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Controls over the strength and timing of fire–grazer interactions in a semi-arid rangeland

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Summary

1. The degree to which large herbivores select and forage within recently burned areas is a key driver of vegetation heterogeneity in rangeland ecosystems. However, few studies have quantified the strength and timing of herbivore selection for burned areas or examined how selection strength varies among ecosystems differing in precipitation and primary productivity.

2. We conducted a 4-year patch-burning experiment in semi-arid rangeland of Colorado, USA, where 25% of the area available to cattle was burned each year and burned patches were shifted annually. We used GPS collars with activity sensors to quantify the distribution of free-ranging cattle at a high temporal resolution (5-min intervals) during the growing season each year. We used a classification tree model to discriminate between cattle grazing vs. non-grazing locations, which significantly increased precision in quantifying burn selection strength. We fit generalized linear models predicting the frequency of cattle use of a given location within each study area and month, enabling comparisons between the relative influence of burns and topography on grazing distribution.

3. Across multiple growing seasons, cattle selectively spent 31% of grazing time on recently burnt areas, which comprised 25% of the landscape; this selection strength was half as strong as that documented in mesic rangeland.

4. At a monthly temporal scale, strong cattle selection for burned areas occurred during periods of rapid vegetation growth regardless of when during the growing season this greening occurred. Outside these intervals, burn selection strength was inconsistent and cattle grazing distribution was primarily influenced by topography. Thus, the relative importance of fire and topography in controlling grazer distribution was temporally contingent upon the timing and size of precipitation pulses.

5. *Synthesis and applications*. Spatiotemporal interactions between fire and herbivores are a consistent feature of both semi-arid and mesic rangelands, with interaction strength varying across gradients of precipitation and primary productivity. Management of semi-arid ecosystems to sustain ecological processes should include strategies that allow ungulate herbivores to shift their grazing distribution seasonally in response to fire, topoedaphic variation and precipitation patterns. Combined management of fire and grazing for conservation objectives can be consistent with, and even complementary to, livestock production goals.

Key-words: foraging behaviour, grazing distribution, patch burn grazing management, pyric herbivory, resource selection, shortgrass steppe, spatial heterogeneity

Introduction

Spatiotemporal interactions between fire and ungulate herbivores are a key driver of the structure, composition and functioning of many rangeland ecosystems worldwide (Archibald *et al.* 2005; Murphy & Bowman 2007; McGranahan *et al.* 2012). Central components of this fire–grazing interaction are (i) selection of recently burned patches as foraging sites by ungulate herbivores, thereby reducing their probability of burning in the future, and (ii) accumulation of fuels in unburned patches reducing

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their use by ungulate herbivores and increasing their probability of burning in the future (Knapp *et al.* 1999; Fuhlendorf & Engle 2004). Preferential use of recently burned patches by ungulates has been widely reported (Fuhlendorf *et al.* 2009) and is often linked to the observation that burns support vegetation with lower biomass but enhanced nutritional quality relative to unburned areas (Sensenig, Demment & Laca 2010; Allred *et al.* 2011). As a result of this forage quality/quantity trade-off, ungulate selection for recent burns is stronger for ruminants compared to hindgut fermenters and stronger for ruminants of smaller body sizes (*c.* 10–500 kg) compared to those larger than 500 kg (Wilsey 1996; Sensenig, Demment & Laca 2010).

Studies of fire–grazer interactions have primarily focused on mesic grasslands and savannas of North America (Biondini, Steuter & Hamilton1999; Allred *et al.* 2011), Africa (Wilsey 1996; Hassan *et al.* 2008; Sensenig, Demment & Laca 2010) and Australia (Murphy & Bowman 2007). These rangelands are characterized by sufficient precipitation (>600 mm annually) for grasses to produce significant quantities of stems and other low-digestibility compounds and tissues over a typical growing season. This creates the potential for burns to remove accumulated low-quality material and enhance quality of post-burn regrowth. In semi-arid rangelands, where above-ground plant productivity is considerably lower (Burke, Lauuenroth & Parton 1997; Derner, Boutton & Briske 2006), fire–grazer interactions have received less attention. This can be attributed to low fuel loads and increased limitation of ungulates by forage quantity reducing the potential for burns to influence ungulate foraging behaviour. However, semi-arid rangelands are characterized by substantial inter- and intra-annual temporal variation in precipitation (Knapp & Smith 2001), where wet pulses could potentially lead to coupled fire–grazing interactions and dry periods could uncouple interactions. Thus, while we understand how characteristics of ungulate herbivores (e.g. digestive strategy and body size) influence responses to burns, little is known about the influence of temporal variation in precipitation on fire–grazing interactions.

