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Cattle Grazing Distribution in Shortgrass Steppe: Influences of Topography and Saline Soils☆

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ABSTRACT

The distribution of livestock across heterogeneous landscapes is often uneven, which has important implications for vegetation dynamics and how rangeland managers achieve desired outcomes from these landscapes. Here, we use data from widely available digital elevation models to classify a landscape in the shortgrass steppe with subtle topographic variation using two different approaches: topographic wetness index (TWI) and topographic position classes (TPCs) derived from topographic position indices. We used global positioning system collars to track the grazing locations of cattle within replicate pastures and fit generalized linear mixed models to their locations to quantify the influence of topography on grazing distribution. In addition, we examine the influence of the presence of saline vegetation communities on cattle use of lowlands. The resulting models indicate that TPC more effectively predicts grazing distribution than TWI and that the patterns are strongest in the second half of the growing season (August—October). Model performance was improved with the inclusion of saline vegetation communities, although the magnitude of cattle grazing time in these communities was not consistent across multiple pastures. These models, in combination with local knowledge, can be used by managers to predict and manage livestock distribution even in landscapes with relatively subtle topographic variability.

Introduction

Understanding and manipulating the distribution of free-ranging livestock in heterogeneous landscapes is central to the discipline of rangeland science, as livestock distribution influences many desired ecosystem services. In addition to direct effects on livestock performance and ranching profitability, the way in which livestock use available forage within rangelands worldwide has potential long-term effects on plant composition and productivity (Milchunas and Lauenroth, 1993; Augustine and McNaughton, 1998), edaphic and hydrological processes (Ludwig et al., 2005; Popp et al., 2009), fire regimes (Fuhlendorf et al., 2009), and habitat for the diverse faunal communities that coexist with livestock (Fuhlendorf et al., 2006; Derner et al., 2009). Many studies have shown livestock distribution is affected by abiotic factors, such as topography and distance to water (Bailey, 2005; Bailey et al., 2015), as well as by biotic factors, including vegetation community composition, nutrient content of plants, and the presence or absence of toxins (Senft et al., 1987; Bailey, 1996; Launchbaugh and Howery, 2005). These factors are also intertwined, as abiotic factors such as soil composition and water availability influence the location, type, and productivity of vegetation communities (Bailey, 2004, 2005). Cattle respond to a combination of both temperature (abiotic) and vegetation (biotic) when making decisions on where to graze (Allred et al., 2013). In addition, cattle have spatial memory, which influences decisions about movements and bite rates within particular patches in the landscape (Provenza and Balph, 1987; Bailey et al., 1996). Understanding and predicting how abiotic and biotic environmental factors and cattle spatial memory influence cattle grazing distributions can therefore help guide the management of rangelands for desired outcomes (Rinella et al., 2011).

Abiotic factors are generally more predictable and better understood than biotic factors for influencing grazing behavior of livestock (Bailey et al., 1996; Bailey, 2005). Distance to water is a primary abiotic factor that is often manipulated to more evenly distribute livestock across pastures (Ganskopp, 2001). Slope is another relatively well understood abiotic factor, as cattle often prefer flat areas with little slope and generally avoid areas with > 10% slope (Ganskopp and Vavra, 1987; Bailey, 1996). Although the effects of topography on cattle grazing distribution in

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rugged terrain have been well documented (Bailey, 2005; Bailey et al., 2015; VanWagoner et al., 2006), surprisingly few studies have examined topographic controls over grazing distribution in the more gentle undulating terrain that characterizes much of the world's rangelands. Furthermore, the few studies addressing this question have used varying metrics to model topographic effects, thereby limiting the generality of model predictions. For example, various researchers have modeled cattle distribution as a function of "topographic zones" derived qualitatively from a topographic map (Senft et al., 1985a), as a function of slope and/or elevation (e.g., Allred et al., 2011; Bailey et al., 2015; Clark et al., 2016) or as a function of topographic indices derived from elevation maps (Augustine and Derner, 2014). Furthermore, measures of topographic variation, particularly in undulating terrain, could influence cattle grazing distribution through factors other than simply the avoidance of steep slopes. Topography also influences and can provide an index of biotic factors, such as areas of moisture accumulation and hence higher forage production or areas of high runoff with lower forage production.

Relating environmental variables to cattle grazing distribution is challenging for several reasons. Biotic factors, such as forage quality and quantity, are more variable and difficult to quantify than abiotic factors, as these vary intra-annually and interannually (Bailey et al., 1996; Bailey, 2005; Augustine and Derner, 2014). Simplistic, one-time or periodic biotic measurements such as standing biomass of the vegetation may also be difficult to relate to grazing distribution because ruminant grazers often avoid high-biomass patches of lower-quality forage in order to enhance intake of higher-quality forage in low biomass patches (Van Soest et al., 1984; Wilmshurst et al., 2000). Singular deterministic variables for predicting cattle grazing distribution, such as standing mass of nitrogen in forage, have limited managerial applicability given that the predictive relationship varies substantially over time as weather, topography, and grazing feedbacks all influence standing nitrogen and forage quality within a given patch (Senft et al., 1985a; Pinchak et al., 1991). One limitation of using parameters such as slope and elevation to model grazing distribution is that resulting model coefficients are site specific, making it difficult to generalize across pastures of varying elevations to derive broader predictions regarding livestock grazing patterns. Furthermore, slope can be a misleading measure of landscape position given that both ridgelines and drainage bottoms often have similar slope. In contrast, models that use topographic indices that can be applied in a standardized manner to many landscapes can provide more generalizable predictions of grazing distribution. To address these limitations, we examined the degree to which two quantitative indices of topography can be used to predict livestock grazing distribution.

Our overarching objective was to build on the foundational but nonreplicated work of Senft et al. (1985a) to evaluate quantitative models of grazing distribution in shortgrass steppe rangeland in central North America. Specifically, we evaluated two different topographic indices, both calculated from digital elevation models that are now available at a 10-m resolution for most of North America (https://www.usgs.gov/core-science-systems/national-geospatial-program/national-map) for predicting variability in grazing distribution. The topographic position index (TPI) is the difference in elevation at a point and the average elevation in a neighborhood surrounding the point (Tagil and Jenness, 2008). By calculating TPI at two different neighborhood scales and combining those values with local slope, a landscape can be classified into multiple topographic position classes (TPC) in a repeatable, quantitative manner (Weiss, 2001; De Reu et al., 2013). The topographic wetness index (TWI) quantifies topographic influences on hydrology, is a function of both the slope at a given point and the size of the upstream area potentially contributing flow to that point (Beven and Kirkby, 1979), and has been previously used to model grazing distribution (Augustine and Derner, 2014).

