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Abstract. Land use, climate change, and their interaction each have great potential to affect grazing systems. With anticipated more frequent and extensive future drought, a more complete understanding of the mechanisms that determine large grazer landscape-level distribution under varying climatic conditions is integral to ecosystem management. Using an experimental setting with contrasting fire treatments, we describe the inter-annual variability of the effect of landscape topography and disturbance from prescribed spring fire on large grazer space use in years of variable resource availability. Using GPS telemetry, we investigated space use of plains bison (*Bison bison bison*) as they moved among watersheds managed with variable experimental burn treatments (1-, 2-, 4-, and 20-year burn intervals) during a seven-year period spanning years of average-to-above average forage production and severe drought. At the landscape scale, bison more strongly favored high-elevation and recently burned watersheds with watersheds burned for the first time in 2 or 4 yr consistently showing higher use relative to annually burned watersheds. In particular, watersheds burned for the first time in 4 yr were avoided to lesser extent than other more frequently burned watersheds during the dormant season. This management type also maintained coupling between bison space use and post-fire regrowth across post-drought growing season months, whereas watersheds with more frequent fire-return intervals attracted bison in only the first month post-fire. Hence, fire frequency played a role in maintaining the coupling of grazer and post-fire regrowth, the fire–grazer interaction, in response to drought-induced reduction in fuel loads. Moreover, bison avoided upland habitat in poor forage production years, when forage regrowth is less likely to occur in upland than in lowland habitats. Such quantified responses of bison to landscape features can aid future conservation management efforts and planning to sustain fire–grazer interactions and resulting spatial heterogeneity in grassland ecosystems.

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INTRODUCTION

The ability of grassland ecosystems to support wildlife and grazing systems is largely determined by grassland productivity, which ultimately determines the limits of secondary productivity (McNaughton et al. 1989, Polis 1999). The potential to support a given level of herbivore biomass in a particular ecosystem is driven by inherent abiotic and biotic factors determining grass production, such as rainfall, topography, and grazing pressure with feedbacks to soil productivity and forage resources (McNaughton et al. 1989, Hopcraft et al. 2010). These interacting factors that drive spatial and temporal variation in forage quantity and quality are further modulated by recursive fire–grazer interactions that can propagate vegetation heterogeneity across landscapes (Fuhlendorf and Engle 2004, Archibald et al. 2005, Anderson et al. 2007, Allred et al. 2011). Heterogeneity of vegetation then may sustain herbivore populations when the feedback of grazing pressure on soil nutrient availability and concomitant forage quantity and quality is hampered by drought-induced climatic variability (Scoones 1993, Ash et al. 2002, Fynn 2012).

In savannas and grasslands, local forage accessibility and availability to large herbivores can be enhanced by fire (Fuhlendorf and Engle 2004, Archibald et al. 2005, Fuhlendorf et al. 2009), where burning removes older, non-palatable vegetation, thereby releasing grassland from light limitation and facilitating new growth of high nutritional value (Hobbs et al. 1991, Seastedt and Knapp 1993, Blair 1997, Allred et al. 2011, Ling et al. 2014). Availability of high-quality forage can then bridge the period when forage elsewhere remains low in quality (i.e., at the onset of the growing season; Albon and Langvatn 1992, Hebblewhite et al. 2008). Ungulates in heterogeneous landscapes often encounter substandard quality forage as the best quality food is patchily distributed with substantial variation among years as a result of climate, recent fire, and grazer activity (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2009, Allred et al. 2011, Augustine and Derner 2014). Thus, the ability to forecast how large grazer distributions and foraging behavior will respond to climate-induced resource availability should benefit ecosystem management (Limb et al. 2016). The availability of animal needs, such as forage and shelter, can change from 1 yr to the next, thus generating inter-annual variability in habitat selection (Schooley 1994, May 1999). However, multi-year evaluations of how animals can alter their behavior to adjust to a changing environment are rarely conducted.

Climate change forecasts include alterations in climatic means, greater climatic variability, and increases in the frequency of climatic extremes such as floods, droughts, and heat waves (Intergovernmental Panel on Climate Change [IPCC] 2007, 2012). Drought defined by the IPCC as a "prolonged absence or marked deficiency of precipitation" is likely to have the most severe, immediate, and long-term impact on terrestrial grassland ecosystems (e.g., Weaver and Albertson 1936, Weaver 1954, Breshears et al. 2005). For example, the Central United States in 2012 experienced the fourth largest drought in a century, with a regional-scale 40% reduction in growing season precipitation (Knapp et al. 2015). Thus, understanding important consumer–resource processes in response to drought is critical (Briske et al. 2015), especially as warming and reduced precipitation are expected to decrease both plant production and nutritive content.

In North American tallgrass prairie, prescribed fire removes standing dead plant tissue, allowing large grazers to forage on undiluted and unobstructed green material (Hobbs et al. 1991, Knapp et al. 1999, Allred et al. 2011, Raynor et al. 2015, 2016), where the rate of daily nutrient intake can be optimized (Fig. 1A; Raynor et al. 2016). Moreover, large grazers increase soil N concentration and availability with urine and fecal deposition, which provides plants with higher amounts of N (Johnson and Matchett 2001). Recursive grazing maintains burned areas in a state of low-to-intermediate biomass until forage senescence occurs (Raynor et al. 2016). With forage senescence, grazers reduce their use of recently burned areas (Fig. 1B), and their spatial distributions are expected to be directed toward areas containing high biomass availability (Vinton et al. 1993). Because large herbivores may use spatial memory to return to profitable areas and avoid undesirable areas (Bailey et al. 1996, Edwards et al. 1996, Merkle et al. 2014), it is likely that the loss of regrowth of high-quality forage can lower within-season site fidelity and trigger shifts in movement behavior (Wittmer
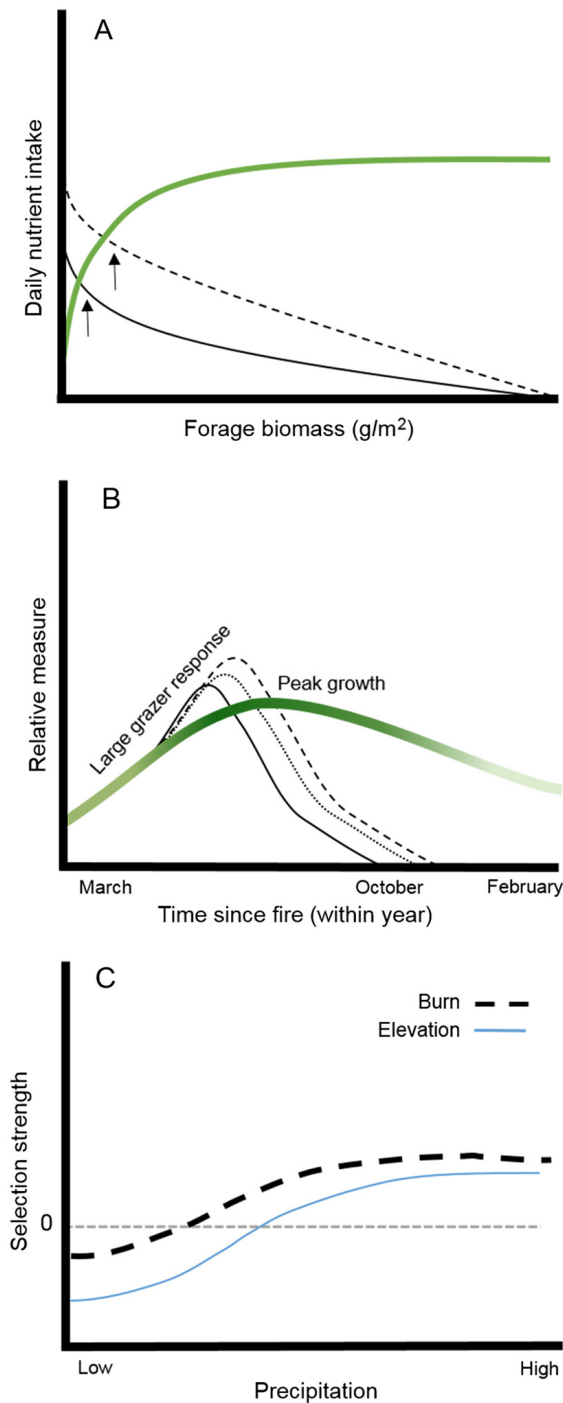
Fig. 1. (A) Foraging constraints of daily cropping (solid line) and digestion for large grazers in frequently burned (fine-dotted line) and infrequently burned (dashed line) grassland predict foraging optima (arrows) at low-to-intermediate biomass (modified from Fryxell 1991, Hebblewhite et al. 2008, Raynor et al. 2015). (B) Predicted large grazer response to prescribed burn frequency in tallgrass prairie, where, when burned, infrequently burned watersheds (dashed line) are expected to more strongly drive space use over not-burned watersheds than biannually (dotted line) and annually burned (solid black line) watersheds; a short duration of response is expected due to high absolute resource requirements. (C) Low rainfall is predicted to decouple large grazer space use from recently burned prairie (dashed line) and upland habitats (solid blue line) due to reduced capacity for nutritious grass regrowth.