In the North American Great Plains, fire–grazing interactions have long been managed and studied in mesic grasslands (Svejcar 1989; Hobbs *et al.* 1991; Knapp *et al.* 1999; Fuhlendorf & Engle 2004). In contrast, there is a lack of research on fire–grazing interactions in semi-arid regions. Studies have consistently found that burning of semi-arid, shortgrass steppe does not reduce herbaceous plant production (Brockway, Gatewood & Paris 2002; Augustine & Milchunas 2009; Augustine, Derner & Milchunas 2010), but fires are widely suppressed due to concerns that loss of standing dead forage may negatively affect livestock production. At the same time, there is interest in using fire and fire–grazing interactions to enhance habitat for native wildlife species of conservation concern, particularly on lands managed for both biodiversity conservation and livestock production (Fuhlendorf *et al.* 2006; Derner *et al.* 2009). We examined how cattle are influenced by a prescribed burning regime that involved burning 25% of the area available to cattle herds each year, thereby allowing animals to choose between burned and unburned patches.

We studied these interactions in the shortgrass steppe of north-eastern Colorado, at a site that receives a mean annual precipitation of 340 mm [corresponding to mean annual net primary production (ANPP) of *c.* 70 g m^{-2}; Lauenroth & Burke 2008;] and hence represents among the driest and least productive rangeland conditions found in grasslands of central North America, central Asia, East Africa and South America (Lauenroth, Burke & Gutmann1999; Sala *et al.* 2012; Lezama *et al.* 2013). We measured the amount of time that cattle spent grazing on burned and unburned patches using GPS collars and associated activity sensors, and the rate at which cattle gained weight with vs. without access to burned patches. We also considered the influence of topographic variation in our analyses, because topography is well known to influence cattle foraging behaviour (Senft, Rittenhouse & Woodmansee 1985) and can influence animal responses to patch burning (Winter *et al.* 2011). Our approach allowed us to measure temporal variability in grazer response to burns, and to quantitatively compare findings with studies that used similar methods in mesic grassland (Allred *et al.* 2011; Limb *et al.* 2011).

Materials and methods

STUDY AREA AND EXPERIMENTAL DESIGN

Research was conducted at the Central Plains Experimental Range (CPER) *c.* 12 km north-east of Nunn, Colorado, USA (40°50′N, 104°43′W). Mean annual precipitation is 340 mm. Soils consisted of very deep, well-drained, fine sandy loams on convex alluvial flats and upland plains. Two C_4 grasses (*Bouteloua gracilis* [Willd. Ex Kunth] Lag. ex Steud and *Buchloe dactyloides* [Nutt.] J. T. Columbus) dominate the vegetation (>80% of ANPP), and *Sphaeralcea coccinia* [Nutt] Rydb. is the dominant forb (Lauenroth & Burke 2008).

We evaluated cattle distribution in three replicate pastures (65 ha each) subjected to a patch-burning treatment consisting of prescribed burns applied to one-quarter of each pasture per year for 4 years. Thus, all areas of a given pasture were burned once over the course of the study. Burned areas were square (16 ha). Burns were implemented in the fall (October or November of 2007–2010) when vegetation was dormant. Cattle responses were measured in the subsequent growing seasons (May–September of 2008–2011). Despite low fuel loads, fuels were spatially contiguous and the burns were homogenous in all 4 years.

Pastures were grazed by yearling steers at a density of 0·52 animal unit months per hectare between 15 May and 1 October each year. We measured cattle distribution using GPS collars (Lotek 3300LR collars; Lotek Engineering, Newmarket, ON, Canada) during 11 time intervals (collar deployments) over the 4-year period (Fig. 1). Deployments lasted *c.* 4 weeks (range 26–34 days) except the first deployment (21 days), with two