Shortgrass steppe occupies $\approx 3.4 \times 10^5$ km^2 in the semiarid, southwestern portion of the Great Plains (Lauenroth et al., 1999). Within this region, cattle account for 97% of grazing pressure by large herbivores and cattle production is the most widespread land use (Hart and Derner, 2008). Uplands throughout the shortgrass steppe are dominated by C_4 shortgrasses (*Bouteloua gracilis* and *B. dactyloides,* typically > 70% of total production), with lesser amounts of perennial C_3 sedges, grasses, and forbs. Uplands include relatively flat, extensive plains dissected by small swales or closed basins (playas), as well as ridgelines and upper hillslopes that alternate with larger drainages containing floodplains and incised stream channels. Soil formation along these topographic gradients typically leads to shallower, less productive soils at the upper, convex portion of hillslopes and productive, deeper soils with increased organic matter content in lowlands, although these differences are less developed in semiarid compared with more mesic rangelands (Kelly et al., 2008). Although runoff is generally infrequent in semiarid rangelands, topographic positions such as swales, playa basins, floodplains, and stream channels that have the potential to collect runoff and better retain precipitation inputs often retain green forage longer into dry periods and support increased production of C_3 perennial graminoids, especially *Pascopyrum smithii* (Milchunas et al., 1989; Lauenroth, 2008). An exception to this pattern occurs on saline lowlands, where two salt-tolerant C_4 grasses, *Sporobolus airoides* and *Distichlis spicata,* often codominate with C_3 graminoids (Costello, 1944).

Our specific objectives were to 1) evaluate the relative ability of TWI versus topographic classes derived from TPI to predict cattle grazing distribution and 2) evaluate how the presence versus absence of saline lowlands affects these topographic models. We modeled cattle grazing distribution throughout the primary grazing season (mid-May to early October) in 130-ha pastures of semiarid shortgrass steppe. Because cattle can typically graze up to 1.6 km from water (Holechek, 1988; Ganskopp, 2001), we did not expect water location to prevent cattle from accessing all portions of these sized pastures. However, because cattle concentrate near water sources and often walk along fence lines, which results in elevated grazing counts near such features, we used a modeling approach that first accounts for distance to water and fencing and then focuses on the role of topography in predicting grazing distribution. Previous work determined that TWI can be used to effectively model cattle grazing distribution under certain forage conditions in the shortgrass steppe (Augustine and Derner, 2014), but that study was conducted in smaller pastures (50% the area, 65-ha) with limited topographical heterogeneity. Here, we examine a more diverse suite of topographic conditions to test our hypothesis that cattle would preferentially graze in nonsaline lowlands over upland plains and upper topographic positions (Senft et al., 1985a; Varnamkhasti et al., 1995), but that this pattern would be reversed in the presence of saline lowlands due to the predominance of productive but lower-quality grasses (Costello, 1944).

Methods

Study Area

Research was conducted at the Central Plains Experimental Range (CPER) c. 12 km northeast of Nunn, Colorado (40°50′N, 104°43′W), a Long-Term Agroecosystem Research (LTAR) network site. Mean annual precipitation is 340 mm with mean elevation of 1 640 m, and the topographic relief in pastures under study averages 29 m (Table 1). Vegetation is generally dominated by two C_4 grasses (*Bouteloua gracilis* [Willd Ex Kunth] Lag. Ex Griffiths and *B. dactyloides* [Nutt.] J.T. Columbus), which frequently comprise > 70% of the abovegrouond net primary production (Lauenroth and Burke, 2008), but topography, grazing, and variable weather all contribute to spatiotemporal variability in plant community composition and productivity (Milchunas et al., 1989). Upper topographic positions, including ridgelines, upper hillslopes, and flat plains, often have plains prickly pear cactus (*Opuntia polyacantha* Haw.) as an important co-occurring species. Conversely, swales and drainages typically lack prickly pear cactus and instead support an increased abundance of C_3 perennial grasses, particularly *Pascopyrum*

Table 1
Variation in elevation, topographic wetness index (TWI) values, topographic position classes, and the proportion of area occupied by salt flat vegetation within six study pastures at the Central Plains Experimental Range in eastern Colorado.

Pasture	Elevation range (m)	TWI values			Pasture % occupied by topographic class					Pasture % occupied by salt flats
		Min	Max	Mean	Lowlands	Flat Plains	Open Slopes	Highlands	Other	
Shortgrass Replicate 1	1640-1666	2.1	14.8	6.8	24.8	49.9	13.4	11.1	0.8	0.0
Shortgrass Replicate 2	1630-1661	3.5	12.3	6.2	6.9	23.1	43.7	26.3	0.0	0.0
Shortgrass Replicate 3	1600-1644	2.8	15.8	5.8	9.8	7.6	35.3	46.6	0.7	0.0
Salt flat Replicate 1	1635-1662	2.8	13.9	6.6	12.7	69.3	12.7	5.3	0.0	9.4
Salt flat Replicate 2	1620-1644	1.8	13.2	6.1	45.1	12.5	18.0	21.9	2.5	22.9
Salt flat Replicate 3	1606-1628	2.9	14.7	6.8	31.4	46.1	19.3	3.2	0.0	19.9

smithii (Milchunas et al., 1989). These lower topographic positions often have enhanced soil moisture during dry periods, as well as increased soil fertility (Schimel et al., 1985). Loamy plains are the most common ecological site (ES) at CPER but intergrade with sandier (Sandy Plains ES) or saline soils (Salt Flat ES) in some of the larger drainages and associated floodplains (USDA, 2007a, 2007b, 2007c).

