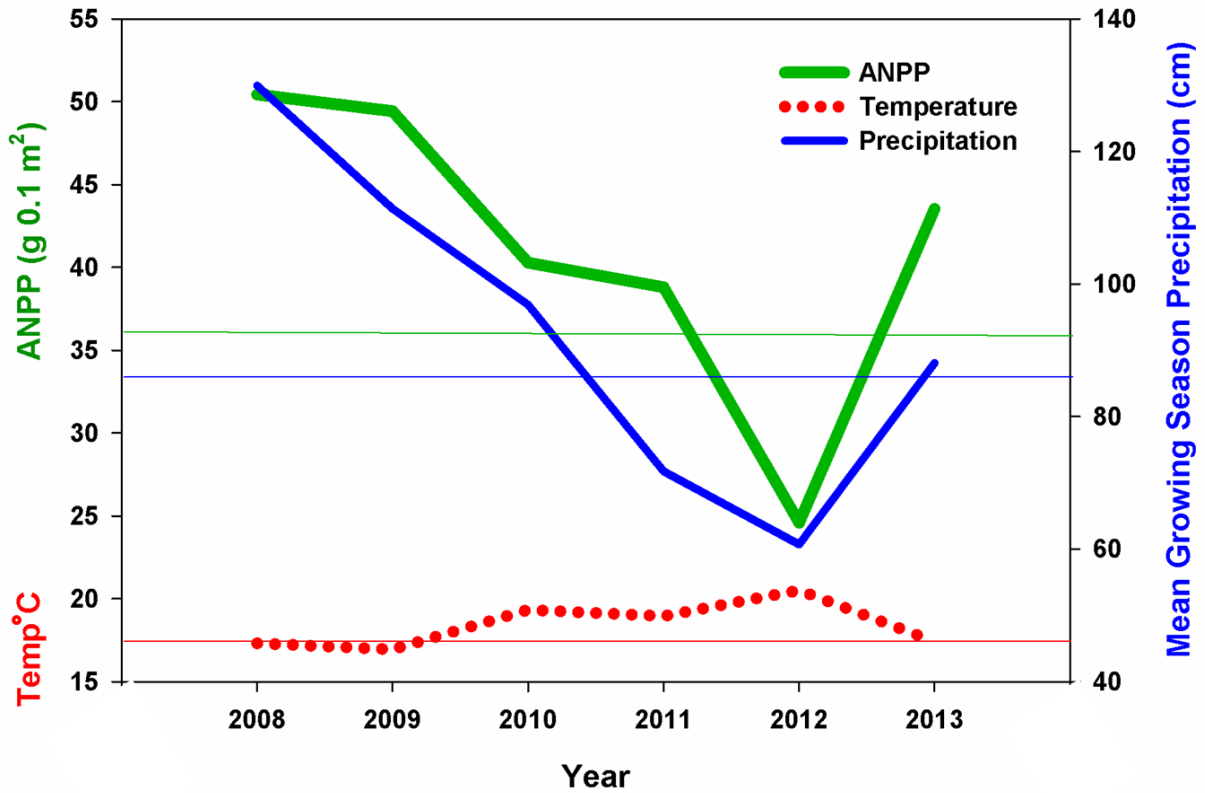
**Table 5-1. Maximum likelihood parameter estimates ( $\bar{x} \pm 95\%$  CI) among all animals and years with for movement, intercept, elevation, slope, cosine of aspect, grass crude protein content, and herbaceous biomass content from 2008-2013 at KPBS.**