individuals move freely among multiple watersheds that differ in fire and grazing history. In this experimental landscape, we assess the use of topography and prescribed fire at varying fire-return intervals for the creation of areas that may restrict bison space use during specific parts of a year. We hypothesize that an inverse relationship occurs between strength in selection for recently burned areas and drought intensity because bison with high resource requirements will be less tightly coupled to watersheds burned in the spring following years of low plant productivity. By evaluating patterns of bison space use in our experimental setting with temporal variability in forage availability, we can identify the topographic features and temporal frequencies of prescribed spring burning that are likely to be important static and management-induced drivers of ruminant grazer distributions. Furthermore, because of their dominant impact on ecosystems (Hobbs 1996, Collins et al. 1998, Holyoak et al. 2005, Joern 2005, Fynn et al. 2016), it is critical to understand how large grazing animals alter their movement behavior in response to climatic events to ultimately assess the full effects of climate change on ecosystem structure and function.

We evaluated resource selection of GPS-tracked female bison across 7 yr in replicated watersheds under varying fire frequency. Using a hierarchical approach to account for the lack of independence associated with repeatedly sampling individual

et al. 2006, Bar-David et al. 2009, Owen-Smith et al. 2010).

Here, we examine the spatial ecology of plains bison (*Bison bison bison*) in tallgrass prairie at Konza Prairie Biological Station (KPBS; Fig. 2) as
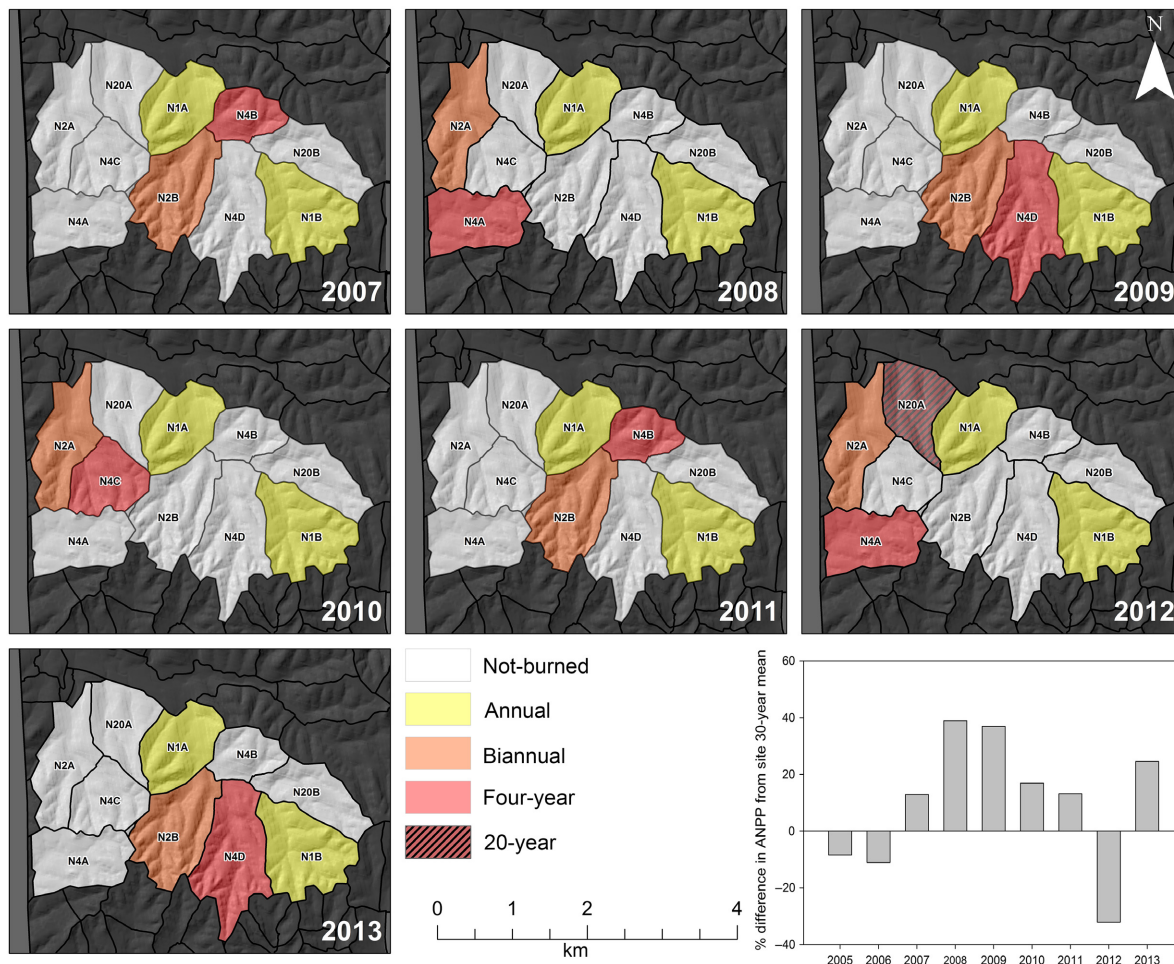
Fig. 2. Map of the bison enclosure at Konza Prairie Biological Station, Manhattan, Kansas, showing topographic relief and watersheds burned each year and percent deviation of aboveground net primary productivity (ANPP) from 30-year (1983–2013) means at Konza Prairie Biological Station, Manhattan, Kansas, USA.

movements, we fit separate models to monthly periods and test the following predictions (P). (P1) During the early growing season, bison select recently burned areas (Fig. 1B), thus bridging the period when forage elsewhere remained low in quality, where they show movement responses similar to those of bison and domestic cattle (*Bos taurus*) observed by Allred et al. (2011, 2013) in tallgrass prairie in Oklahoma.