We studied two sets of pastures containing different plant communities, both with season-long (May–October) cattle grazing at moderate stocking rates. The first set consisted of pastures ($n = 3$; pasture area of 130–152 ha, hereafter shortgrass pastures) that typify large portions of the shortgrass steppe with topography varying from shortgrass-dominated upland plains, ridgelines, and upper slopes to intervening swales and lower hillslopes with increased abundance of C_3 midgrasses (see Schimel et al., 1985; Milchunas et al., 1989, 1990, 1998; Varnhamski et al. 1995; Burke et al., 1998; Lauenroth et al., 1999). The second set of pastures ($n = 3$, pasture area of 130 ha, hereafter salt flat pastures) contained flat uplands dissected by a drainage in which a narrow, incised stream channel was bordered by floodplains with saline soils that support a distinct plant community characterized by the presence of C_4 saltgrasses, *Sporobolus airoides,* and *Distichlis spicata* (the "dry meadow" community described by Costello, 1944, or Salt Flat ES; NRCS 2007). The Salt Flat ES is distributed widely but infrequently across the shortgrass steppe region and supports notably more forage production than upland communities (USDA, 2007c). Salt flats occur in lowland topographic positions that appear similar to other types of lowlands in the shortgrass steppe in terms of topographic indices that can be derived from a digital elevation map (see later) but differ in plant composition due to soil salinity.

Field Methods

We studied cattle grazing distribution in these two sets of pastures during years with contrasting environmental conditions: 1) a relatively wet, productive yr in 2014 (370 mm mean annual precipitation [MAP]) and 2) a relatively dry, low-productivity yr in 2016 (256 mm MAP). To illustrate the temporal pattern of plant growth in these 2 yr, we calculated the mean normalized difference vegetation index (NDVI; Tucker and Sellers, 1986) from the MOD13Q1 16-d, 250-m^2 resolution data product derived from the MODIS instrument on board the Terra spacecraft, for all pixels occurring within the boundaries of CPER (Fig. 1).

Study pastures were grazed by yearling steers from 16 May to 2 October at a density of 0.64 animal unit months (AUM) ha^{-1} in 2014 and from 13 May to 30 September at a density 0.68 AUM ha^{-1} in 2016 (20–24 steers per pasture). We measured cattle distribution during each grazing season by placing GPS collars (Lotek 3300LR collars; Lotek Engineering, Newmarket, ON, Canada), which recorded positions at 5-min intervals, on two randomly selected steers per pasture. Within-pasture similarity in model coefficients for the two replicate steers within each pasture indicated they adequately represented the distribution patterns of the entire herd (see Appendix A). We divided each year into two analysis periods of equal length (~70 d each): 1) the first half of the grazing season, when vegetation is growing rapidly, and 2) the second half of the grazing season, when vegetation is largely senescing. For analyses, we excluded 1) days in which 10% or more of expected fixes ($n = 288$) were missing due to GPS performance and 2) days when batteries were replaced. Due to changes in precipitation between study years, NDVI varied between years and analysis periods (see Fig. 1).

Collars also contained an activity sensor that recorded movements of the neck along X- and Y-axes and the estimated percent of each 5-min interval in which the neck angle indicated the animal's head was down, which we previously used to distinguish between 5-min intervals in which the animal was grazing versus not grazing (i.e., grazing vs. resting/walking; Augustine and Derner, 2013). Because most of the activity sensors did not function properly in 2016, in both study years we classified grazing behavior for each 5-min interval as follows. First, we removed all fixes occurring within 50 m of a pasture corner, within 100 m of a pasture corner with a water source, or within 75 m of a water source not in a corner, as these are heavily trampled areas with minimal available forage, so actual grazing here is improbable. For the remaining fixes, we classed as grazing those in which steer velocity was > 5 m 5 min^{-1} and < 105 m 5 min^{-1}. Analyses of grazing predictions from 10 collars deployed in 2014 (when activity sensors were functional) showed that the method of Augustine and Derner (2013) classified 35.8% + 2.6% (mean $\pm$ 95% CI) of all collar fixes as grazing fixes, whereas our method based only on velocity classified 46.9% $\pm$ 1.5% of all fixes as grazing fixes. We did not conduct direct behavioral observations of cattle grazing behavior in 2014 to calibrate the collars. These results suggest the velocity method increased the proportion of nongrazing locations that are misclassified as grazing locations but still gives a reasonable estimate of where and when cattle are grazing each day.

For the three pastures containing salt flats, we mapped the boundaries of the saltgrass community by starting with soil maps (Soil Survey Geographic [SSURGO] database for Weld County, Colorado; https://datagateway.nrcs.usda.gov), which we refined during field visits where boundaries of patches containing *Sporobolus airoides* and/or *Distichlis spicata* were mapped. Vegetation composition of these communities was measured in June of 2014 and 2016 as follows. In each pasture containing the salt flats, we selected two randomly located points within the salt flat boundary and then established four, 30-m transects in a systematic grid surrounding each point (104 m spacing between transect centroids; total of 8 transects per pasture). Along each transect, we measured foliar cover of all vegetation by inserting a laser vertically through the vegetation at 50-cm intervals along the first 25 m of each transect and recording the number of foliar contacts by species per laser. Cover of "standing dead" vegetation represents contacts with standing vegetation (any species) that was produced in a previous growing season.

Topographic Indices

We obtained a 1-m resolution digital elevation model (DEM) for CPER derived from LiDAR (NEON, 2015). Before calculating topographic indices, we aggregated the 1-m DEM to a 10-m resolution because most DEMs widely available for North America are at a 10-m resolution.

Using the 10-m DEM, we calculated the topographic wetness index (TWI) for each pixel using the Landscape Connectivity and Pattern Analysis extension for ArcGIS (v1; Theobald, 2007). We also created a