id	Year	Movement	Intercept	Elevation	Slope	Aspect	Foliar Protein	Biomass
w514	2008	6.31 (6.27, 6.35)	-8.96 (-11.03, -6.90)	0.02 (0.01, 0.03)	-0.16 (-0.20,-0.14)	-0.23 (-0.39, -0.08)	0.20 (0.12, 0.28)	-0.01 (-0.01, -0.00)
w531	2008	6.23 (6.20,6.27)	-14.94 (-64.02, 34.14)	0.02 (0.01, 0.02)	-0.14 (-0.16,-0.13)	-0.06 (-0.16, 0.07)	0.05 (0.02, 0.08)	0.00 (-0.00,0.00)
w651	2008	6.45 (6.41,6.49)	-9.35 (-11.13,-7.57)	0.02 (0.01, 0.02)	-0.19 (-0.21, -0.16)	-0.10 (-0.21, 0.02)	0.14 (0.08, 0.20)	-0.00 (-0.01, 0.00)
w753	2008	6.26 (6.21, 6.29)	-10.99 (-13.53, -8.44)	0.02 (0.02, 0.03)	-0.18 (-0.21, -0.15)	-0.02 (-0.17, 0.13)	0.23 (0.17, 0.29)	-0.01 (-0.01, -0.00)
w764	2008	6.32 (6.28, 6.35)	-11.64 (-13.85, -9.43)	0.03 (0.02, 0.03)	-0.18 (-0.21, -0.15)	-0.21 (-0.35, -0.07)	0.23 (0.16, 0.29)	-0.01 (-0.01, -0.00)
y139	2008	6.34 (6.30, 6.38)	-10.60 (-12.72, -8.47)	0.02 (0.02, 0.03)	-0.19 (-0.22, -0.16)	-0.14 (-0.28, -0.00)	0.17 (0.11, 0.24)	-0.00 (-0.01, -0.00)
y274	2008	6.32 (6.28, 6.36)	-8.19 (-10.3403, -6.04)	0.02 (0.01, 0.02)	-0.16 (-0.19, -0.13)	-0.15 (-0.30, -0.01)	0.18 (0.11, 0.25)	-0.01 (-0.01, -0.00)
w630	2009	6.22 (6.18, 6.26)	-9.78 (-12.06, -7.51)	0.02 (0.01, 0.03)	-0.14 (-0.17, -0.12)	-0.18 (-0.34, -0.02)	0.16 (0.11, 0.22)	-0.01 (-0.01, -0.00)
w531	2009	6.18 (6.14, 6.22)	-8.61 (-10.59, -6.63)	0.02 (0.01, 0.02)	-0.13 (-0.16, -0.11)	-0.20 (-0.33, -0.07)	0.12 (0.07, 0.17)	-0.00 (-0.01, -0.00)
w651	2009	6.23 (6.19, 6.27)	-9.20 (-11.14, -7.26)	0.02 (0.01, 0.02)	-0.18 (-0.20, -0.15)	-0.03 (-0.16, 0.10)	0.18 (0.12, 0.23)	-0.00 (-0.01, -0.00)
w753	2009	6.24 (6.19, 6.28)	-8.58 (-20.40, 3.25)	0.01 (0.01, 0.02)	-0.12 (-0.16, -0.09)	-0.08 (-0.22, 0.06)	0.08 (0.03, 0.13)	-0.00 (-0.01, -0.00)
w764	2009	6.19 (6.16, 6.23)	-10.93 (-13.11, -8.75)	0.02 (0.02, 0.03)	-0.18 (-0.20, -0.15)	-0.25 (-0.40, -0.10)	0.14 (0.09, 0.19)	-0.00 (-0.01, -0.00)
y269	2009	6.22 (6.18, 6.26)	-10.93 (-13.05, -8.81)	0.02 (0.02, 0.03)	-0.14 (-0.17, -0.12)	-0.18 (-0.33, -0.03)	0.17 (0.12, 0.22)	-0.01 (-0.01, -0.00)
y274	2009	6.19 (6.16, 6.23)	-7.28 (-9.39, -5.18)	0.02 (0.01, 0.02)	-0.15 (-0.18, -0.12)	-0.25 (-0.41, -0.10)	0.11 (0.06, 0.17)	-0.00 (-0.01, -0.00)
w026	2010	6.33 (6.29, 6.36)	-6.09 (-7.85, -4.33)	0.01 (0.00, 0.01)	-0.17 (-0.19, -0.14)	-0.08 (-0.21, 0.04)	0.35 (0.29, 0.40)	-0.01 (-0.01, -0.01)
w531	2010	6.25 (6.21, 6.29)	-7.10 (-8.94, -5.18)	0.01 (0.01, 0.02)	-0.16 (-0.18, -0.13)	-0.19 (-0.32, -0.05)	0.26 (0.19, 0.32)	-0.01 (-0.01, -0.00)
w651	2010	6.37 (6.33, 6.40)	-8.74 (-10.44, -7.04)	0.01 (0.01, 0.02)	-0.16 (-0.18, -0.14)	-0.05 (-0.17, 0.07)	0.35 (0.29, 0.41)	-0.01 (-0.01, -0.01)
y036	2010	6.30 (6.26, 6.33)	-9.73 (-10.46, -7.00)	0.02 (0.01, 0.02)	-0.15 (-0.17, -0.13)	-0.20 (-0.33, -0.07)	0.37 (0.32, 0.43)	-0.01 (-0.02, -0.01)
w764	2010	6.35 (6.31, 6.38)	-7.46 (-9.18, -5.74)	0.01 (0.01, 0.02)	-0.16 (-0.17, -0.14)	-0.16 (-0.28, -0.05)	0.27 (0.22, 0.32)	-0.01 (-0.01, -0.01)
y072	2010	6.34 (6.30, 6.38)	-7.87 (-9.50, -6.24)	0.01 (0.01, 0.02)	-0.14 (-0.16, -0.12)	-0.13 (-0.25, -0.01)	0.35 (0.30, 0.41)	-0.01 (-0.01, -0.01)
y116	2010	6.28 (6.25, 6.32)	-7.16 (-8.91, -5.40)	0.01 (0.01, 0.02)	-0.16 (-0.18, -0.14)	-0.15 (-0.27, -0.03)	0.29 (0.24, 0.35)	-0.01 (-0.01, -0.01)
y139	2010	6.35 (6.32, 6.39)	-5.29 (-7.02, -3.55)	0.01 (0.00, 0.01)	-0.16 (-0.18, -0.13)	-0.23 (-0.36, -0.10)	0.38 (0.32, 0.44)	-0.01 (-0.01, -0.01)
y270	2010	6.31 (6.27, 6.35)	-7.66 (-9.36, -5.95)	0.01 (0.01, 0.02)	-0.13 (-0.15, -0.11)	-0.07 (-0.20, 0.05)	0.34 (0.28, 0.39)	-0.01 (-0.01, -0.01)