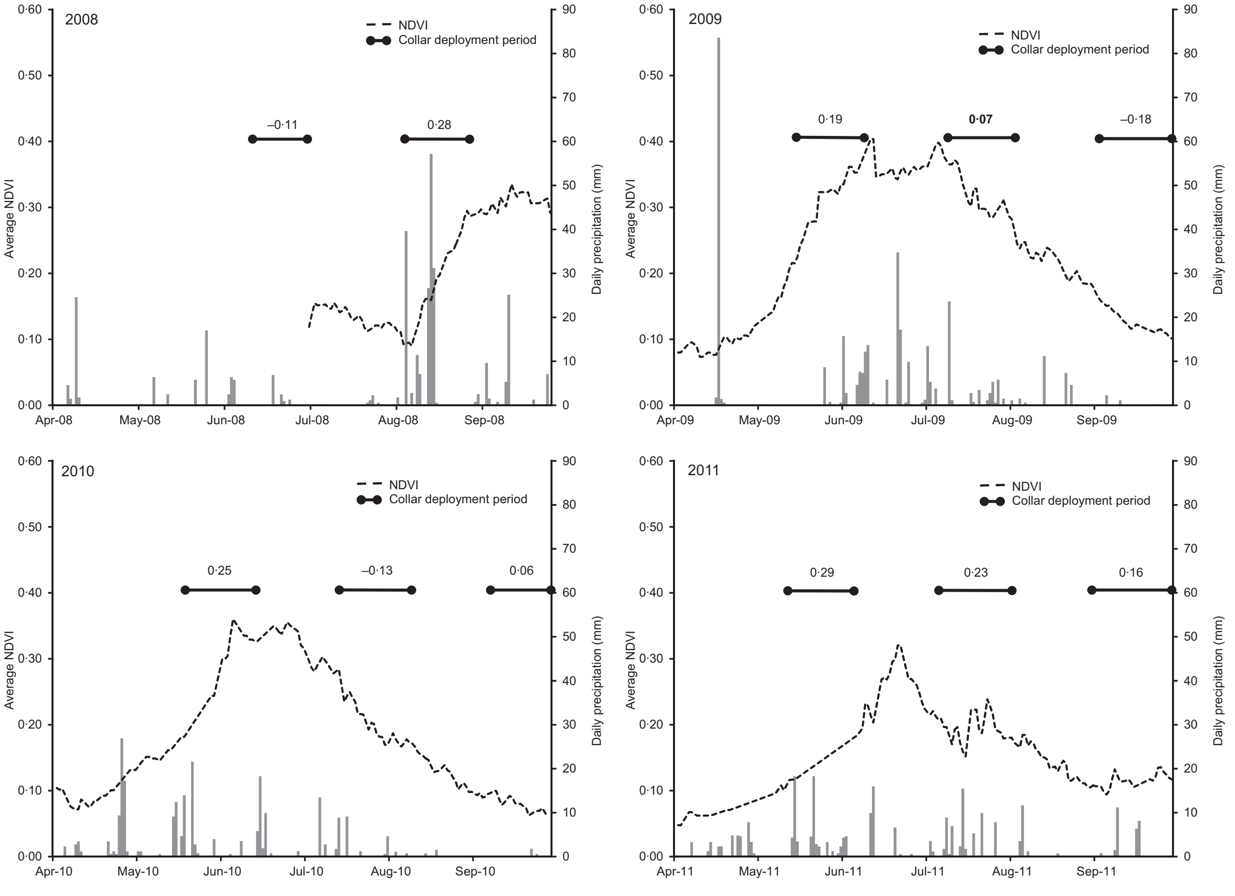

Fig. 1. Temporal variation in precipitation and vegetation greenness (NDVI) in relation to the timing of measurements of cattle responses to patch burns during 2008–2011 at the Central Plains Experimental Range in north-eastern Colorado, USA. Vertical grey bars show daily precipitation from 1 April to 30 September each year. Numbers above the black bars indicating the GPS collar deployment intervals show the mean burn selection coefficient for that interval (Table 1). NDVI, normalized difference vegetation index.

deployments in 2008 (June–July and August) and three in 2009, 2010 and 2011 (May–June, July–August and September; Fig. 1). For each deployment, we placed GPS collars on three randomly selected steers in each pasture (nine in total). Collars weighed 1·2 kg were set to record GPS positions at 5-min intervals and included a dual-axis activity sensor that recorded up-down (y-axis) and side-to-side (x-axis) movements and percentage of time the y-axis sensor was in the 'down' position. Due to a programming error, collars only collected fixes at 20-min intervals during the first deployment of 2011. Steers were of mixed European breed, weighed ~270 kg at the beginning of the grazing season (15 May) and weighed *c.* 410 kg at the end of the grazing season (1 October).

During each deployment, we directly observed each collared steer for a portion (~4–6 h) of 1 day. We used a classification tree model based on the distance travelled in a 5-min interval and activity sensor measurements to discriminate between GPS fixes associated with grazing vs. fixes associated with non-grazing behaviour (Augustine & Derner 2013). We analysed cattle distribution based on those fixes associated with grazing behaviour, referred to hereafter as grazing locations. For the 2011 deployment when fixes were collected at 20-min intervals, we resampled the data base analysed by Augustine & Derner (2013) to 20-min intervals and generated a histogram of movement distances (in 1-m increments) for 20-min intervals when cattle were observed grazing (>50% of the time) and a histogram for all other intervals. Histograms showed a breakpoint in activity at movement distances of 11 m. Assuming that fixes associated with movement <11 m were non-grazing fixes correctly removed 54% of non-grazing locations from the data set while only incorrectly removing 3·3% of grazing locations. We therefore applied this 11-m movement rule to data collected in the first 2011 deployment.

PRECIPITATION AND VEGETATION

The amount and timing of precipitation varied substantially over the 4 years (Fig. 1). Precipitation during April–August was 240, 353, 288 and 245 mm in 2008, 2009, 2010 and 2011, respectively. We used nine ground-based, two-channel radiation sensors (Skye Instruments, Powys, UK) to quantify seasonal patterns of vegetation growth and senescence. Each year, three sensors were located on burned patches, three in unburned patches, and three in adjacent unburned pastures. Sensors were mounted at a height of 2 m, monitored an area of ~4 m^2 and had two channels centred on 660 and 730 nm wavelengths. Data were used to calculate the normalized difference vegetation index (NDVI) at a daily time step for the period from 10:00–14:00 on days when photosynthetically active radiation was above a threshold equivalent to full sun. Sensors were not operational until late June of 2008; we note that vegetation in June 2008 was senescing due to below-average precipitation (Fig. 1). For the time interval corresponding to each collar deployment, we calculated the net change in NDVI as mean NDVI for the last 3 days minus the mean NDVI for the first 3 days.