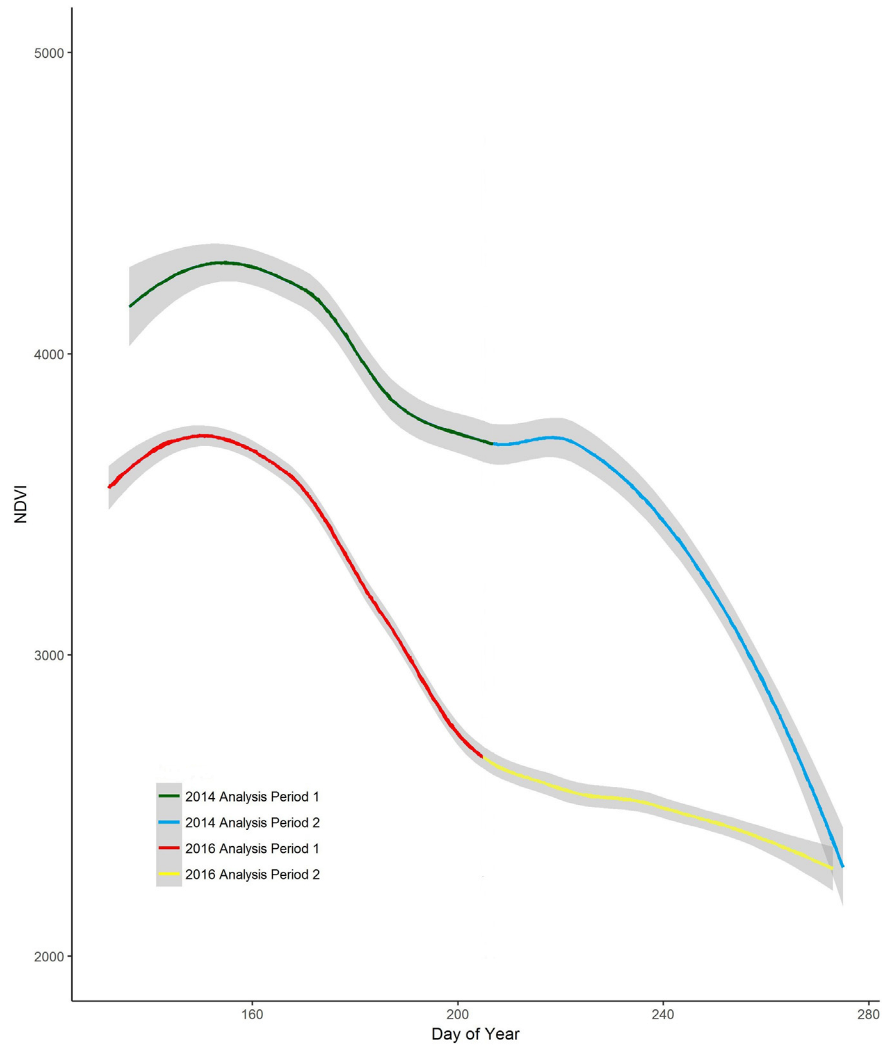

Figure 1. Temporal patterns of greenness as measured by the normalized difference vegetation index (NDVI) averages across the Central Plains Experimental Range in eastern Colorado during 2014 and 2016. Lines are smoothed trend lines fit to the data using the loess method. Cattle grazing distribution was measured during 15 May to 2 October 2 in 2014 and from 12 May to 30 September 30 in 2016.

topographic position classification map of CPER following Weiss (2001). To create this classification, we calculated the TPI of each pixel based on 1) a neighborhood radius of 50 m (TPI_{50}) and 2) a neighborhood radius of 500 m (TPI_{500}) using the Land Facet Corridor Designer extension for ArcGIS (v1.2.884; www.CorridorDesign.org). Each TPI raster was standardized by subtracting the mean, dividing by the standard deviation, and rounding up to a whole number (Weiss, 2001) and then used in combination with the slope of each pixel to define five topographic position classes (Table 2). Weiss (2001) considered TPI values < 1 standard deviation from the mean as low topographic features and TPI values > 1 standard deviation from the mean as high topographic features. Weiss's method was designed for a region with rugged terrain, including mountaintops, which are absent from the shortgrass steppe. Here, however, we shifted these thresholds to 0.8 standard deviations and 1.2 standard deviations, respectively, because of the gently rolling topography of the western Great Plains. This shift accentuated differences in

Table 2
Definitions of five topographic position classes used to model cattle grazing distribution in the shortgrass steppe of eastern Colorado. We calculated the topographic position index (TPI) at a spatial scale of 50 m and 500 m surrounding each pixel (TPI_{50} and TPI_{500} respectively) using a 10-m resolution digital elevation model of the study area and used these values in combination with slope to identify 10 types of topographic position classes following Weiss (2001). These were grouped into five classes (Lowlands, Flat Plains, Open Slopes, Highlands, and Other) for purposes of modeling variation in cattle grazing distribution.

Topographic position	TPI 50	TPI 500	Slope	TPI description	Example
Lowlands	≤ −0.8	≤ −0.8	NA	Locally low, broadly low	Incised stream channel or canyon
Lowlands	−0.8 < x < 1.2	<= −0.8	NA	Locally even, broadly low	Floodplain near channel; playa basin
Lowlands	≤ −0.8	−0.8 < x < 1.2	NA	Locally low, broadly even	Shallow valley
Flat Plains	−0.8 < x < 1.2	−0.8 < x < 1.2	≤ 2	Locally even, broadly even, flat	Flat plains
Open Slopes	−0.8 < x < 1.2	−0.8 < x < 1.2	> 2	Locally even, broadly even, sloped	No elevation extremes, sloped
Highlands	≥ 1.2	−0.8 < x < 1.2	NA	Locally high, broadly even	Ridge on hillside
Highlands	−0.8 < x < 1.2	≥ 1.2	NA	Locally even, broadly high	Slope on hillside
Highlands	≥ 1.2	≥ 1.2	NA	Locally high, broadly high	Hilltop, highest point in area
Other	≥ 1.2	≤ −0.8	NA	Locally high, broadly low	Hill in valley, ridge in lowland
Other	≤ −0.8	≥ 1.2	NA	Locally low, broadly high	Drainage in hillside

low-lying topographic features and limited the overclassification of upper topographic features. Low topographic features are common across the shortgrass steppe landscape, whereas extreme high topographic features are rare. Classification was implemented using the raster package (Hijmans and van Etten, 2012) in R Studio (R Core Team 3.5.1 2018). To use TWI and topographic position classes in models of cattle grazing distribution within each pasture, we resampled the 10-m resolution TWI map and the 10-m resolution topographic classification map to a 25-m resolution (see explanation for selection of this spatial resolution under *Resource Selection Analysis*) using the nearest neighbor method in the ArcGIS Spatial Analyst resampling tool (ESRI).

Distance to Fence and Water

We clipped a 25-m resolution cell grid to the boundaries of each study pasture. For each cell, we calculated the distance to surface water and distance to fencing (in meters) using the Euclidian distance tool in the ArcGIS spatial analyst toolbox (ArcGIS v10.2.2). To account for the tendency of yearling steers to travel and graze along fencelines (e.g., Augustine et al., 2013), we set all pixels > 30 m from fences to a value of 30, thereby modeling the fence influence at local (0–30 m) spatial scale. Similarly, to model the localized effect of water sources on cattle distribution, we set all pixels > 300 m to water to a value of 300, thereby modeling the water influence at a local (0–300 m) spatial scale and focusing on the influence of topography and vegetation at larger scales (Augustine and Derner, 2014).