y269	2010	6.33 (6.29, 6.37)	-8.33 (-10.02, -6.63)	0.01 (0.01, 0.02)	-0.14 (-0.16, -0.12)	-0.05 (-0.17, 0.07)	0.26 (0.21, 0.32)	-0.01 (-0.01, -0.00)
y274	2010	6.33 (6.29, 6.37)	-7.07 (-8.94, -5.20)	0.01 (0.01, 0.02)	-0.14 (-0.16, -0.11)	-0.15 (-0.28, -0.02)	0.32 (0.25, 0.38)	-0.01 (-0.01, -0.01)
w026	2011	6.28 (6.24, 6.31)	-6.43 (-8.10, -4.76)	0.01 (0.01, 0.02)	-0.16 (-0.18, -0.14)	-0.17 (-0.29, -0.05)	0.25 (0.20, 0.30)	-0.01 (-0.01, -0.01)
y036	2011	6.32 (6.28, 6.35)	-6.95 (-8.71, -5.18)	0.01 (0.01, 0.01)	-0.15 (-0.17, -0.13)	-0.19 (-0.31, -0.07)	0.26 (0.21, 0.31)	-0.01 (-0.01, -0.01)
w764	2011	6.37 (6.33, 6.40)	-17.02 (-309.54, 275.50)	0.01 (0.01, 0.01)	-0.15 (-0.16, -0.13)	-0.24 (-0.34, -0.14)	0.27 (0.24, 0.31)	-0.01 (-0.01, -0.01)
y116	2011	6.33 (6.30, 6.37)	-5.59 (-7.51, -3.68)	0.01 (0.00, 0.01)	-0.16 (-0.18, -0.14)	-0.20 (-0.31, -0.09)	0.24 (0.19, 0.29)	-0.01 (-0.01, -0.01)
y139	2011	6.27 (6.23, 6.30)	-6.11 (-8.26, -3.97)	0.01 (0.00, 0.01)	-0.14 (-0.16, -0.12)	-0.18 (-0.29, -0.07)	0.20 (0.16, 0.24)	-0.01 (-0.01, -0.01)
y270	2011	6.30 (6.27, 6.34)	-4.77 (-6.67, -2.86)	0.01 (0.00, 0.01)	-0.15 (-0.17, -0.12)	-0.09 (-0.21, 0.03)	0.27 (0.21, 0.33)	-0.01 (-0.01, -0.01)
y269	2011	6.31 (6.27, 6.34)	-6.90 (-8.78, -5.01)	0.01 (0.01, 0.02)	-0.11 (-0.13, -0.09)	-0.09 (-0.23, 0.05)	0.29 (0.22, 0.35)	-0.01 (-0.02, -0.01)
y274	2011	6.32 (6.28, 6.35)	-6.88 (-8.67, -5.09)	0.01 (0.01, 0.02)	-0.14 (-0.16, -0.12)	-0.21 (-0.33, -0.09)	0.26 (0.21, 0.31)	-0.01 (-0.01, -0.01)
y520	2011	6.27 (6.23, 6.30)	-6.37 (-8.15, -4.59)	0.01 (0.01, 0.02)	-0.13 (-0.15, -0.11)	-0.21 (-0.34, -0.09)	0.30 (0.24, 0.35)	-0.01 (-0.02, -0.01)
y605	2011	6.36 (6.32, 6.39)	-8.16 (-9.85, -6.47)	0.02 (0.01, 0.02)	-0.14 (-0.16, -0.12)	-0.21 (-0.33, -0.08)	0.27 (0.22, 0.32)	-0.01 (-0.01, -0.01)
y678	2011	6.35 (6.31, 6.38)	-5.99 (-7.73, -4.25)	0.01 (0.01, 0.01)	-0.16 (-0.18, -0.13)	-0.34 (-0.47, -0.21)	0.27 (0.22, 0.31)	-0.01 (-0.01, -0.01)
y720	2011	6.35 (6.32, 6.39)	-6.76 (-8.38, -5.14)	0.01 (0.01, 0.02)	-0.15 (-0.17, -0.13)	-0.31 (-0.43, -0.19)	0.24 (0.20, 0.29)	-0.01 (-0.01, -0.01)
y072	2011	6.37 (6.33, 6.42)	-10.80 (-184.43, 162.83)	0.01 (0.00, 0.01)	-0.12 (-0.13, -0.10)	-0.21 (-0.33, -0.10)	0.20 (0.17, 0.24)	-0.01 (-0.01, -0.01)
w651	2011	6.37 (6.33, 6.42)	-12.71 (-182.84, 157.43)	0.01 (0.00, 0.01)	-0.14 (-0.16, -0.12)	-0.17 (-0.30, -0.04)	0.21 (0.18, 0.25)	-0.01 (-0.01, -0.01)
y026	2012	6.30 (6.26, 6.33)	-15.82 (-84.36, 52.70)	0.01 (0.01, 0.02)	-0.12 (-0.13, -0.10)	-0.06 (-0.16, 0.03)	0.19 (0.16, 0.23)	-0.01 (-0.01, -0.00)
y036	2012	6.32 (6.28, 6.35)	-12.05 (-68.14, 44.04)	0.01 (0.01, 0.01)	-0.12 (-0.14, -0.11)	0.04 (-0.06, 0.14)	0.16 (0.13, 0.19)	-0.01 (-0.01, -0.00)
w764	2012	6.32 (6.28, 6.35)	-7.74 (-42.60, 27.12)	0.01 (0.00, 0.01)	-0.13 (-0.17, -0.10)	-0.16 (-0.27, -0.04)	0.25 (0.14, 0.36)	-0.01 (-0.01, -0.01)
y072	2012	6.40 (6.37, 6.44)	-12.58 (-109.91, 84.76)	0.01 (0.00, 0.01)	-0.16 (-0.18, -0.14)	-0.09 (-0.18, 0.01)	0.24 (0.20, 0.27)	-0.01 (-0.01, -0.01)
y116	2012	6.36 (6.33, 6.40)	-14.38 (-199.90, 171.15)	0.01 (0.00, 0.01)	-0.13 (-0.15, -0.11)	-0.08 (-0.18, 0.01)	0.15 (0.12, 0.18)	-0.01 (-0.01, -0.00)
y139	2012	6.40 (6.36, 6.44)	-14.44 (-274.03, 245.15)	0.01 (0.00, 0.01)	-0.12 (-0.14, -0.11)	-0.04 (-0.14, 0.05)	0.22 (0.18, 0.25)	-0.01 (-0.01, -0.01)
y270	2012	6.34 (6.31, 6.38)	-4.20 (-6.25, -2.16)	0.00 (0.00, 0.01)	-0.16 (-0.18, -0.13)	-0.17 (-0.29, -0.05)	0.23 (0.18, 0.28)	-0.01 (-0.01, -0.01)
y274	2012	6.36 (6.32, 6.40)	-3.29 (-6.07, -0.51)	0.00 (-0.00, 0.01)	-0.14 (-0.16, -0.11)	-0.15 (-0.26, -0.03)	0.24 (0.18, 0.30)	-0.01 (-0.01, -0.00)
y520	2012	6.24 (6.20, 6.27)	-10.32 (-32.25, 11.61)	0.01 (0.00, 0.01)	-0.13 (-0.15, -0.12)	0.01 (-0.09, 0.11)	0.15 (0.11, 0.18)	-0.00 (-0.01, -0.00)
y605	2012	6.36 (6.32, 6.40)	-5.90 (-7.80, -4.00)	0.01 (0.00, 0.01)	-0.15 (-0.17, -0.12)	-0.18 (-0.30, -0.06)	0.26 (0.21, 0.32)	-0.01 (-0.01, -0.01)

y678	2012	6.32 (6.28, 6.35)	-13.14 (-86.62, 60.34)	0.01 (0.01, 0.01)	-0.12 (-0.14, -0.10)	0.03 (-0.06, 0.13)	0.16 (0.13, 0.20)	-0.01 (-0.01, -0.00)
y720	2012	6.40 (6.37, 6.44)	-6.81 (-10.56, -3.05)	0.01 (0.00, 0.01)	-0.15 (-0.18, -0.13)	-0.07 (-0.17, 0.03)	0.22 (0.18, 0.27)	-0.01 (-0.01, -0.01)
y389	2012	6.38 (6.34, 6.41)	-3.18 (-5.38, -0.98)	0.00 (-0.00, 0.01)	-0.17 (-0.20, -0.14)	-0.05 (-0.19, 0.08)	0.28 (0.21, 0.34)	-0.01 (-0.01, -0.01)
y026	2013	6.28 (6.26, 6.33)	-8.91 (-10.69, -7.12)	0.02 (0.01, 0.02)	-0.15 (-0.17, -0.12)	-0.15 (-0.27, -0.02)	0.10 (0.05, 0.15)	-0.00 (-0.00, 0.00)
y269	2013	6.34 (6.31, 6.38)	-8.63 (-10.48, -6.78)	0.02 (0.01, 0.02)	-0.11 (-0.14, -0.09)	-0.19 (-0.33, -0.05)	0.12 (0.07, 0.18)	-0.00 (-0.01, -0.00)
w764	2013	6.27 (6.23, 6.30)	-11.31 (-54.61, 31.98)	0.01 (0.01, 0.02)	-0.14 (-0.16, -0.12)	-0.07 (-0.17, 0.03)	0.09 (0.04, 0.13)	-0.00 (-0.00, 0.00)
y116	2013	6.28 (6.24, 6.31)	-8.46 (-10.38, -6.54)	0.02 (0.01, 0.02)	-0.18 (-0.21, -0.14)	-0.14 (-0.27, -0.00)	0.14 (0.06, 0.22)	-0.00 (-0.00, 0.00)
y139	2013	6.26 (6.23, 6.30)	-16.09 (-106.73, 74.55)	0.01 (0.01, 0.02)	-0.14 (-0.15, -0.12)	-0.04 (-0.14, 0.06)	0.10 (0.06, 0.13)	0.00 (0.00, 0.00)
y270	2013	6.28 (6.25, 6.32)	-9.14 (-0.17, -1.03)	0.01 (0.01, 0.02)	-0.14 (-0.18, -0.11)	-0.08 (-0.20, 0.04)	0.09 (0.02, 0.16)	-0.00 (-0.00, 0.00)
y274	2013	6.36 (6.33, 6.40)	-13.92 (-72.16, 44.31)	0.01 (0.01, 0.02)	-0.13 (-0.14, -0.11)	-0.07 (-0.16, 0.03)	0.07 (0.04, 0.10)	0.00 (-0.00, 0.00)
y507	2013	6.30 (6.27, 6.34)	-10.14 (-11.99, -8.28)	0.02 (0.02, 0.03)	-0.15 (-0.18, -0.13)	-0.11 (-0.24, 0.02)	0.20 (0.15, 0.25)	-0.01 (-0.01, -0.00)
y605	2013	6.39 (6.35, 6.42)	-8.39 (-10.11, -6.67)	0.02 (0.01, 0.02)	-0.17 (-0.20, -0.14)	-0.06 (-0.19, 0.07)	0.15 (0.09, 0.21)	-0.00 (-0.01, -0.00)
y720	2013	6.41 (6.37, 6.44)	-9.76 (-13.78, -5.74)	0.02 (0.01, 0.02)	-0.16 (-0.18, -0.13)	-0.16 (-0.27, -0.05)	0.10 (0.05, 0.16)	-0.00 (-0.00, 0.00)
y389	2013	6.35 (6.31, 6.38)	-6.63 (-8.63, -4.64)	0.01 (0.01, 0.01)	-0.15 (-0.18, -0.13)	-0.21 (-0.33, -0.09)	0.17 (0.11, 0.23)	-0.00 (-0.00, 0.00)