Each year, we measured standing herbaceous biomass in the recently burned quarter and in an unburned area in each patch-burned pasture during the first week of June and the first week of August by clipping 10, 20 × 50 cm quadrats to ground level. Biomass was oven-dried and sorted into the current year's production vs. residual standing biomass remaining from the previous year.

TOPOGRAPHY

The study site encompasses subtle variation in elevation and topography, which influences cattle grazing distribution (Senft, Rittenhouse & Woodmansee 1985). Study sites were underlain by fine sandy loam soils and contained gently rolling terrain (10–17 m change in elevation within each 65-ha area) dominated by C_4 shortgrasses, representative of the overall landscape. The four quarters within each pasture contained variation in topography and drainage patterns that was not reflected in available soil maps, but could be quantified from a digital elevation model (DEM). We calculated a topographic wetness index (TWI) for each pixel using a 10-m resolution DEM following Theobald (2007); see Augustine *et al.* (2012) for a details on this index applied to shortgrass landscapes. TWI varied from 2 on ridges and convex upper hillslopes to 25 in swales and playas.

ANALYSES OF CATTLE DISTRIBUTION

Averaged over all 4 years, the percentage of grazing time that cattle spent on current-year burns was tested against the expected value of 25%. However, when examining variation in burn selection strength among deployments and years, we accounted for topographic variation among the four quarters of each study site. We overlaid steer grazing locations with the 10-m DEM and calculated the number of grazing locations occurring in each pixel for each deployment. We created a binary burn variable by assigning pixels a burn value of 1 for those within the recently burned quarter of the pasture, and 0 otherwise. We also calculated the distance of each pixel to a fence and a water source. Pixels more than 20 m from a fence or water source were all assigned a value of 30 m, to account for local attraction to fences and water in all models.

We examined histograms of the number of pixels with varying counts of cattle grazing locations for each deployment and pasture. The means, variances and shapes of these histograms indicated they were best described by a negative binomial distribution rather than by a Poisson or overdispersed Poisson distribution. We fit general linear models predicting the number of cattle grazing locations per pixel for each pasture and collar deployment based upon distance to water, distance to fence, TWI and presence of burn (0 or 1), using a logarithmic link function assuming a negative binomial distribution. To examine the relative influence of topography and patch burns on cattle distribution, we standardized these two variables by subtracting their mean and dividing by their standard deviation (Gelman & Hill 2007). We fit models with TWI, burn and TWI plus burn as predictors (Proc GLIMMIX, SAS, v9.3, SAS Institute, Cary, NC, USA) and selected the model that minimized Akaike Information Criteria. We calculated mean burn and TWI coefficients for each deployment and identified those where selected models included significant positive or negative coefficients for all three replicate pastures. Distance to water and fence were significant in all models and consistent in their sign (negative) and magnitude across all years and deployments. We included them in models to account for their effect on cattle distribution, but do not consider them in detail, given our focus on the relative role of topography and patch burning under varying vegetation conditions.

Results

We recorded and analysed 685 232 GPS measurements of cattle locations. Averaged across all deployments and years, 26·4% of cattle locations were on recently burned areas that comprised 25% of the pastures (*t*-test for comparison of use vs. availability, $t_2 = 1{\cdot}15$, $P = 0{\cdot}37$). Application of the classification tree to separate GPS fixes into grazing vs. non-grazing locations reduced the data set to 253 303 cattle grazing locations. Averaged across all deployments and years, 31·4% of cattle grazing locations were on recently burned areas that comprised 25% of the pastures (*t*-test for comparison of burn use vs. availability, $t_2 = 5{\cdot}92$, $P = 0{\cdot}027$). Thus, cattle selectively grazed on recently burned areas in this semi-arid rangeland, but the magnitude of the selection was small enough that it could not be detected when non-grazing locations were included in the analysis. Non-grazing locations, which were primarily bedding or standing locations, made up a large proportion (63%) of the fixes, were strongly clustered in space and were unrelated to the locations of recent burns (Fig. 2). As expected, general linear models of cattle grazing distribution consistently included a negative coefficient for distance to water (mean across all replicates and deployments = −0·153) and a negative coefficient for distance to a fence (mean across replicates and deployments = −0·027), reflecting a significantly greater probability of cattle grazing fixes occurring in the immediate proximity of water and fences, with water having a stronger influence than fences.