However, the predictability of this space use strategy may be influenced by habitat productivity (Bell 1970, Hopcraft et al. 2010, Augustine and Derner 2014). Following extremely dry years with low vegetation production and low soil moisture availability, reduced selection strength for recently burned watersheds will likely result

because less fuel is available to carry fire uniformly across the landscape and provide highly sought-after grass regrowth. Unlike small-bodied herbivores such as gazelles that have low absolute resource requirements and can therefore meet their intake requirements on short grass, such as a short grazing lawn (Illius and Gordon 1987, Hobbs and Swift 1988, Hopcraft et al. 2010, 2012, Bhola et al. 2012), foraging decisions of bison with high absolute resource requirements are likely to be influenced by the availability of areas known to offer reliably high primary productivity. In tallgrass prairie, during drought years when soil moisture is limiting for forage production (Briggs and Knapp 1995), there may be insufficient regrowth after fire to sustain a

large-bodied herbivore. Thus, we predict (P2) bison will avoid recently burned watersheds during the periods when conditions are poor and vegetative regrowth is not possible, resulting in use of areas with greater availability of low-quality forage. This response would be associated with reduced nutrient intake (e.g., maintenance of the protein–energy balance [Odadi et al. 2013, 2016]). Because large-bodied herbivores such as African buffalo (*Syncerus caffer*), and bison that utilize a tongue sweep strategy to maximize bite size in areas where long grass leaves can be swept into the mouth (Bell 1970, Prins and Beekman 1989, Bergman et al. 2000, Augustine and Springer 2013), we expect (P3) the availability of lowland areas to be a strong predictor of space use in sub-optimal forage production years (Fig. 1C). At KPBS, upland sites on dry shallow soils and lowlands on wetter and deeper soils contrast in availability of soil moisture, which is critical for post-fire grass regrowth (Knapp et al. 1993, 1999, Briggs and Knapp 1995, Nippert et al. 2011). Thus, lowland sites during dry years are likely to constrain bison distributions. On the other hand, we expect bison to select upland sites during wetter growing seasons when post-fire regrowth is possible (Fig. 1C). In general, upland sites offer high-quality forage in the growing season (Schimel et al. 1991), a key to meeting both forage quality and quantity requirements.

Time since last fire has been shown to be a key predictor of large grazer resource selection as forage quality in recently burned grassland is greater than in unburned grassland (Allred et al. 2011). However, the duration of this attraction to recently burned grassland may be short-lived (e.g., ~1 month; Augustine and Derner 2014) because large grazers with high absolute intake requirements may seek additional, low-quality forage to meet metabolic demands (Hobbs and Swift 1988, Sensenig et al. 2010). How this attraction to recently burned grassland varies by grassland fire-return interval is unknown, which is a cause for concern because fire management is becoming a more common tool to manage the structure and function of grassland ecosystems (Twidwell et al. 2013, Limb et al. 2016). In the Flint Hills tallgrass prairie region of the Central United States, annual spring burning is a common practice to create homogeneous and highly nutritious grassland habitats for livestock production that may negatively affect grassland structural heterogeneity and concomitant species diversity (Fuhlendorf et al. 2012, Ratajczak et al. 2012, McNew et al. 2015). Understanding the role of fire-return interval in guiding grazer distribution may be critical to reversing homogeneous grassland management practices.

In this study, we examine relative preference for the experimental watersheds at KPBS to test the prediction (P4) that bison are more attracted to watersheds burned for the first time in several years relative to annually burned watersheds due to the greater availability of high-quality post-fire regrowth in less frequently burned watersheds burned that year (Seastedt and Knapp 1993, Blair 1997, Raynor et al. 2015, Fig. 1B). With frequent fire, soil nutrients become limiting to plant growth, even while sufficient light exists to promote growth (Seastedt and Knapp 1993, Blair 1997). Enhanced grass productivity and quality is seen immediately following infrequent fires (e.g., 3–4 yr) that last over a relatively short non-equilibria transition stage (e.g., one growing season) in response to the relatively high availability of both light and soil nutrients in areas burned at intermediate frequencies compared with sites burned annually or left unburned for long periods (Blair 1997). Moreover, sites burned for the first time in several years are more likely to carry fire uniformly across the landscape and maintain large grazer use (Fig. 1B).

Our basic approach includes quantifying the extent to which utilization distributions of bison relate to these varying fire frequencies and landscape features. In addition, we assess the strength of recently burned watershed selection in relation to previous-year primary productivity, which reflects both fuel loads and over-winter animal food needs (Hobbs 1996). These non-mutually exclusive factors likely underpin the strength of the fire–grazer interaction and are expected to be of particular importance in shaping the spatial–temporal dynamics of large herbivore space use in grazing systems managed with fire. We evaluate the degree to which departures from average primary production reduce the strength of selection for recently burned areas and topography and how different prescribed fire-return intervals can maintain coupling between space use and post-fire regrowth.

Table 1. Experimental watershed prescribed burning assignments at Konza Prairie Biological Station near Manhattan, Kansas.

Year	N1A	N1B	N20A	N20B	N2A	N2B	N4A	N4B	N4C	N4D	Total
2007	X	X	–	–	–	X	–	X	–	–	4
2008	X	X	–	–	X	–	X	–	–	–	4
2009	X	X	–	–	–	X	–	–	–	X	4
2010	X	X	–	–	X	–	–	–	X	–	4
2011	X	X	–	–	–	X	–	X	–	–	4
2012	X	X	X	–	X	–	X	–	–	–	5
2013	X	X	–	–	–	X	–	–	–	X	4

Note: "X" indicates watersheds that burned and "–" indicates watersheds that did not burn in early spring of that year.

Methods

Study system

Konza Prairie Biological Station is a native tallgrass prairie preserve located in the Flint Hills grassland near Manhattan, Kansas, United States (39°05′ N, 96°35′ W; Fig. 1). An extreme drought occurred from mid-summer of 2011 to the beginning of the growing season in 2013, which reduced forage production (~30% less than 30-year mean, Fig. 1; Appendix S1: Fig. S1; Knapp et al. 2015). Mean monthly temperatures range from −2.7°C (January) to 26.6°C (July) and mean (±SE) precipitation is ~835 ± 60 mm, with 75% falling during the growing season. Vegetation is mostly dominated by C_4 grasses (*Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Panicum virgatum*) along with a diverse mixture of warm- and cool-season graminoids. Forbs constitute ~75% of species richness, and vegetation biomass is >75% from grasses (Towne 2002, Collins and Calabrese 2012). During the dormant season, watersheds not burned in the spring typically offer more grass biomass than is found in watersheds burned in the spring, a result of recursive grazing in the burned watersheds and removal of standing dead biomass by spring burning (Vinton et al. 1993, Raynor et al. 2015). Elevation of the KPBS bison enclosure ranges from 334 to 443 m with a mean (±SD) of 394 ± 24 m and slope ranges from 0 to 46° with a mean of 8 ± 5°. Upland Florence soils are shallow, rocky, cherty silty clay loams, while lowland Tully soils area deeper, non-rocky silty clay loams. Slopes vary from shallow and rocky near the uplands to deeper and finer textured where they grade into lowland areas, which are generally more productive than uplands (Collins and Calabrese 2012).