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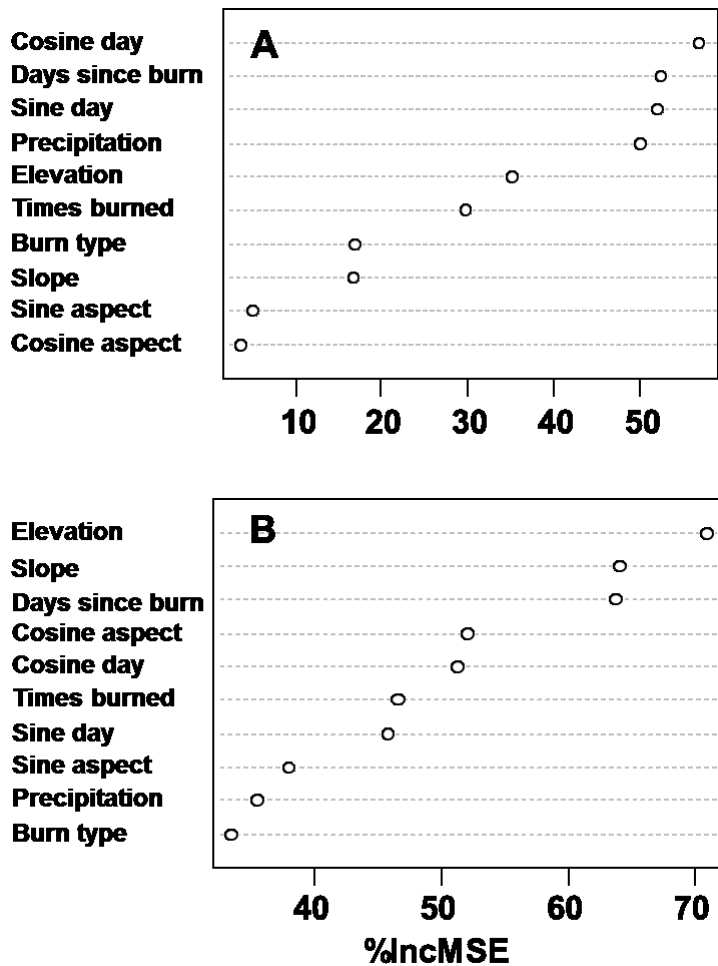
3566 **Figure 5-1. Cumulative growing season (Mar-Oct) precipitation (blue line) with 30-year**  
 3567 **mean of cumulative growing season precipitation (dashed blue line), annual net primary**  
 3568 **productivity (ANPP) averaged across ungrazed watersheds: 04B, 1D, 20B (green line) with**  
 3569 **29-year mean (dashed green line; Konza-LTER dataset PAB01), and average growing**  
 3570 **season ambient temperature (°C; red line) with 32-year mean (dashed red line) during**  
 3571 **2008-2013 at Konza Prairie Biological Station, Manhattan, Kansas, U.S.A.**

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3577 **Figure 5-2. Variable importance plots for (a) grass nitrogen content and (b) herbaceous**  
 3578 **biomass content generated by the random forest algorithm included in the *randomForest***  
 3579 **package for R software. The plot shows the variable importance measured as the increased**  
 3580 **mean square error (%IncMSE), which represents the deterioration of the predictive ability**  
 3581 **of the model when each predictor is replaced in turn by random noise. Higher %IncMSE**  
 3582 **indicates greater variable importance. Variables include cosine of day, days since last burn**  
 3583 **of watershed, sine of day, cumulative precipitation since March 1, elevation (m; scaled),**  
 3584 **number of times burned since 1980, burn type [frequent, infrequent, not-burned that year],**  
 3585 **slope (degrees), sine of aspect (radians), and cosine of aspect (radians).**