Resource Selection Analysis

Following the approach of Augustine and Derner (2014) and Clark et al. (2014, 2016), we overlaid cattle grazing locations for each collared animal onto the 25-m cell grid described earlier and calculated the number of grazing locations within each pixel for each of the two activity periods per study year. A "grazing location" refers to a position within the pasture where we estimated that a given collared steer spent the majority of the prior 5 min grazing. For each pasture-steer-yr-analysis period combination, we fit generalized linear models (GLMs) predicting the number of cattle grazing locations per pixel (625 m^2) as a function distance to water, distance to fence, TWI or TPC, and presence of C_4 saltgrass vegetation in a given pixel. Probability of cattle use was modeled as a continuous response variable in the GLM, and each model included an offset term (McCullagh and Nelder, 1989), such that model predictions were in the form of a relative frequency of cattle use of a pixel. Model coefficients were estimated using Equation [2] published in Sawyer et al. (2009) and discussed in greater detail by Nielson and Sawyer (2013):

$$\ln(E[l_i/\text{total}]) = \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p,$$

where, l_i is number of GPS locations within sampling pixel i ($i = 1, 2, \ldots, n$), n is number of pixels in study pasture, *total* is total number of GPS locations within the pasture study area, β_o is an intercept term, $\beta_1, \ldots, \beta_p$ are unknown coefficients for the predictor variables $X_1, \ldots, X_p$, and $E[.]$ represents the expected value.

First, we evaluated cattle grazing distribution in shortgrass pastures ($n = 3$) by fitting GLMs of grazing locations per pixel as a function of distance to water, distance to fence, and either TWI or TPC. Models addressing topographic classes as a predictor variable used "Flat Plains" as the reference class that other class coefficients are related to. Next, for pastures containing salt flat vegetation, we evaluated models with and without salt flat vegetation as a categorical predictor (0 or 1 for salt flat presence). For each pasture, we fit separate models for each collared steer ($n = 2$ per pasture) and then calculated mean model coefficients for a given pasture. We then calculated model predictions for grazing distribution as a function of TWI or TPC, given mean values for distance to fence and water and plotted these model predictions for each of the three replicate "shortgrass" pastures and each of the three replicate "salt flat" pastures. Finally, we examined how model predictions for the latter three pastures changed in response to the presence of lowlands containing salt flats.

For all our analyses, we used 25 × 25 m pixels to subdivide pastures because this resolution resulted in a distribution of grazing fixes per pixel that approximated a negative binomial distribution, which allows us to use the modeling approach of Nielson and Sawyer (2013). Smaller cell sizes would increase the probability that a given cell contained no grazing fixes, resulting in a zero-inflated distribution. The offset term converts the integer counts of the response variable to relative frequency values, which are an estimate of the true probability of use of a given pixel and therefore represent resource selection probability functions (RSPFs; Manly et al., 2002).

Relative frequencies are small on a per-pixel basis (typically varying from 0 to 0.002), so we multiplied the relative frequencies by 1 000 to express grazing distribution in units of relative frequency of grazing locations per pixel per steer per 1 000 grazing locations (typically varying from 0 to 2.0; Fig. 2) when reporting or presenting model predictions. Using these units, a perfectly even grazing distribution by one steer in a 130-ha pasture would result in a relative frequency of 0.50 grazing locations per pixel. For the one shortgrass pasture that was larger (152 ha) than the other study pastures (130 ha), the expected relative frequency given perfectly even distribution is 0.43 grazing locations per pixel. To account for this difference, we rescaled all predicted relative frequencies for the 152-ha pasture to be expressed in units that are equivalent to a 130-ha pasture.

Results

Growing Season and Pasture Conditions

Vegetation growth was substantially greater during the wet year of 2014 compared with the below-average precipitation year of 2016 (see Fig. 1). In 2014, greenness (as measured by NDVI) increased rapidly from the start of the grazing season (15 May) until reaching peak value on 1 June. NDVI declined steadily from 1 June until the midpoint of the growing season (25 July). During the second half of that grazing season (25 July–2 October), NDVI continued to decline steadily. Greenness followed a similar temporal pattern in 2016, but NDVI was approximately 20–40% lower across the growing season (see Fig. 1).

Study pastures varied in their relative extent of different topographic classes, with ~8–50% classified as flat plains, 7–45% lowlands, and 4–47% highlands (see Table 1). For the salt flat pastures, ~9–23% of total pasture area contained salt flat vegetation (see Table 1). The salt flat in replicate 1 contained notably lower cover of the two saltgrasses (*Sporobolus airoides* and *Distichlis spicata*) and greater cover of a palatable C_3 midgrass *(Pascopyrum smithii)*, as well as C_4 grasses (primarily *Bouteloua* spp.) relative to replicates 2 and 3 (Table 3).

Cattle Grazing Distribution

Within each study pasture, the relative frequency of grazing locations per collared steer per pixel per 1 000 grazing locations varied from 0 to > 2.0 (see Fig. 2). Model coefficients for the two replicate steers within each pasture showed a high degree of spatial and temporal congruence (see Appendix A), indicating that the two collared animals adequately represented the distribution patterns of the entire herd. Within pastures, cattle grazed unevenly, demonstrated by 4–16% of the pixels containing no grazing locations and 1–5% of pixels containing a relative frequency > 2.0, which is > 4 × greater than the expected value under perfectly even grazing during the first half of the grazing season in 2014 (see Fig. 2).