The KPBS bison enclosure is divided into long-term, watershed-level experimental treatments that cross bison grazing with fire frequency (Fig. 2). Bison have unrestricted access to 10 experimental watersheds ($\bar{x} \pm$ SD; 97 ± 23 ha) over approximately 970 ha managed with prescribed spring burns (occurring in mid-March–early April) at 1-, 2-, 4-, and 20-year intervals, where four watersheds are burned each year with the exception of watersheds on a 20-year fire-return interval, N20A and N20B. In this 7-year study, only one 20-year watershed burned, N20A, while one 2-year and one 4-year watershed burned each year as well as two annually burned watersheds (Table 1). In our evaluation of monthly drivers of space use described below, we refer to watersheds that were burned in the spring of the year in question as "recently burned" and watersheds that did not burn that spring as "not burned." Four watersheds were burned and six did not burn between 2007 and 2013, except in 2012 when five watersheds burned and five were not burned; N20A burned in 2012 for the first time in 20 yr (Table 1). Here, we consider April, May, and June as early growing season months, while July, August, and September are transitional, peak growth months, and December, January, and February are treated as dormant season months. The current bison herd was established in 1987, and the population size (adults and calves) during the growing season has been maintained at ~370 ± 31 ($\bar{x} \pm$ SD) individuals from 2002 to 2013. Adult bison typically lose during the dormant season at KPBS (−11.3%) and rapidly gain body mass in the spring post-burning (Towne 1999).

Movement data

Individual bison were tracked from 2007 to 2013 using Telonics TGW-3700 GPS collars (commercial accuracy 8–20 m for both longitude and latitude; Telonics, Mesa, AZ, USA). Four individuals were tracked in 2007, 7 in 2008–2009, 11 in 2010, 13 in 2011, 12 in 2012, and 11 in 2013. All individuals fitted with collars were older, matriarchal females; no males were collared. Bison cows are more likely than males to prefer recently burned areas in tallgrass prairie (Post et al. 2001). Collars were fitted annually at the autumn bison roundup in late October, using the same individuals in consecutive years when possible. We removed two-dimensional data points with a dilution of precision (DOP) of >5.0 to avoid using data that may have large spatial errors (Lewis et al. 2007). Two-hour collar fixes spanning the entire 24-h day were used to determine resource utilization for all collared bison. The bison herd was restricted to only part of the site twice a year (~3 weeks in October–November for roundup, and again in March to accommodate other research needs); data for these periods were excluded from movement analyses.

Landscape attributes

Landscape attributes were mapped using a 30 × 30 m grid of the entire bison enclosure created in ArcMap 10.1 (ESRI, Redlands, CA, USA). For each burn cycle, watershed raster layers were coded in binary fashion as those watersheds that did not burn that spring in year of question (0) and watersheds that were burned that spring (1) with respect to burn type as dummy variables. This resulted in three watershed layers for 1-, 2-, and 4-year prescribed fire intervals in each year of this study except 2012 when a 20-year watershed, N20A, also burned (Table 1). Thus, inference for space use in relation to prescribed burning for April to the following February is based on watersheds that burned that spring (March–early April 2007–2013). This approach allows evaluation of bison response to the watersheds managed under different long-term burn intervals (1, 2, 4, and 20 yr) that burned in the year bison were followed, and how bison habitat response to fire potentially decays each month leading up to February of the next year just before spring burning at KPBS. Therefore, we are investigating how spring burning (March to early April) of

watersheds under different fire-return intervals sets the stage for bison space use over the following 9 months. In addition, to understand effects of topography on space use, we included topographic information (elevation and slope) from a digital elevation model (2-m^2 resolution) that was hypothesized a priori as good predictors of space use in the RUF. We resampled the DEM raster to a 30-m resolution using the majority rule in order to match the grain of the prescribed burn watershed layers. Slope was then mapped to generate a slope raster with values measuring the maximum change in slope between a target cell and its eight neighbor cells.

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

We created a 30 × 30 m grid for the entire 970-ha bison enclosure and created enclosure-wide utilization distributions for each bison because each individual moved across the entire enclosure each month. Separate utilization distributions (UDs) were calculated for monthly distributions of each individual bison using the biased-random bridge (BRB) method, which uses serial autocorrelation in location data to improve the utilization distribution rather than requiring temporally independent locations and ignoring finer-scale movements (Benhamou and Cornelis 2010, Benhamou 2011, Papworth et al. 2012). All individual UDs were bounded within the enclosure prior to estimation. All individuals for each month met the minimum number of 200 locations recommended for UD development (Millspaugh et al. 2006, Benhamou and Cornelis 2010). The diffusion coefficient was calculated using the function BRB.D (Benhamou 2011) in the package adehabitatHR for Program R (Calenge 2006, R Development Core Team 2013). We set the minimum smoothing parameter for the BRB formula to one-half of the mean distance moved between locations by all bison in a given month (Benhamou and Cornelis 2010). The next step in our RUF analysis (sensu, Marzluff et al. 2004) was to link landscape attributes to each 30 × 30 m grid cell in the bison enclosure. We used the Spatial Analyst Extraction tool in ArcMap 10.1 to create spatially explicit data files as input for the ruf package, version 1.5.2 in Program R (Kertson and Marzluff 2010, Handcock 2012). Next, the ruf.fit function was used to create RUF for assessing the

differential patterns in monthly space use for each individual, third-order selection (Johnson 1980), across the seasonal cycle. RUFs employ a multiple linear regression approach to relate multiple landscape variables, in this case: burn treatment indicators, elevation, and slope, to the height of the UD (a probabilistic, continuous measure of space use, $\hat{f}_{UD}(x, y)$, where x, y represent a location) describing how intensely an animal uses each part of its territory (Seaman and Powell 1996, Hepinstall et al. 2005, Papworth et al. 2012). To account for the spatial autocorrelation generated by natural environmental autocorrelation (Schleig 2003), the RUF uses a maximum-likelihood procedure with a Matern correlation function (Marzluff et al. 2004). The outer 5% of the UDs was removed, because the tails of a distribution are typically estimated less reliably (Vanak and Gompper 2010). Following Kertson et al. (2011), the UDs were then changed from density functions to volume, so that the UD values ranged from 0 to 95, where 0 represents no use. We log$_e$-transformed each cell's UD value to meet the assumptions of linear multiple regression models. We allowed the RUF algorithm to determine the appropriate spatial range for the Matern autocorrelation function via maximum-likelihood methods, but set the smoothness parameter to 1.5 after Marzluff et al. (2004). For some utilization distributions, the range parameter was not estimable with a smoothness of 1.5, so we reduced the value by increments of 0.5 until the range was estimable. In a few instances, the range parameter was not estimable at a smoothness of 0.5, so we reduced the value by increments of 0.1 until the range could be estimated.