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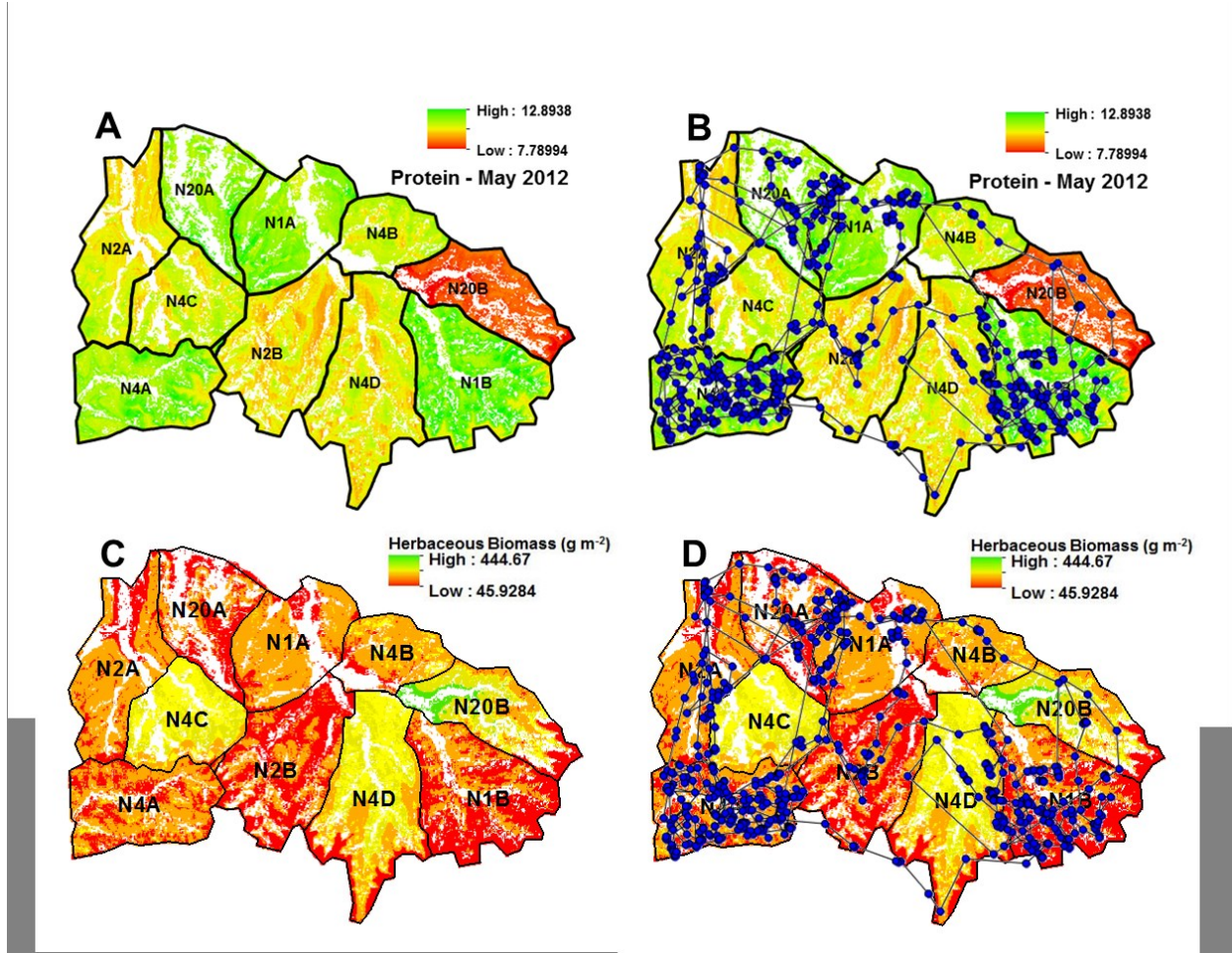
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3594 **Figure 5-3. Map showing the prediction of (a) grass crude protein content (10 m resolution)**  
3595 **in the Konza Prairie Biological Station bison enclosure obtained by the application of the**  
3596 **random Forest model for May 2012, (b) with movement path of bison #W674 for May**  
3597 **2012, (c) map showing the prediction of herbaceous vegetation content (10 m resolution),**  
3598 **and (d) with movement path of bison #W674 for May 2012.**

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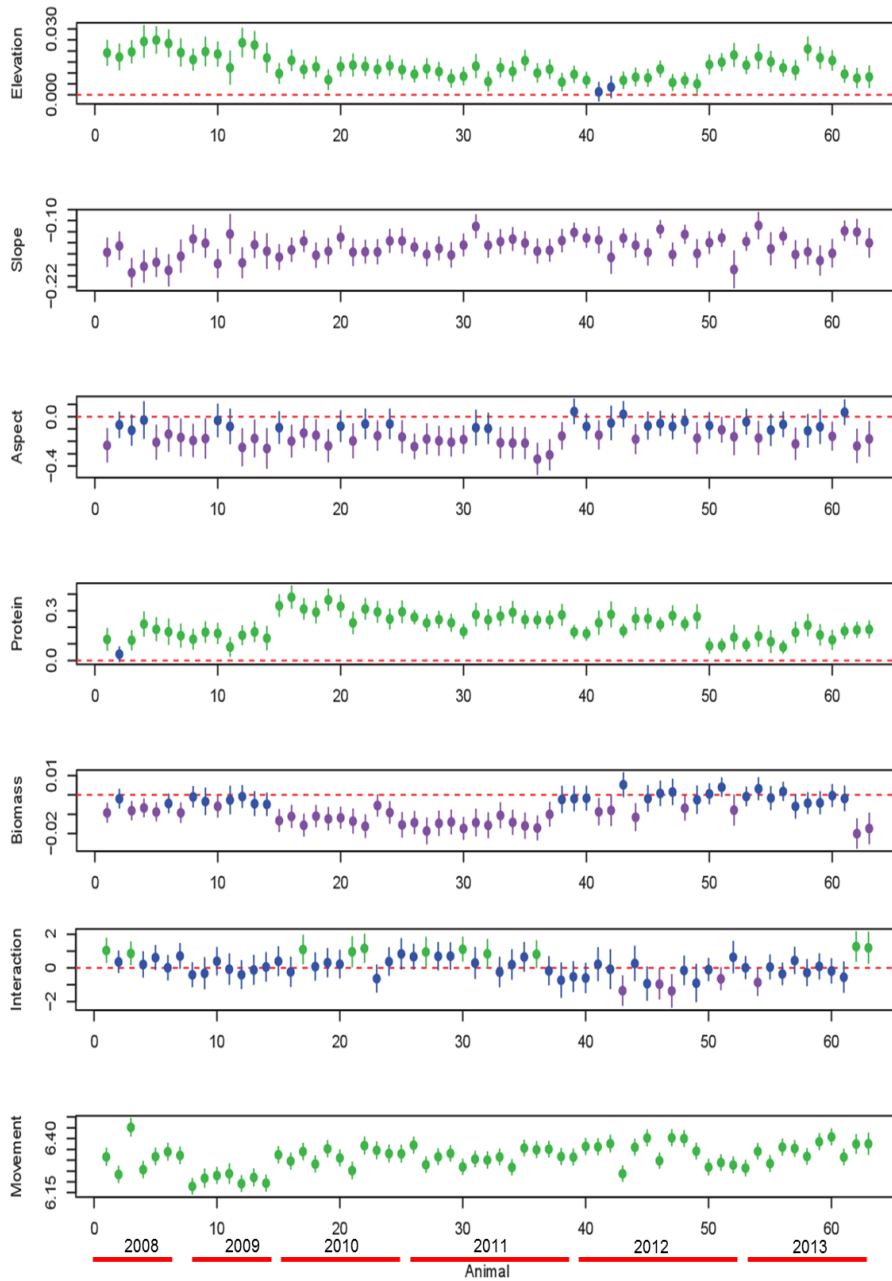
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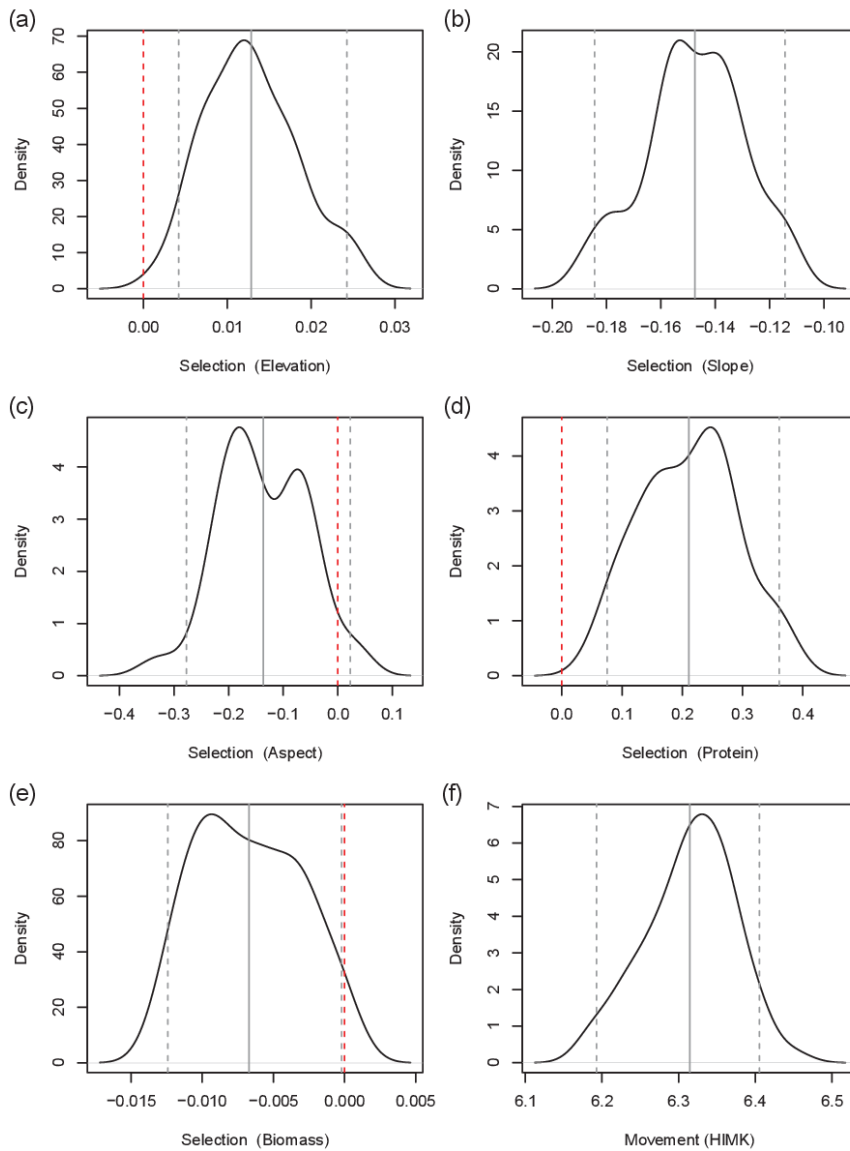