TWI was significantly and positively correlated with the frequency of cattle grazing locations throughout 2014 in the shortgrass pastures, and the strength of this relationship increased markedly for all three

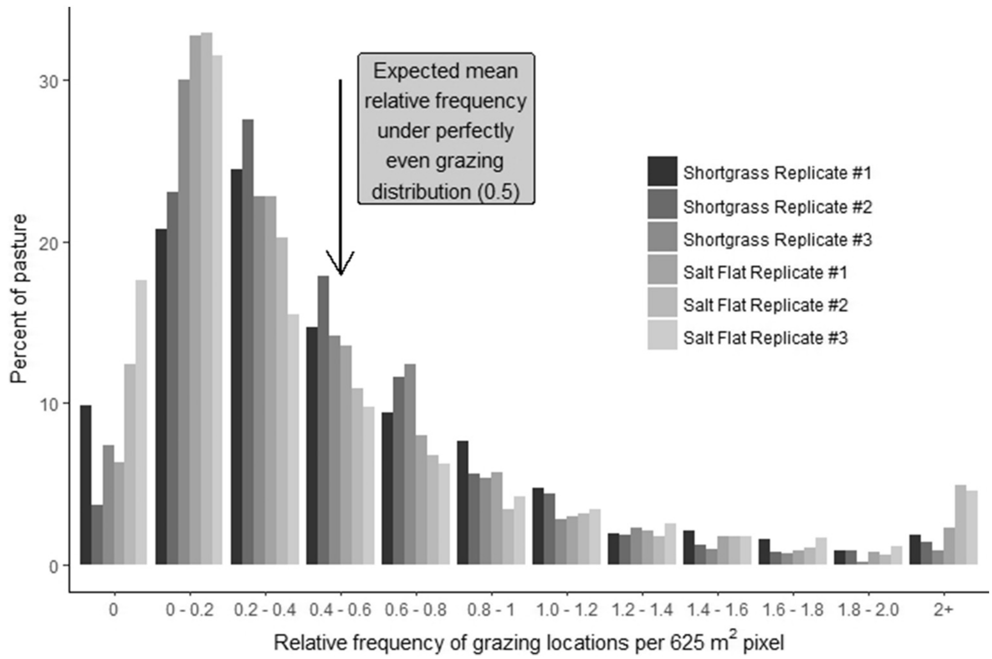

Figure 2. Histogram illustrating the percent area of each of six study pastures experiencing varying relative frequencies of cattle grazing locations in the shortgrass steppe of eastern Colorado. Grazing frequency distributions are shown for each of three pastures containing only shortgrass vegetation and each of three pastures that contained both shortgrass and saltgrass vegetation. For each pasture, the expected mean relative frequency of cattle grazing locations per pixel under perfectly even grazing distribution is 0.5.

replicates during the second half of the grazing season (Fig. 3a). In 2016, we found that TWI was not consistently related to cattle grazing distribution during the first half of the growing season but then was strongly positively associated with TWI during the second half of the growing season (see Fig. 3b). When viewed relative to growing season conditions measured in terms of NDVI (see Fig. 1), topographic controls on soil moisture appear to most strongly influence cattle grazing distribution after vegetation reaches peak biomass.

When we modeled grazing distribution in shortgrass pastures as a function of the five topographic position classes (TPC), results were equivocal in terms of whether TPC provided more parsimonious models than TWI (Table 4). The TWI model was more parsimonious than the TPC model in replicate 1 of the shortgrass pastures and also more parsimonious than the TPC models for all shortgrass pastures in analysis period 2 of 2016 (see Table 4), whereas TPC models were more parsimonious in other time periods. TPC models revealed similar shifts in the magnitude of topographic influences on grazing distribution over the course of the growing season. On the basis of model predictions averaged across all three replicates, the relative frequency of grazing locations was lower (based on nonoverlapping confidence intervals; see Fig. 4) in highlands relative to both lowlands and flat plains in the second half (but not the first half) of both growing seasons. Maps of one shortgrass pasture illustrate the high degree of consistency in grazing distributions for both collared steers (Fig. 5a) and the degree to which the RSPF map derived from the average TPC models predicts an increase in grazing location density across the toposequence from highlands to lowlands (see Fig. 5b).

When we fit TWI and TPC models for the pastures containing salt flats, TPC models were consistently more parsimonious than TWI models across all years, analysis periods, and replicates (Table 5). For the salt flat pastures, TPC models that included presence/absence of salt flat vegetation were more parsimonious than models based on TPC alone, for most pastures and analysis periods, and in particular were always more parsimonious during the second half of the growing season in both years (see Table 5). Although including salt flat vegetation consistently improved model fit, it did not produce consistent predictions for the degree to which cattle grazed in salt flat vegetation. In one salt flat pasture, the presence of salt flats substantially increased the relative frequency of grazing locations in both lowlands and flat plains (the two primary topographic positions where salt flats occur). In a second pasture, presence of salt flats slightly reduced the relative frequency of grazing locations, while in a third pasture, presence of salt flat vegetation dramatically reduced relative frequency of grazing locations (Figs. 6 and 7). This inconsistency was substantial throughout the 2014 growing season and in the second half of the 2016 growing season (see Fig. 6). We also found that cattle in these pastures used open slopes and highlands to a lesser degree than other topographic positions, similar to findings for shortgrass pastures. The variable response of cattle to salt flat vegetation is clearly reflected in the RSPF maps for these three pastures, with strong selection of salt flats evident in replicate 1 and strong avoidance of salt flats (the latter matching our original hypothesis) evident in replicate 3 (see Fig. 7).

Table 3
Foliar cover of plant functional groups in salt flats occurring in three study pastures at the Central Plains Experimental Range in eastern Colorado. Saltgrasses consist of *Sporobolus airoides* and *Distichlis spicata*. C_4 grasses other than the saltgrasses consist predominantly of *Bouteloua* spp., and C_3 gramminoids other than western wheatgrass *(Pascopyrum smithii)* consist predominantly of *Hesperostipa comata* and *Carex* spp. Values shown are the mean of measurements from June 2014 and 2016.

Pasture	Foliar cover of plant functional groups (%)					
	Saltgrasses	Western wheatgrass	Other C_4 grasses	Other C_3 graminoids	Forbs	Standing dead
Salt flat replicate 1	10	22	42	13	4	88
Salt flat replicate 2	53	20	6	13	4	181
Salt flat replicate 3	66	12	14	15	2	129