To develop population-level inferences from all of the collared individuals each month, we calculated mean standardized β coefficients (±95% confidence intervals) for each landscape attribute by monthly period with a variance that incorporated inter-individual variation (Marzluff et al. 2004). Standardized β coefficients were used to compare the relative importance of landscape factors on the concentration of space use by bison, calculated as:

$$\widehat{\beta j} = \hat{\beta}_j^* \frac{S_{xj}}{S_{RUF}} \tag{1}$$

where $\hat{\beta}_j^*$ is the maximum-likelihood estimate of the partial regression coefficient from the multiple regression estimate (unstandardized β; Appendix S1: Table S1) and S_{xj} is the standard deviation of the UD values (Marzluff et al. 2004). For inferences at individual and population levels, standardized coefficients with 95% confidence intervals that did not overlap zero were considered significant predictors of space use. We ranked the relative importance of significant landscape metrics using the absolute value of their mean standardized β coefficients and tallied the number of individual-months that a particular variable had the highest relative importance (Marzluff et al. 2004). If 95% confidence intervals did not overlap zero, we drew inferences about the direction and magnitude of relationships between intensity of space use and values of landscape characteristics at the individual and population level (Marzluff et al. 2004, Kertson et al. 2011). We inferred that resource use was greater (+) or less (−) than expected based on availability of the resource within the enclosure.

To investigate the effect of temporal variability in climatic conditions on bison space use, we evaluated the relationship between recently burned watershed selection strength irrespective of burn history and previous-year aboveground net primary productivity (ANPP). We re-fit all individual-month landscape attribute-UD files with a burn variable coded as 1 for all burned watersheds or 0 for all not-burned watersheds and not separated into indicator variables for the four burn frequencies as described above. The growing season month standardized β coefficients at the population level were averaged for May through September of each year for use in simple linear regression to investigate the relationship between previous-year ANPP and burned area selection. Previous-year ANPP values are derived from mean values of live tissue clipped outside of the bison enclosure during the end of the previous growing season (~15 September) at study plots in non-grazed watersheds, 1D, 04B, 20B (LTER dataset: PAB011, http://www2.konza.ksu.edu/content/pab011).

RESULTS

Resource utilization functions

RUF analyses revealed that areas highly used by bison within the 95% UD were associated with a greater availability of grassland burned in
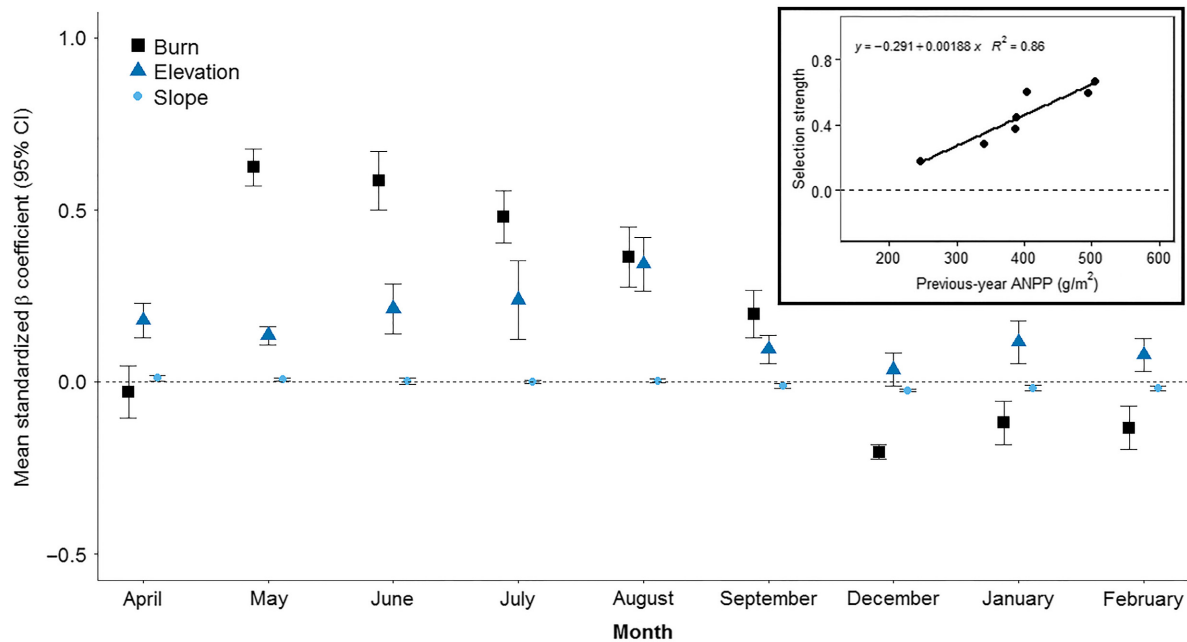
Fig. 3. Monthly standardized beta coefficients ($\bar{x} \pm$ SE) for adult female bison resource utilization functions for burned watersheds in response to utilization of watersheds not burned in the year being compared (dashed line) and landscape attributes, elevation and slope, from 2007 to 2013 at Konza Prairie Biological Station, near Manhattan, Kansas, USA. Points and standard errors that do not overlap the dashed line either use the resource selectively (positive values) or avoid the resource more than would be expected at random (negative values). Inset: coefficient of determination for the linear relationship between mean monthly burn selection coefficient from 2007 to 2013 and mean ANPP from 2006 to 2012 growing seasons.

the spring compared to watersheds not burned that spring, and selection or avoidance for burned watersheds was the greatest predictor of bison space use over the seasonal cycle (Fig. 3). Overall, 76% of individual-month beta coefficients were positively related to the recently burned watersheds over the growing season (April to September), while 63% of individual-month beta coefficients showed that watersheds burned that spring were significantly avoided (i.e., both upper and lower confidence intervals were below 0) in the dormant season (December to February; Table 2). Over 2007–2013, RUFs for the entire growing season (April to September) showed an ascending pattern of selection for the three recently burned watershed types: annual ($\bar{\beta} = 0.23$), biannual ($\bar{\beta} = 0.27$), and four ($\bar{\beta} = 0.28$). However, confidence intervals of population-level β coefficients for each burn type overlapped in all months except in December when quadrennial-burned watersheds burned that spring were avoided to a significantly lesser

extent than other burned watersheds burned in spring (Fig. 4). Furthermore, population-level β coefficients for annually burned watersheds in December showed this type was avoided to a significantly greater extent than all other burn types. Two watersheds, N1A and N1B, were burned every year, whereas only one of the biannual- and 4-year watersheds burned in each spring of the study. Thus, although two annually burned watersheds were available to be grazed each year, bison tended to use the biennial- and quadrennial-burned watersheds more often in the year of burn than the watersheds burned every spring despite the reduced area of these less frequently burned watersheds.