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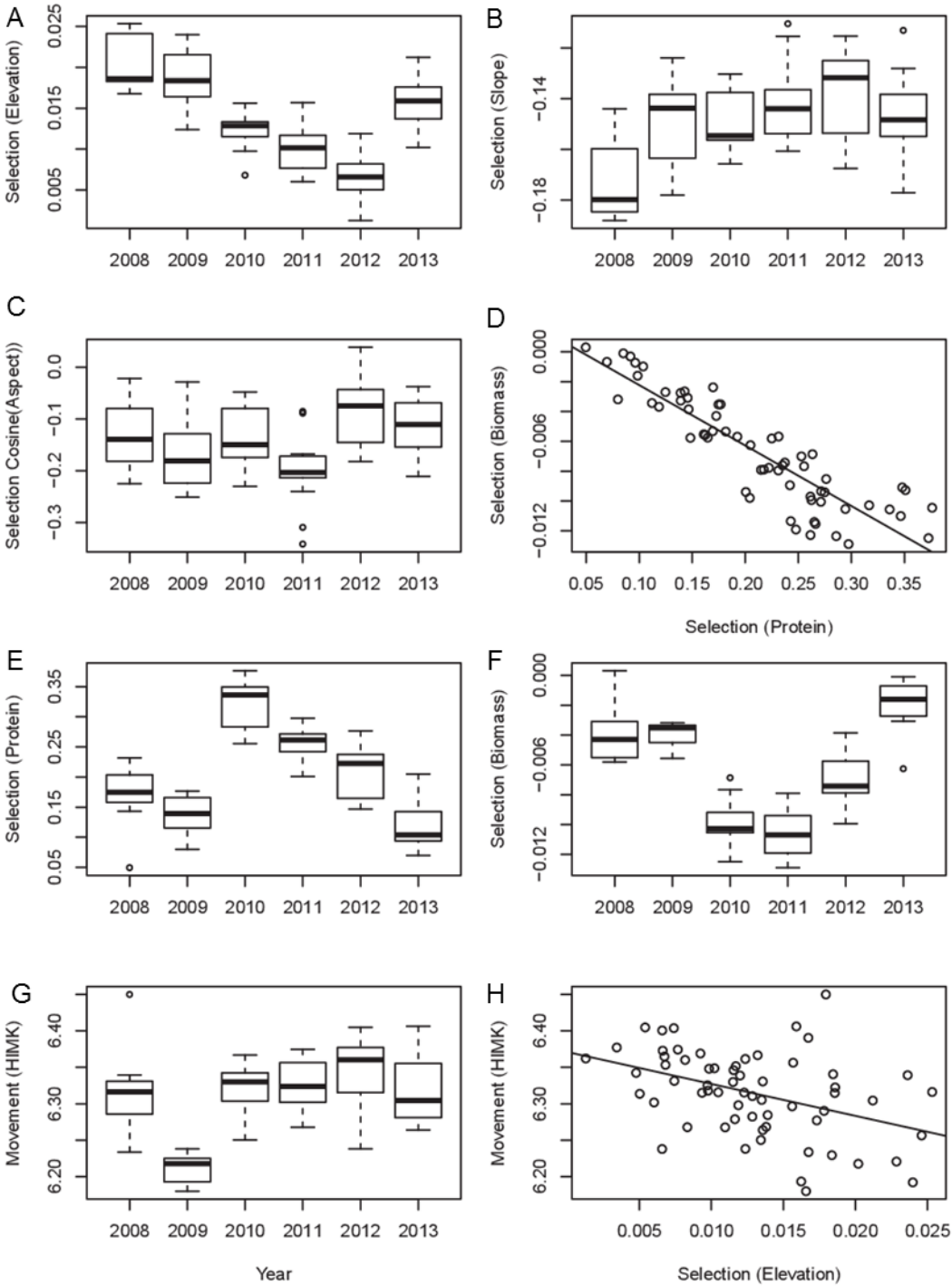
3608 **Figure 5-4. Maximum likelihood parameter estimates among all animals with mean**  
3609 **(circle), 95% confidences (lines) and 0 (no selection) as the redline for (a) elevation, (b)**  
3610 **slope, (c) cosine of aspect, (d) grass crude protein content, (e) herbaceous biomass content,**  
3611 **(f) protein-biomass interaction, and (g) habitat-independent movement kernel parameter.**  
3612 **Points that are green are positively associated with the variable, purple are negatively**  
3613 **associated with the variable, and blue are not different from random.**