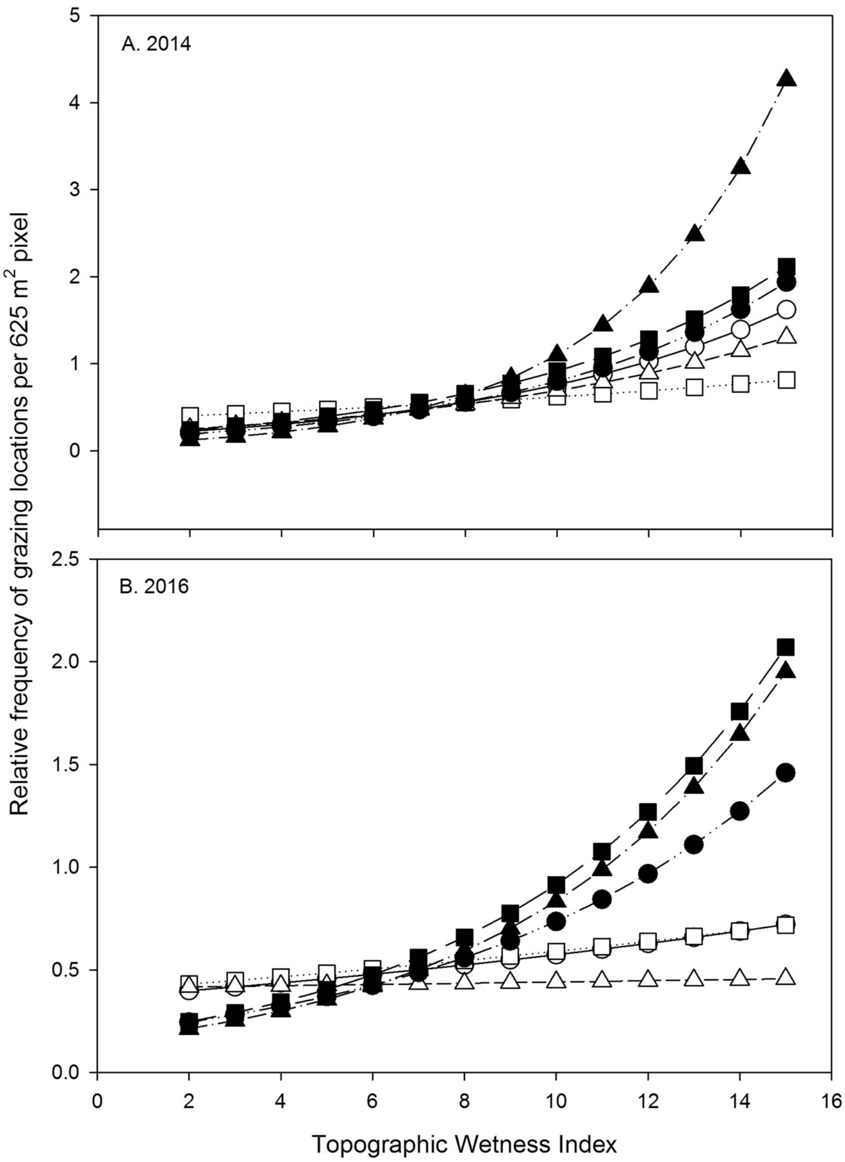

Figure 3. Relative frequency of grazing locations as a function of the topographic wetness index (TWI) per pixel (625 m^2) for the first half of the growing season (analysis period 1; open symbols) and the second half of the growing season (black symbols) for each of three pastures encompassing shortgrass vegetation in eastern Colorado. Cattle grazing distribution response to TWI increased substantially relative to the first half of the growing season in both a wet yr (2014; **A**) and a dry yr (2016; **B**). Symbol shapes show the same pasture in any given year and season.

Discussion

Understanding drivers of grazing distribution patterns within pastures is central to livestock management. Several past studies have employed detailed vegetation maps or intensive spatial sampling of forage quantity and quality in order to derive maps that are used to predict cattle grazing distribution (e.g., Senft et al., 1985a; Ganskopp and Bohnert, 2009). However, such maps are labor intensive and costly to obtain and often impractical to employ in management contexts. Furthermore, in rangelands where plant species composition varies continuously across subtle gradients in topoedaphic characteristics, boundaries between plant communities can be difficult or arbitrary

Table 4
Akaike Information Criterion (AIC) scores for shortgrass pastures comparing topographic wetness index (TWI) model with topographic position class (TPC) model. The TWI model consistently performed better in replicate #1. In other replicates, the most parsimonious model varied between the two models. Values in bold indicate the selected model (TPI vs. TPC) based on AIC.

Dataset	Akaike information criterion							
	2014 Analysis period 1		2014 Analysis period 2		2016 Analysis period 1		2016 Analysis period 2	
Shortgrass pastures	TWI	TPC	TWI	TPC	TWI	TPC	TWI	TPC
Shortgrass replicate 1A	**9349.1**	9374.8	**9408.2**	9520.3	**9715.2**	9716.1	**9535.8**	9696.3
Shortgrass replicate 1B	**9402**	9454	**9322.5**	9343.1	**9771.8**	9776.1	**9859.1**	9894.5
Shortgrass replicate 2A	9607.6	**9607.5**	9934.5	**9924**	9102.3	**9087.6**	**9093.5**	9122
Shortgrass replicate 2B	**9512.8**	9531.5	7133.7	**7118.5**	9612.4	**9567.7**	3072.2	**3064.6**
Shortgrass replicate 3A	10798	**10754**	10183	**10111**	10699	**10568**	**8262**	8275.5
Shortgrass replicate 3B	10635	**10567**	**10264**	10316	10516	**10449**	**10294**	10429