The most frequent significant predictor of bison space use during the early growing season months (April through June) was the availability of quadrennial-burned watersheds compared to not-burned watersheds ($\bar{\beta} = 0.27$; ranging from −0.22 to 0.71; Fig. 4; Appendix S1: Fig. S2) for 77% (149 of 195) of all collared individuals

Table 2. Mean standardized resource utilization function coefficients ($\bar{\beta}$) for each female bison each month at Konza Prairie Biological Station.

Landscape metric	$\bar{\beta}$	95% CI	+	−	$\bar{\beta}$	95% CI	+	−	$\bar{\beta}$	95% CI	+	−
		April (n = 65)				May (n = 65)				June (n = 65)		
Annual	0.011	−0.110, 0.132	13	36	0.437	0.360, 0.515	60	0	0.356	0.241, 0.471	61	1
Biannual	−0.056	−0.195, 0.084	21	27	0.440	0.309, 0.572	58	0	0.430	0.265, 0.594	58	1
Four	−0.038	−0.173, 0.097	25	29	0.406	0.257, 0.555	60	3	0.435	0.286, 0.584	64	0
Twenty	0.012	−0.033, 0.058	3	1	0.334	0.295, 0.373	12	0	0.405	0.374, 0.437	12	0
Elevation	0.151	0.072, 0.231	42	11	0.108	0.043, 0.172	36	6	0.209	0.067, 0.351	50	10
Slope	0.016	0.001, 0.030	7	0	0.019	0.000, 0.018	1	0	0.010	−0.001, 0.022	1	0
		July (n = 64)				August (n = 64)				September (n = 61)		
Annual	0.280	0.150, 0.410	59	2	0.177	0.016, 0.339	44	10	0.088	−0.018, 0.195	35	13
Biannual	0.361	0.205, 0.518	57	1	0.293	0.135, 0.451	53	3	0.150	0.006, 0.294	38	14
Four	0.364	0.266, 0.461	64	0	0.297	0.195, 0.399	60	2	0.194	0.109, 0.279	48	3
Twenty	0.278	0.245, 0.311	12	0	0.185	0.094, 0.276	10	2	0.049	−0.047, 0.144	7	2
Elevation	0.280	0.047, 0.512	48	12	0.401	0.221, 0.581	55	7	0.105	−0.016, 0.225	27	18
Slope	0.006	−0.001, 0.013	0	0	0.011	0.004, 0.018	1	0	−0.004	−0.010, 0.002	0	0
		December (n = 62)				January (n = 59)				February (n = 60)		
Annual	−0.214	−0.258, −0.170	0	52	−0.101	−0.185, −0.017	10	39	−0.105	−0.166, −0.044	6	36
Biannual	−0.136	−0.185, −0.087	9	38	−0.110	−0.185, −0.034	8	40	−0.120	−0.244, 0.004	14	36
Four	−0.045	−0.113, 0.023	11	34	−0.052	−0.157, 0.053	11	35	−0.040	−0.127, 0.046	20	23
Twenty	−0.127	−0.221, −0.034	3	9	−0.208	−0.297, −0.118	0	9	−0.342	−0.399, −0.285	0	11
Elevation	0.023	−0.076, 0.122	24	21	0.120	0.012, 0.227	30	14	0.076	−0.033, 0.184	31	14
Slope	−0.024	−0.032, −0.015	0	11	−0.017	−0.030, −0.005	0	9	−0.021	−0.035, −0.008	0	9

Note: The table illustrates the monthly standardized coefficient averaged across the study period and the number of significant and non-significant coefficients (where the 5–95% CI did not include 0) for each RUF variable.

(Table 2). During the transitional, peak growth period (July to September), the most frequent, significant predictor of space use was also the availability of quadrennial-burned watersheds compared to not-burned watersheds ($\bar{\beta}$ = 0.29; ranging from 0.07 to 0.53; Fig. 4) for 91% (172 of 189) of all collared individuals. Thus, this four-year fire-return interval was a relatively strong driver of bison space use for the duration of the entire growing season.

In contrast, during the dormant season prior to the next burn cycle at KPBS (December to February), the most frequent, significant predictor of space use was the proportional availability of watersheds not burned in spring compared to annually burned watersheds ($\bar{\beta}$ = −0.14 ranging from −0.31 to 0.08; Fig. 4) for 69% (125 of 181) of individuals (Table 2). Throughout the dormant season, mean standardized β coefficients of individual-months revealed that annually ($\bar{\beta}$ = −0.14) and biannually burned ($\bar{\beta}$ = −0.12) watersheds burned that spring were avoided to a greater extent than watersheds burned for the first time in 4 yr ($\bar{\beta}$ = −0.05), although differences in mean β coefficients (±95% CI) of burned watersheds were

significant only in December. The watershed, N20A, that burned in 2012 after 20 yr of no burning had the highest level of avoidance ($\bar{\beta}$ = −0.23) during the 2012–2013 dormant season (Fig. 4).

Elevation was the strongest topographic driver of space use during the transitional season months of July through September ($\bar{\beta}$ = 0.26; ranging from −0.35 to 0.62; Fig. 3), while elevation tended to be less important during the early growing season months of April through June ($\bar{\beta}$ = 0.16; ranging from −0.15 to 0.47) and dormant season months of December through February ($\bar{\beta}$ = 0.07; ranging from −0.18 to 0.38; Table 2). During the growing season of 2012, bison avoided upland habitat (Fig. 4, inset), whereas selection for elevation was evident for all other years. Slope was most frequently a significant topographic predictor of space use during the dormant season months when behavioral avoidance was evident ($\bar{\beta}$ = −0.02; ranging from −0.05 to 0.006; Fig. 3).