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3617 **Figure 5-5. Distributions of maximum likelihood parameter estimates among all animals**  
3618 **with mean (solid gray), 95% confidences (dashed lines) and 0 (no selection) as the redline**  
3619 **for (a) elevation, (b) slope, (c) cosine of aspect, (d) grass crude protein content, (e)**  
3620 **herbaceous content, and (f) habitat-independent movement kernel parameter.**  
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**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

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3633 This study offers insights on the foraging behavior, habitat selection, and landscape-level  
3634 distribution of bison that can help answer the seemingly simple question raised in the dissertation  
3635 prologue: how does foraging behavior and space use respond to varying grassland burn  
3636 frequencies? Bison prefer recently-burned watersheds that are burned every four years. Here,  
3637 forage items have greater protein content than watersheds burned more frequently. Selection of  
3638 foraging areas is related to high foliar crude protein content and low vegetation structure at the  
3639 patch spatial scales. This dissertation further outlines the importance of the degree of disturbance  
3640 in terms of prescribed fire intervals on habitat selection and resource use by a large, ruminant  
3641 ecological engineer.

### 3642 *Fine-scale foraging behavior*

3643 Active selection of forage at the fine scale as a function of nutritional quality is the most  
3644 immediate response in the foraging hierarchy. In Chapter 2, I first investigated the plant-bison  
3645 interaction by examining feeding station intake rates for the area in between steps in a foraging  
3646 bout (Bailey et al. 1996). During short foraging bouts, bison increased their intake rate with  
3647 increasing availability of grass biomass at a greater rate in the early growing season compared to  
3648 the mid-summer transitional season in infrequently-burned watersheds, whereas the slope of  
3649 intake rate was gradually increasing with grass biomass in watersheds that did not burn that  
3650 previous spring or burned that previous spring and are annually or biannually burned. This early  
3651 growing season behavior corresponds with a time-minimizing short-term feeding strategy  
3652 (Bergman et al. 2001, Fortin et al. 2002). When forage is in a state of greatest nutritional value,  
3653 foragers may intensely utilize this resource as a means to free time for non-foraging behavior  
3654 activities (e.g. social activities or nursing young). However, as the growing season progressed

3655 and bison remained in this habitat, a shift towards a long-term feeding strategy, where daily  
3656 nutrient gains may be maximized by feeding in nutrient-laden, low-stature vegetation, likely  
3657 occurred.

3658 My primary field seasons in 2012 and 2013 included a drought and non-drought period,  
3659 respectively, when ANPP was well below-average and average for the KPBS LTER long-term  
3660 mean. The contrasting ANPP that resulted from these periods allowed me to assess potential  
3661 differences in late growing season foraging behavior at the feeding station-scale. When  
3662 precipitation is markedly reduced in a growing season, grass protein concentrations increase  
3663 (Milchunas et al. 1995, Joern and Mole 2005). To determine if feeding station foraging behavior  
3664 responds to this climate-driven variation in forage resource I compared bite mass and  
3665 instantaneous intake rate at the end of the two growing seasons as this is the period when  
3666 nutrient-levels would be most reduced prior to the dormant season. Both feeding measures were  
3667 greater in 2013 than 2012. This result suggests bison may have been compensating for lower  
3668 nutrient availability in forage by taking larger bites and ingesting more grass as the dormant  
3669 season approached (Chapter 2).

3670 Animals often face temporal and spatial heterogeneity in the distribution of resources,  
3671 and the decision of where to forage can influence the spatial dynamics of consumer-resource  
3672 processes. Optimal diet theory reworked for grazing provides a useful theoretical framework to  
3673 understand how and why animals include prey items in their diet (MacArthur and Pianka 1966,  
3674 Pulliam 1974, Fryxell 1991, Spalinger and Hobbs 1992). In landscapes where food patch quality  
3675 is temporally stable, forage attributes such as protein concentration may be consistently  
3676 responsible for feeding-site selection during that season. Despite the variation in forage quality  
3677 among watersheds burned at different frequencies, I found plant-form characteristics guiding

3678 feeding-site selection to be generally static within seasons (Chapter 3). Bison grazed  
3679 preferentially in areas of higher foliar protein content, higher grass: forb ratio, and lower  
3680 herbaceous biomass content than observed in nearby, randomly-selected locations in the early  
3681 growing and mid-summer transitional seasons. However, bison grazed selectively in areas of  
3682 higher uniformity in vegetation structure between used and available locations during the  
3683 dormant season in primarily unburned watersheds. This suggests that the availability of forage  
3684 irrespective of quality, which was uniformly low in this period, was driving feeding-site  
3685 selection during periods of plant dormancy. In contrast, when plant regrowth was possible, bison  
3686 were likely re-using previously grazed sites that could still offer higher quality forage items than  
3687 that available in randomly selected areas nearby. Furthermore, diurnal time spent feeding  
3688 increased as the dormant season approached, which suggests that bison's ability to locate high-  
3689 quality forage decreases as high quality foraging items became scarcer. Moreover, the isotopic  
3690 history of diet selection for collared female bison documents a shift from a pure warm-season  
3691 grass diet to a mixed diet of warm- and cool-season plants in the dormant season. Study animals  
3692 disproportionately used unburned habitat during this period, which bolsters an environmentally-  
3693 induced shift in diet and foraging behavior in response to reduced availability of high-quality  
3694 forage during periods of plant dormancy.

3695         These findings are consistent with predictions for the forage maturation hypothesis,  
3696 which posits that aggregations of large herbivores reflect optimal combinations of forage quality  
3697 and quantity to maximize net intake rate (Fryxell 1991). In turn, collective consumption pressure  
3698 at intermediate to high grazer densities may maintain vegetation in a state of low to intermediate  
3699 forage quantity but high quality through regrowth of young forage tissue (McNaughton 1979,  
3700 Fryxell 1991); i.e., seasonal maturation to high biomass is repressed by repeated foraging

3701 pressure. McNaughton and Fryxell's observations originated in stable, tropical environments but  
3702 our findings extend the use of this hypothesis to temperate environments for predicting patch use  
3703 and the spatial and temporal distributions of grazing herbivores when plant regrowth is possible  
3704 during the growing season. Furthermore, these findings of fine-scale foraging behavior in plains  
3705 bison show that the initial attraction to infrequently-burned watersheds burned that year in  
3706 response to the pulse of high quality forage dictates growing season space use as long as  
3707 regrowth is possible. This observation links two prominent ecological hypotheses, one developed  
3708 in Africa (FMH; Fryxell 1991) and one developed and tested at KPBS (Seastedt and Knapp  
3709 1993, Blair 1997).