The influence of recent burns and topography on the distribution of grazing locations varied dramatically within and among years. For one deployment in each of the 4 years (August 2008, May–June 2009, May–June 2010 and May–June 2011), cattle grazing distribution was positively associated with recently burned areas in all three replicates (Table 1). Mean burn coefficients within these deployments were 0·28, 0·19, 0·25 and 0·29 respectively, with a mean of 0·25 (Table 1). In none of these four deployments did topography have a consistent influence on cattle grazing distribution across replicates; corresponding mean coefficients for the influence of topography were 0·15, 0·07, −0·003 and 0·00, respectively (Table 1), with an average of 0·05.

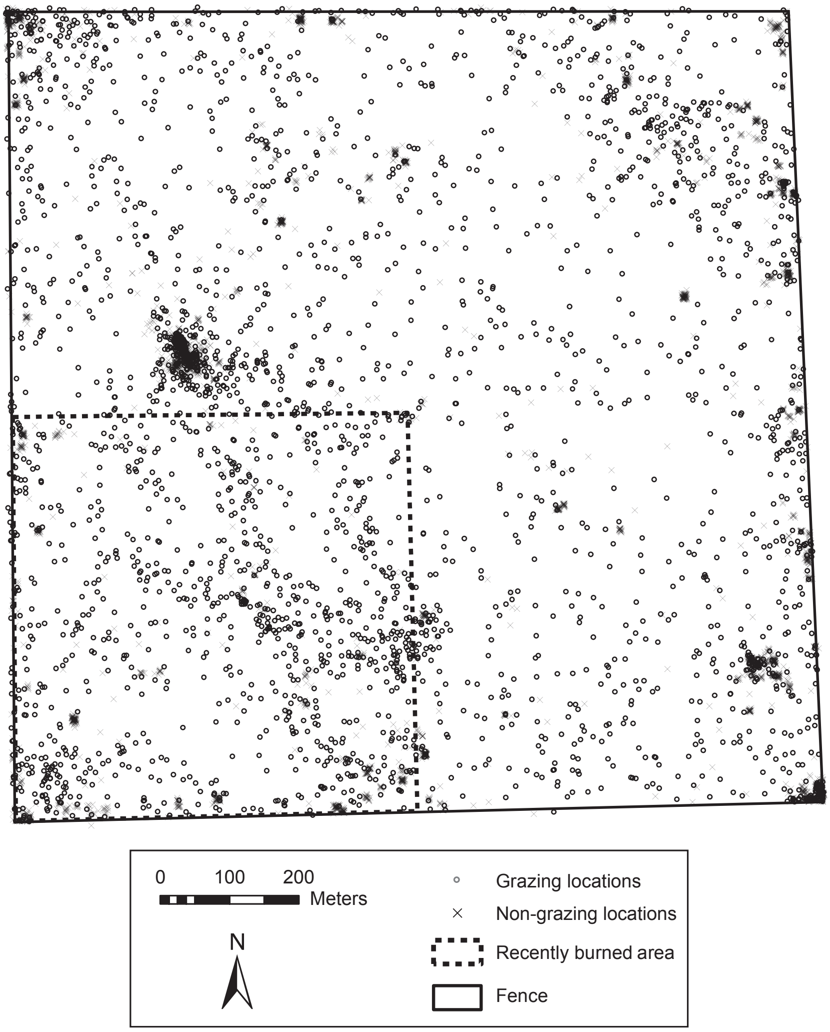

Fig. 2. Distribution of GPS locations for a yearling steer collected at 5-min intervals from 16 May to 10 June 2009, at one replicate study site in patch-burned shortgrass steppe of eastern Colorado, USA. In this example, 25% of all GPS locations occurred within the burned area. However, classifying locations into those associated with grazing (circles) vs. those associated with non-grazing behaviours (crosses) revealed that 32% of grazing locations occurred in the burned area, which comprised 25% of the pasture. Note the clustered distribution of non-grazing locations relative to grazing locations. The general linear model predicting cattle grazing distribution for this time interval and location included a significant burn coefficient of 0·20 (selection for the burned area), and a significant topography coefficient of 0·13 (selection for lowlands). The dense cluster of crosses just north of the burned area is the location of the water source.

Table 1. Summary of the degree to which patch burning and topography influenced cattle grazing distribution for 11 GPS tracking intervals during 2008–2011 in shortgrass steppe of eastern Colorado, USA. Values represent mean coefficients from models of cattle grazing distribution fit to each of three experimental replicates, where predictors (recently burned area use and topographic wetness index) were scaled so that the magnitude of coefficients are directly comparable. Values with * indicate time periods where a significant positive coefficient for that predictor was included in models for all three replicate sites

Year	Time	Conditions	Mean burn coefficient	Mean topography coefficient
2008	June–July	Dry	−0·11	0·07
	August	Greening	0·28*	0·15
2009	May–June	Greening	0·19*	0·07
	July–August	Transition	0·07	0·17*
	September	Dry	−0·18	−0·04
2010	May–June	Greening	0·25*	−0·003
	July–August	Transition	−0·13	0·06*
	September	Dry	0·06	0·16*
2011	May–June	Greening	0·29*	0·00
	July–August	Transition	0·23	0·19*
	September	Dry	0·16	−0·07