Primary production and burn selection strength

The two years preceding this study experienced lower-than-average rainfall and concomitant
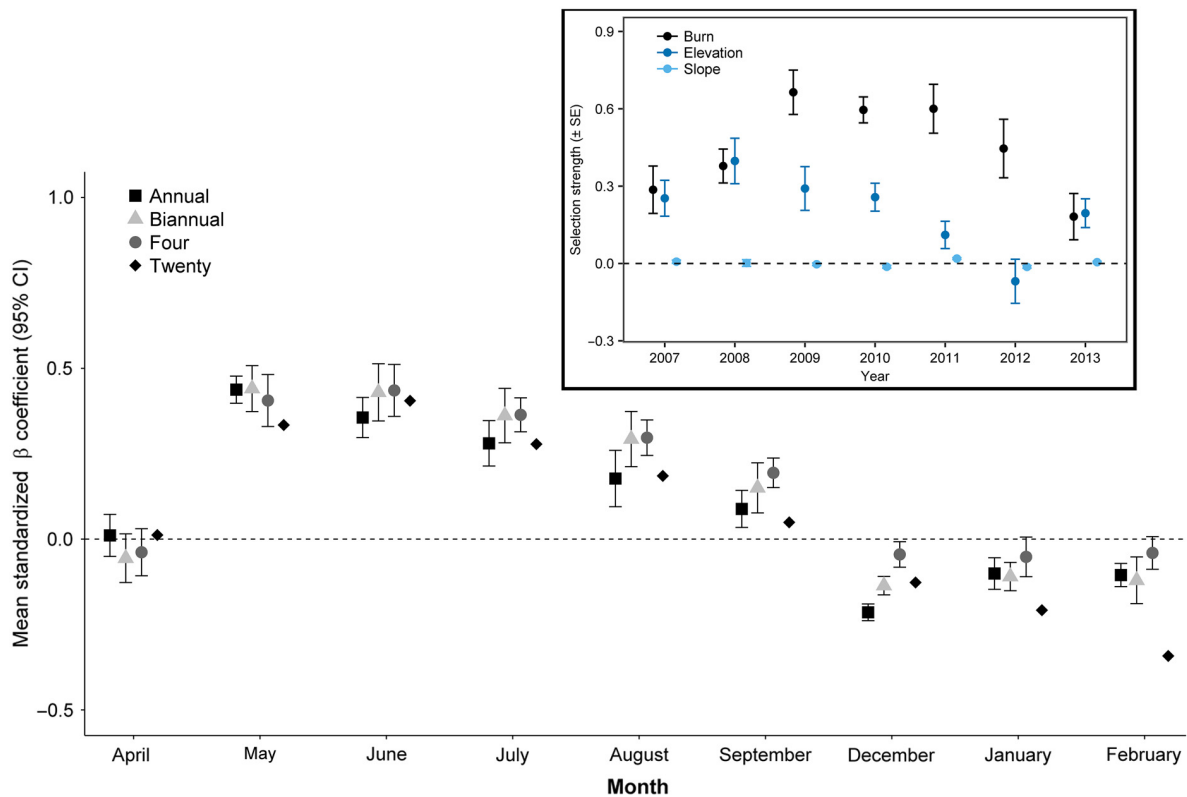
Fig. 4. Monthly standardized beta coefficients ($\bar{x} \pm$ SE) for adult female bison resource utilization functions for burned watersheds on different burn schedules in response to utilization of watersheds not burned in the year being compared at Konza Prairie Biological Station, near Manhattan, Kansas, USA. Points and standard errors for each month that do not overlap the dashed line either use the resource selectively (positive values) or avoid the resource more than would be expected at random (negative values). Inset: mean monthly selection coefficients ($\pm$SE) over growing season (May–September) from 2007 to 2013.

forage production for the 30-year record at KPBS (Fig. 1), while rainfall for 2012 was the fourth lowest in a century, with a 40% reduction in growing season precipitation (Knapp et al. 2015). The mean β standardized coefficient for all recently burned watersheds at the population level during the growing season (May through September) was positively correlated with previous-year ANPP at KPBS (simple linear regression; $F_{1,5} = 23.48$, $P = 0.005$, adjusted $R^2 = 0.86$; Fig. 3, inset). Thus, past growing season forage production is a critical component of the fire–grazer interaction that depends on rainfall.

DISCUSSION

Spatial heterogeneity in forage quality and quantity in tallgrass prairie is driven by fire–grazer interactions and topography, leading to a shifting mosaic of not only vegetation characteristics, but also the landscape-level distribution and foraging behavior of grazers (Fuhlendorf et al. 2009, Allred et al. 2011). At KPBS, we found strong support for restricted space use by bison that is oriented toward recently burned areas (P1), and that short-term climatic events modulate the use of experimental watersheds treated with varying fire-return intervals. A range of fire frequencies manipulated experimentally at the watershed level were critical for teasing apart the effects of temporal variability in plant productivity on bison distributions. We provide empirical support for the expectation that grazer attraction to recently burned areas is dependent on past forage production (P2). Although lower total forage biomass was available during an extreme drought year, the

quadrennial-burned watershed remained the top driver of space use in the enclosure (Appendix S1: Fig. S2). This result suggests that watersheds with several years of rest from fire can serve as important buffering resources for animal performance irrespective of previous-year forage productivity, a proxy for fuel loads. Because this experimental watershed type had not burned in several years, sufficient fuel was likely available for ignition leading to the "magnet effect" (Archibald et al. 2005).

Understanding the role that various habitat types play in limiting movement of a large grazer population across the seasonal cycle is critical for grassland conservation. While responses by cattle to recent burning in semi-arid, short grass steppe grasslands can be short-lived (i.e., ~1 month; Augustine and Derner 2014), we found that the use of burned areas compared to not-burned areas by bison in mesic grassland lasted from May through September. We hypothesize that plant productivity interacted with soil N availability in recently burned watersheds to maintain the availability of high-quality forage well into the summer (Blair 1997). The consistent, elevated use by bison of the less frequently burned watersheds in year of ignition (two- and four-year burns) indicates that these experimental burn frequencies can act as critical resources to bridge periods of low resource availability for herbivore populations as well as to dampen the effect of extreme drought on the strength of the fire–grazer interaction. Although these burn treatments constitute half of the area occupied by annual burns (one vs. two watersheds) at KPBS, their relative importance for driving space use was consistently higher than annual burns, indicating these rest habitats are resource hotspots for large herbivores.

In temperate systems, herbivore site fidelity over the seasonal cycle can decrease as accessibility to high-quality forage declines (Van Beest et al. 2010). Here, bison exhibited a pattern of relative avoidance of not-burned watersheds during the growing season and diminished avoidance of not-burned watersheds during the dormant season (Fig. 4). This result met our prediction (P3) that a behavioral response in space use shifting away from highly utilized watersheds burned in spring would occur when overall resource conditions are poor (i.e., favoring lowland areas with available forage of low

digestibility). As the dominant C_4 forage senesces and becomes less digestible in burned tallgrass prairie late in the growing season, bison may shift foraging behavior to locate C_3 plants in not-burned watersheds (Vinton et al. 1993, Raynor et al. 2016). In a concurrent study, Raynor et al. (2016) found that isotopic signatures in tail hair from GPS-tracked bison showed evidence of a mixed C_3–C_4 diet during the dormant season when these animals avoid burned, upland areas. Moreover, when preferred forage resources are scarce, grazing ruminants may supplement grass diets with forbs to maintain protein–energy balance (Odadi et al. 2013). Reduced forage quantity in grassland systems with intact fire–large grazer processes can lead to reductions in forage intake rates that are associated with reduced bite depth and bulk density (Odadi et al. 2016). The not-burned watersheds at KPBS provide higher biomass availability although of lower forage quality than recently burned watersheds in the dormant season (Raynor et al. 2015), which indicates that not-burned grassland acts a buffer habitat during the period of plant dormancy.

Habitat use

The drought of 2011–2012 provided an opportunity to investigate bison space use when resource availability was low overall in an otherwise productive tallgrass prairie. Our results showing that bison generally avoided recently burned areas during periods of low forage production further demonstrate that while fire is one factor influencing consumer–resource processes, it may have a negative effect during drought when soil moisture is already strongly limiting to forage production and becomes further limiting from the effect of fire, thereby increasing resource limitation for large-bodied herbivores. On the other hand, topographic influences on soil moisture availability and grass productivity (e.g., Knapp et al. 1993, Hopcraft et al. 2010) can be a critical factor generating functional heterogeneity for herbivores during droughts and during the dormant season because of the ability of more productive, wetter parts of the landscape to produce reserves of forage for the dormant season and for droughts. African pastoralists burn floodplains during the dry season in order to remove the tall productive but low-quality grass and stimulate high-quality regrowth for their

livestock, but regrowth is only possible because of the topographic position (poor drainage). Similarly, dry season fires were shown to produce regrowth and benefit sable antelope (*Hippotragus niger*) dry season protein intake in lowland, but not in upland positions (Parrini and Owen-Smith 2010). Our data provide new insight into large grazer space use of topography during periods of poor forage productivity (Fig. 4, inset) but also how fire plays a more diminished role during such low productivity years in a usually productive mesic grassland.