3710 *Coarse-scale behavior*

3711 Studies of large grazer responses to fire-induced variation in forage quality and quantity has  
3712 primarily been conducted in reference to spatial extent of fire and binary applications of fire or  
3713 the lack thereof– i.e., comparisons of reactions by herbivores to recently burned vs. not-burned  
3714 sites (Archibald and Bond 2004, Allred et al. 2011). In this dissertation, I investigated large  
3715 grazer response to shifting maxima in forage resources resulting from prescribed burning of  
3716 watersheds at different frequencies, which provides insight into dynamic, temporally-based  
3717 variation in ungulate response to fire. In Chapter 4, I investigated the likelihood of GPS-collared  
3718 female bison occurring at any given location in their enclosure and linked the likelihood to  
3719 watersheds burned at different frequencies. Then, I tested whether the likelihood of using  
3720 different burn types was different from using unburned watersheds. Without the watershed-level  
3721 experimental design in place in the KPBS bison enclosure, a long-term investigation of bison use  
3722 of different burn frequencies of mesic grassland would not have been possible anywhere in the  
3723 world. The finding that annually-burned watersheds are most strongly avoided compared to

3724 unburned watersheds during the dormant season offers further evidence that this management  
3725 strategy in the Flint Hills of Kansas may not offer adequate forage cover for herbivore  
3726 consumers, especially in years of low ANPP. Furthermore, I demonstrated that infrequently-  
3727 burned watersheds were more extensively used by bison than not-burned or frequently-burned  
3728 watersheds throughout the growing season (May to September), which implies that infrequent-  
3729 burning of pasture may not only collectively offer suitable habitat for other wildlife species  
3730 (Fuhlendorf et al. 2009, McNew et al. 2015) but also for economically-important cattle (Limb et  
3731 al. 2011, Allred et al. 2014).

3732           Understanding how the biotic and abiotic environment affects the movement and  
3733 distribution of organisms is a central objective of resource and movement ecology. As discussed  
3734 in earlier chapters, digestive and time constraints faced by herbivores can limit rates of daily  
3735 intake (Belovsky 1978, Langvatn and Hanley 1993, Wilmshurst et al. 1995, 1999). To reduce  
3736 these constraints on daily food intake, herbivores may select foraging areas in efforts to  
3737 maximize forage intake as seen in free-ranging domestic sheep (*Ovis aries*) or to simultaneously  
3738 feed and thwart predation as in roe deer (*Capreolus caprolus*) (Myysterud et al. 1999).

3739           In Chapter 5, using a novel mechanistic movement model (Beyer et al. 2014), I  
3740 demonstrated that spatial and temporal variation in forage quality and quantity was a biotic  
3741 feature of the landscape that shaped the distribution of bison. In the predator-free system at  
3742 KPBS, it seems safe to assume that bison distribution is food-motivated. However, I also found  
3743 topography to be a driver of space use. Over several growing seasons, bison tended to prefer high  
3744 elevation, avoid steep slopes and areas that did not face south. These habitat preferences may be  
3745 fitness-based as locomotion on steep slopes is energy-demanding (Dailey and Hobbs 1989),  
3746 whereas wind-prone, elevated southern-facing areas offer relief from insect harassment and high

3747 temperatures, which induce sub-clinical effects on fitness (Skarin et al. 2004, Witter et al. 2012).  
3748 Moreover, the flat, upper bench habitat at KPBS offers high quality forage (Blair 1997) as well  
3749 as relief from warm temperatures and insects that likely influences growing season space use in  
3750 the Konza Prairie bison herd in addition to fire-induced variation in forage resources. These  
3751 results suggest that management strategies should consider biotic and abiotic characteristics of  
3752 the landscape in which preferred habitat features are found (Pearson et al. 1995).

3753 *Ecological hierarchy of foraging*

3754 Animals should select habitats that simultaneously satisfy several of their needs that may result  
3755 in behavioral trade-offs, which may vary at different spatio-temporal scales (Johnson 1980, Allen  
3756 and Starr 1982, Senft et al. 1987, Mysterud et al. 1999, Fortin et al. 2004, St-Louis and Cote  
3757 2012). Scale-dependence in trade-offs has been suggested by Senft et al. 1987 and Bailey et al.  
3758 (1996), and observed in empirical studies such as these of Wallace et al. (1995), Schaefer and  
3759 Messier (1995), and Fortin et al. (2003).

3760 I found that bison distribution and resource use were influenced by both abiotic and biotic  
3761 factors with variation of relative importance at different scales and time periods. Fire-induced  
3762 enhancement of forage quality influenced feeding station- and landscape-level decisions. In  
3763 response to this abiotic factor, bison increased feeding rates at a greater rate in the most  
3764 nutritious grassland than grassland of lower nutritive value (Chapter 2). The feeding station is the  
3765 finest resolution of the ecological hierarchy in foraging by large herbivores and is where the  
3766 strength of the plant-herbivore interaction is strongest as diet is selected at this level (Senft et  
3767 al.1987, Bailey et al. 1996). As forage availability waned in the most profitable habitat by mid-  
3768 summer, bison instantaneous intake responded by taking large bites of poorer quality forage in a  
3769 year of average ANPP, 2013, or smaller bites of the more stressed yet higher quality forage in a

3770 year of very low ANPP, 2012 (Chapter 2). At the intermediate level of the foraging hierarchy,  
3771 the patch or feeding site scale, bison preferred to graze in burned areas of low vegetation  
3772 structure (Chapter 3), where high quality items that maximize daily nutrient gains are easier to  
3773 find (Fryxell 1991). Decreasing forage availability with the approaching dormant season, likely  
3774 drove bison to feed in more homogenous, unburned areas where satiation was more likely  
3775 although at the cost of reduced nutrient intake.

3776         In response to fire-induced variation in forage quality and temporal forage availability,  
3777 bison foraging tactics to meet metabolic requirements at two scales dictated space use in the  
3778 landscape as predicted by Senft et al. (1987). At the landscape-level, bison shifted patterns of  
3779 space use in response to fire-induced resource variability but topographical features of the  
3780 landscape also affected space use (Chapter 4). Preference for the upper bench features of the  
3781 enclosure, which offer flat terrain, southerly winds, and high-quality food, reduced movement  
3782 during the growing season (Chapter 5). In this empirical study, I documented behavioral  
3783 mechanisms driving resource use at each of the levels of the ecological hierarchy available at  
3784 KPBS (feeding station to patch to landscape). These findings shed light on a historically,  
3785 important consumer's multi-scale behavioral tactics to maintain basic metabolic requirements in  
3786 a nutritionally heterogeneous grassland managed to mirror ecological processes in tallgrass  
3787 prairie with an intact-fire grazer interaction.

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