During the other seven deployments, grazing cattle did not consistently select or avoid recently burned areas (Table 1). In some cases, cattle avoided recently burned areas in two of three replicates, but never in all three. For the seven deployments where we did not detect consistent burn selection, the mean burn coefficient varied from −0·18 to 0·23 and averaged 0·01 (Table 1). During four of these seven deployments (July–August of 2009, 2010 and 2011, and September of 2010), cattle grazing distribution was consistently and positively associated with TWI, indicating selective grazing in lowlands regardless of burn location. In the remaining three deployments, all corresponding to dry periods when NDVI was declining (June–July 2008, September 2009 and September 2011), neither recent burns nor topography had a consistent influence on cattle grazing distribution (Table 1).

We measured current-year and residual standing dead herbaceous biomass within and outside of burnt areas at times corresponding to eight of the collar deployments. Four of these biomass measurements occurred when cattle were selecting recently burned areas and four occurred when cattle were not selecting burned areas (Table 2). Differences in the amount of herbaceous biomass in burned vs. unburned areas were primarily due to burns removing residual standing dead material from the previous year, as current-year herbaceous biomass was generally similar at any given time regardless of burn status (Table 2). Variation in burn selection strength was not correlated with the magnitude of the difference in herbaceous biomass on vs. off burns ($r^2 = 0{\cdot}02$, $F_{1,6} = 0{\cdot}11$, $P = 0{\cdot}75$), or with variation in the amount of current-year herbaceous biomass ($r^2 = 0{\cdot}05$, $F_{1,6} = 0{\cdot}34$, $P = 0{\cdot}58$). The lack of correlation with differences in standing dead biomass in burned vs. unburned areas reflected the finding that selective grazing on burned areas occurred both when differences were low (August 2008 and May–June 2009, mean difference of 21 g m^{-2}) and when this difference was nearly twice as large (May–June 2010 and 2011, mean difference of 41 g m^{-2}; Table 2).

Consistent with the lack of relationship between burn selection strength and herbaceous biomass, we found that burn selection strength was not significantly correlated with mean NDVI for the 10 deployments where NDVI was measured (Fig. 1; $r^2 = 0{\cdot}20$, $F_{1,8} = 2{\cdot}00$, $P = 0{\cdot}19$). Rather, strong selection for recently burned areas occurred during periods of rapid vegetation growth, regardless of whether this greening occurred early (2009–2011) or late (2008) in the growing season (Fig. 1). As a result, variation in burn selection strength was significantly and positively related to the rate of change in NDVI (Fig. 3; $r^2 = 0{\cdot}56$, $F_{1,8} = 10{\cdot}3$, $P = 0{\cdot}012$).

Cattle weight gains over the grazing season were similar in patch-burned vs. patch-unburned treatments in 2008, 2009 and 2011 ($P > 0{\cdot}1$), whereas weight gains were significantly greater in the patch-burned vs. patch-unburned treatment in 2010 ($P = 0{\cdot}038$; Fig. 4).

Discussion

The degree to which large herbivores select and forage in recently burned areas is a key driver of vegetation heterogeneity in rangeland ecosystems (Knapp *et al.* 1999;

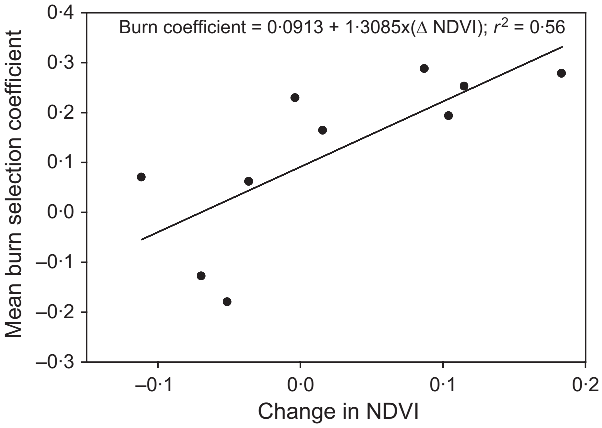

Fig. 3. Relationship between the net change in vegetation greenness (NDVI) during a tracking interval (mean NDVI during last three days – mean NDVI during first 3 days) and the strength of cattle selection for recent burns, as measured by the mean burn selection coefficient in models of cattle grazing distribution fit for each of three experimental replicates (Table 1). NDVI, normalized difference vegetation index.