At KPBS, soil N often limits the quality of vegetation regrowth in annually burned watersheds, while light limitation from litter accumulation becomes more important in not-burned watersheds (Blair 1997). Watersheds burned at two- and 4-year intervals at KPBS typically show increased ANPP and foliar N concentrations compared with annually burned watersheds in the growing season following a burn (Seastedt and Knapp 1993, Blair 1997, Raynor et al. 2015). This increase in ANPP for infrequently burned watersheds during a burn year when light is no longer limiting is linked to greater availability of soil N after several years without fire. Because annually burned sites are more soil N-limited than infrequently burned sites in the year of burn, foliar N is higher in plants from watersheds in the recently burned sites subjected to longer rest intervals (Blair 1997, Raynor et al. 2015), leading to greater foliar protein concentrations available to bison in infrequently burned watersheds burned that year. The high ANPP in recently burned sites with longer rest intervals combined with high forage protein content likely explains why bison spend more time in these watersheds than in annually burned watersheds (Fig. 1A). Bison and other ungulate grazers routinely respond positively to forage with higher protein content (Allred et al. 2011, Raynor et al. 2015), and actively select the highest quality patches (Senft et al. 1985, Ranglack and du Toit 2015, Raynor et al. 2016) as long as sufficient vegetation standing crop exists. One therefore expects that the strength of attraction for recently burned watersheds to be greater in sites burned after not being burned for several years. Our results indicate this occurs during the growing season in the year of burn as the 2- and 4-year burns consistently exhibited the highest relative importance of landscape attributes for bison space use (support for P4). Because grazing lawns that inhibit the spread of fire develop in grazing systems (Archibald 2008, Hopcraft et al. 2010), we surmise that litter buildup at infrequently burned sites allows fire to carry more uniformly and provide more reliable regrowth than at frequently burned sites with less litter buildup.

Large herbivores are known to select burned over unburned grassland from months to years post-ignition (Schuler et al. 2006, Ranglack and du Toit 2015). However, our dormant season observations in this experimental landscape indicate bison use recently burned prairie that has not burned in several years to a greater extent than more frequently burned prairie. To our knowledge, this result extends our understanding of large grazer space use beyond the growing season and in response to variable burn history.

Although infrequently burned watersheds including N20A had higher concentrations of crude protein in forage than the frequently and not-burned watersheds in spring 2012 (Raynor et al. 2015), bison did not use this 20-year burn to a greater degree than the 4-year burn as one would expect for an area not burned in 20 yr (lack of support for P4). A confounding factor that may have affected use of the 20-year watershed is that almost half of this watershed could not be used for grazing due to encroaching woody vegetation (J. Briggs, *personal observation*). The effect of woody encroachment on the movement ecology of grassland ungulate species remains mostly unexplored (but see Allred et al. 2013), for a cause for global concern as grassland biomes are facing a major risk of conversion to woodland (Bond et al. 2005, Anadon et al. 2014). Furthermore, woody plant encroachment reduces livestock production (Anadon et al. 2014) and increases losses in grassland species diversity (Ratajczak et al. 2012). Our finding that bison favor watersheds burned for the first time after 2 or 4 yr without burning and not annually is especially applicable to future grazing system management decisions in grasslands threatened by woody encroachment. For example, Ratajczak et al. (2016) showed that this range of fire-return intervals has high potential for lowering the susceptibility of Flint Hills tallgrass prairie to conversion to shrub or tree dominance.

Furthermore, the topography of the landscape (e.g., hills, creeks) affects the quality and abundance of primary production available to herbivores (Senft et al. 1985, Hopcraft et al. 2010). In general, herbivores favor upland sites during the growing season because they are dominated by shorter more digestible grasses but switch to lowland sites during the dormant season because they support warmer conditions, they are often snow free in winter, and forage quantity is sufficient. This observation is true for both African and northern ecosystems (Bell 1970, Festa-Bianchet 1988, Albon and Langvatn 1992, Hopcraft et al. 2010). We show bison in tallgrass prairie select lowlands during the dormant season and during years of low forage production, whereas high elevation is favored in productive years (Fig. 1C). At KPBS, investigations of soil moisture availability and topographic position on forage production determined lowland areas offered a high abundance of lowland herbaceous biomass (Briggs and Knapp 1995, Nippert et al. 2011). Raynor et al. (2015) found not-burned lowland areas offering high amounts of low-quality forage were the same areas where bison bite size was increased to meet nutrient intake demands in the late summer, transitional period; such results indicate lowland areas are key reserve areas during periods of plant dormancy. Studies of ungulates in both hemispheres revealed contrasting space use of topography based on herbivore body size (Hopcraft et al. 2010, 2012). Large-bodied herbivores with a tongue sweep strategy to maximize bite size require ample herbaceous biomass. Thus, buffalo are excluded from high-quality but short heavily grazed upland grassland in livestock areas outside the Mara, whereas small-bodied gazelles are most abundant in these short grasslands (Bell 1970, Bhola et al. 2012).

Implications for large herbivores in heterogeneous landscapes

In this study, we document how landscape features modulate the spatial and temporal dynamics of large grazer distributions throughout the year, which allows us to characterize habitat use as two habitat types, recently burned and not burned that year, reflecting season-specific restricted space use. This spatial restriction forms the basic limitation underlying large grazer

seasonal distributions in systems with an intact fire–grazer interaction, a key process for maintaining functionally diverse landscapes (Fuhlendorf and Engle 2004, Fahrig et al. 2011, Fynn 2012, Fynn et al. 2016). Reduced selection strength for recently burned prairie in response to past forage conditions provides evidence for density-dependent consumer–resource coupling under a variable resource base. In addition, our results provide insight into how fire may be used as a tool to modulate grazer distributions under variable climatic conditions. Recently, adaptive management strategies utilizing weather and climate predictions, fire, and pasture rest have enabled rangeland managers to meet multiple objectives of vegetation, profitability of ranching operations, and wildlife habitat (Limb et al. 2016). Furthermore, efforts to restore large herbivores to their historic range benefit from evaluations of the effects of inter-annual variability of large herbivore movement in response to land management techniques (Kuemmerle et al. 2011).

Fire-induced heterogeneity in vegetation quantity and quality is an important landscape-scale process that links foraging and fire ecology. Increasing spatial heterogeneity in savannas and grasslands acts to decrease temporal variability in aboveground biomass that could destabilize consumer–resource dynamics and concomitant ecosystem structure and function (Fynn 2012, McGranahan et al. 2016), thereby buffering ecosystem response from global environmental change (Turner 2010). Differences in selection for post-fire forage regrowth in watersheds under different burn intervals should prove effective in understanding how landscape- and climate-related changes affect gradients in resource availability that animals rely on (Avgar et al. 2013), and for identifying when habitat manipulation will benefit herbivores that move across large landscapes.

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