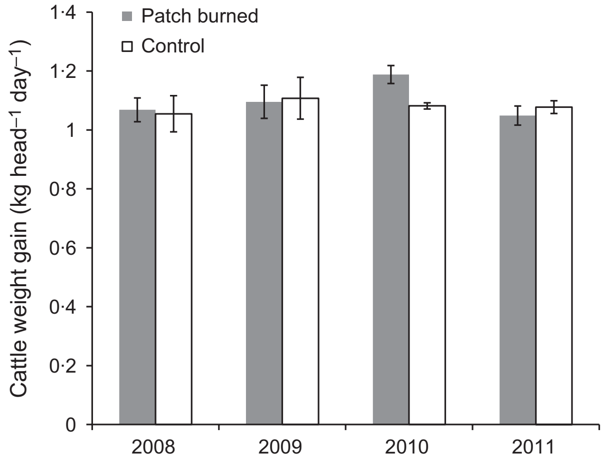

Fig. 4. Weight gained by cattle between 15 May and 1 October on patch-burned and patch-unburned shortgrass steppe ($n = 3$ replicates per treatment) in north-eastern Colorado, USA, 2008–2011. Error bars show 1 SE. Patch burning significantly increased cattle weight gain in 2010 ($P = 0{\cdot}038$).

Table 2. Current-year herbaceous plant production and residual standing dead biomass remaining from previous years (means with 1 SE in parentheses) measured during the first week of June and August in three patch-burned pastures at the Central Plains Experimental Range in north-eastern Colorado, USA. Columns with values in bold correspond to time periods when cattle showed significant selection for recent burns. Measurements were from patches within each pasture that were either burned or not burned during the fall (October or November) preceding the growing season. All values are in grams per square metre

	2008		2009		2010		2011	
	June	August	June	August	June	August	June	August
Current-year growth								
Burned	36·4 (11·5)	**48·0 (10·9)**	**46·6 (1·9)**	121·9 (6·4)	**49·5 (3·3)**	109·0 (3·7)	**19·7 (5·4)**	71·7 (13·6)
Unburned	30·7 (7·6)	**49·9 (9·1)**	**63·7 (22·5)**	159·5 (20·1)	**56·5 (4·0)**	107·1 (7·1)	**32·7 (3·1)**	69·6 (5·4)
Old standing dead								
Burned	1·0 (0·3)	**1·8 (1·0)**	**1·5 (0·6)**	0·4 (0·4)	**0·9 (0·1)**	1·4 (0·5)	**0·9 (0·4)**	1·3 (0·3)
Unburned	39·8 (8·9)	**22·8 (8·9)**	**22·5 (4·2)**	9·7 (2·2)	**45·0 (9·1)**	26·5 (1·8)	**39·6 (4·3)**	25·1 (5·0)

Fuhlendorf & Engle 2004; Archibald *et al.* 2005; McGranahan *et al.* 2012). Yet few studies have quantified the strength of herbivore selection for burns (Allred *et al.* 2011) or examined how burn selection strength varies across gradients of productivity. We showed that cattle selectively grazed on recently burned areas in semi-arid rangeland with substantially lower ANPP than previous studies of fire–grazing interactions. The selection strength that we measured, where cattle spent an average of 31% of their grazing time on recently burned areas that comprised 25% of the landscape, was approximately half as strong as in a mesic grassland, where cattle and bison spent 58% and 68% of their time, respectively, on burned areas that comprised 25% of the landscape (Allred, Fuhlendorf & Hamilton 2011; Allred *et al.* 2011). Our study and that of Allred *et al.* (2011) represent nearly opposite extremes of conditions occurring in grasslands of central North America in terms of mean annual precipitation, ANPP, soil nitrogen dynamics, and plant height and species composition (Burke, Lauuenroth & Parton 1997; Lauenroth, Burke & Gutmann 1999), with peak standing biomass at our semi-arid site (48–160 g m^{-2}, Table 2) being an order of magnitude lower than peak standing biomass at the mesic grassland (600–800 g m^{-2}; Allred *et al.* 2011). These two sites also represent similar extremes in ANPP that occur across precipitation gradients in grasslands of central Asia, East Africa and South America (Sala *et al.* 2012; Lezama *et al.* 2013). Our findings indicate that spatiotemporal interactions between fire and herbivores (i.e. pyric herbivory, sensu Fuhlendorf *et al.* 2009) are a consistent feature of rangelands encompassing a wide range of abiotic and biotic conditions, but that interaction strength is likely to vary substantially across gradients of grassland productivity.

Previous studies showed that prescribed fires in shortgrass steppe enhanced forage quality by increasing nitrogen content 1·3–2·2-fold (Augustine & Milchunas 2009) and to a lesser extent by increasing *in vitro* dry matter digestibility (from 63% in unburned to 70% in burned areas; Augustine, Derner & Milchunas 2010). In mesic grassland, fires enhanced forage quality to a substantially greater degree, increasing nitrogen content 2·7–4·8-fold early in the growing season (Allred *et al.* 2011). Collectively, these findings show that the magnitude of fire effects on forage quality and burn selection strength were both approximately twice as large in the mesic compared to the semi-arid grassland. Results support the idea that fire effects on forage quality are the primary driver of herbivore selection for burned areas during the growing season, and furthermore suggest that measures of forage quality in burned vs. unburned areas may provide an index of the strength of responses by large ruminants to fire across rangeland ecosystems.

Semi-arid ecosystems are characterized by substantial variation in precipitation within and among years, and these fluctuations are predicted to increase with climate change (Sala *et al.* 2012). We showed that variation in burn selection strength is also highly variable within a growing season, with the strongest selection for burned areas consistently occurring during periods of rapid vegetation growth (Fig. 3). This was true both when greening occurred late in the summer in association with monsoonal rains (2008) or early in the growing season (2009–2011; Fig. 1). During periods of rapid plant growth, cattle grazing distribution was consistently more strongly affected by burns than topography. Burn selection strength was not related either to the amount of forage produced in the current growing season or the amount of residual standing dead biomass remaining on unburned areas (Table 2), suggesting that forage quantity was generally not so limiting as to override selection of burned areas. For example, we even detected strong selection for burned areas in May–June of 2011, when burned patch biomass averaged only 21 g m^{-2}. Given that burn selection strength was not related to standing dead biomass in unburned areas, increased N content of current-season growth (Augustine & Milchunas 2009) and more rapid initial plant growth in burned areas during greening are likely reasons for cattle selection of burned areas at this time.

Outside periods of rapid plant growth, cattle grazing distribution either was consistently and positively associated with lowlands, as indexed by TWI, or inconsistent across replicates in terms of response to burns and topography. These findings show that the relative importance of fire and topography in controlling grazer distribution was temporally contingent upon precipitation patterns, revealing the complexity of interactions between biotic and abiotic factors shaping rangeland vegetation heterogeneity. Selection of lowlands during periods of plant senescence may be related to landscape variation in both forage quantity and quality, as lowlands retain green, actively growing vegetation longer into the dry periods. To the extent that sustaining ecological processes is a land management goal, our results emphasize the importance of allowing ungulate herbivores to shift grazing distribution at daily to seasonal temporal scales in response to fire, topographic variation and precipitation patterns.

Strategies to manage rangelands for conservation objectives, such as restoring fire regimes to enhance habitat for grassland birds (Fuhlendorf *et al.* 2006; Derner *et al.* 2009; Little, Hockey & Jansen 2013), frequently generate concerns among livestock managers as to effects on livestock production. In mesic rangelands, recent studies have shown that patchy application of fire designed to enhance wildlife habitat (Limb *et al.* 2011) can be just as effective for livestock production as more traditional homogenous applications of fire (Svejcar 1989). However, previous studies have not examined the effect of patch burning on livestock production in semi-arid rangeland. We found that patch-burn grazing in semi-arid shortgrass steppe had no negative effects on cattle weight gains in three of 4 years, and a significant positive effect in the fourth year. The positive effect in 2010 was associated with the accumulation of standing dead biomass due to above-average precipitation and plant production in 2009. Even in semi-arid rangelands where forage quantity limits livestock weight gain during dry periods, accumulations of standing dead biomass can suppress cattle weight gain in the wettest years (Derner & Hart 2007). Early in the growing season of 2010, accumulated dead biomass may have been of sufficiently low quality to reduce digestible forage intake rates of cattle that only had access to unburned vegetation. This interpretation is also consistent with the finding that strong selection of burned patches in 2010 only occurred early in the growing season.

The methods we used to link animal locations with grazing behaviour were essential for detecting the relative influence of fire and topography on ungulate grazing distribution. Larger-scale processes such as migration, dispersal and range fidelity can be studied without linking animal behaviour and location (Faille *et al.* 2010; Williams, Dechen Quinn & Porter 2012), but our study shows this may not be true for within-season patterns of habitat selection. Our study is one of the first to use GPS technology to analyse behaviour-specific animal distribution, revealing different selection processes operate during foraging vs. non-foraging periods. In some cases, animal foraging response to the factor of interest may be so strong (Sensenig, Demment & Laca 2010; Allred, Fuhlendorf & Hamilton 2011 for ungulate response to burns) that it can be detected even with error resulting from inclusion of other behaviours. However, as we seek to understand trade-offs and multiple interacting factors shaping habitat selection, precise measures of foraging distribution based on combined measurements of animal behaviour and location will be needed.

Applied ecologists increasingly recognize that sustaining or enhancing spatiotemporal heterogeneity in ecosystems is central to the biodiversity conservation (Wiens 1997; du Toit, Rogers & Biggs 2003; Tews *et al.* 2004; Fynn 2012). Management of rangelands by allowing large herbivores to choose among burned and unburned patches in the landscape, and thereby interactively influence vegetation heterogeneity through grazing of recently burned patches, is one means by which managers can sustain rangeland heterogeneity (Fuhlendorf *et al.* 2006, 2012). As society increasingly values multiple rangeland ecosystem services, including producing livestock, sustaining ecosystem processes and conserving biodiversity, management strategies that restore spatiotemporal interactions between fire and grazers are needed. Our work shows that fire–grazing interactions are a temporally variable yet significant component of semi-arid ecosystems, and that the combined management of fire and grazing can be consistent with and even complementary to livestock production goals.

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