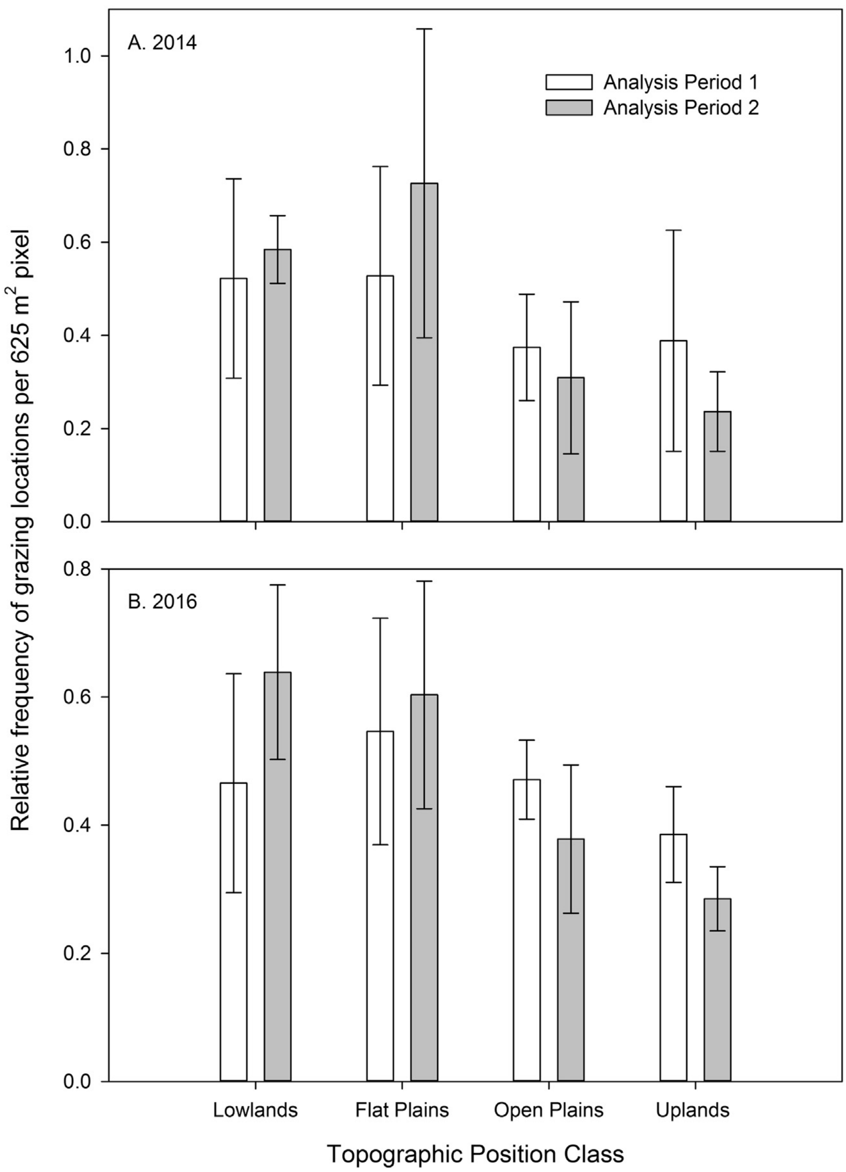

Figure 4. Variation in the mean predicted relative frequency of grazing locations per pixel (and 95% confidence intervals derived from models for 3 different pastures) for each of four topographic position classes in the shortgrass steppe of eastern Colorado during 2014 (**A**) and 2016 (**B**). White bars show predicted grazing frequency for the first half of the growing season (analysis period 1), and gray bars show the second half of the growing season (analysis period 2). See Figure 1 for temporal patterns in vegetation greenness during these analysis periods in both years.

to define. Under these conditions, models that quantify variation in cattle grazing distribution in relation to quantitative topographic indices can provide valuable baseline understanding of how cattle grazing distribution will vary in the absence of management factors (e.g., rotational grazing systems, prescribed burning) that would further alter grazing patterns.

Alternatively, the integration of biophysical, topographical, and ecological components of landscapes, which can be derived from widely available DEMs, through two metrics of topographic variability (TWI and TPC) consistently predicted spatial variability in cattle grazing distribution during the second half of contrasting (relatively wet vs. relatively dry) growing seasons in shortgrass steppe rangeland with gently rolling topography. Less robust relationships between grazing distribution and topography during the first half of the growing season are not surprising, as both forage quality and quantity are concurrently high at this time of rapid growth following green-up. As a result, livestock move regularly among grazing patches as they satiate to local characteristics of any given patch in a pasture (Bailey and Provenza, 2008). As plants phenologically advance during the growing season, they differentially exhibit changes in biomass production and forage quality declines, which, combined with soil water heterogeneity associated with topoedaphic conditions, substantially enhances differences in spatial variability of vegetation within a pasture. As such, lowland and flat plains topographical positions exhibit substantially greater relative greenness in vegetation compared with higher topographical positions. During the growing season, forage quality (digestibility and crude protein content) is likely to be more important than total forage quantity in driving these patterns (Wilmshurst et al., 2000; Ganskopp and Bohnert, 2009; Allred et al., 2011).

Although topographic indices derived from DEMs are useful tools for describing a landscape, there is no bona fide method of using these tools to replicate the intricacies of a real landscape (De Reu et al., 2013). Both methods we used in our analyses (TWI and TPC) have shortcomings in reflecting the realities of a landscape. One notable topographic feature of the pastures containing salt flats was the presence of an incised stream channel cutting through the terrace in which the salt flats occur. These incised channels are the lowest topographic feature in the pasture, occasionally contain flowing water following large storm

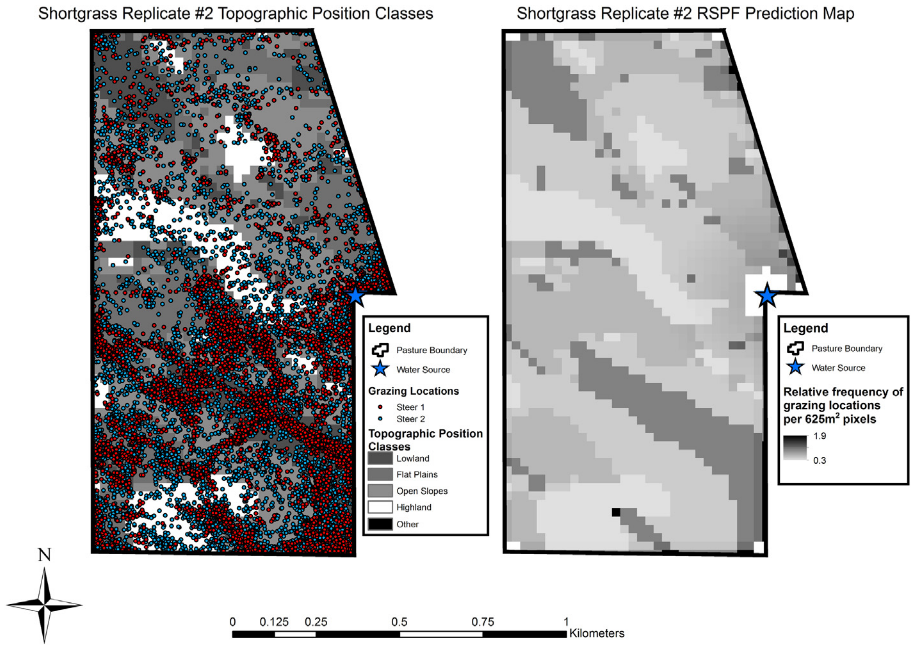

Figure 5. Example of grazing location distribution for two steers in relation to topographic position classes in a pasture encompassing shortgrass vegetation in eastern Colorado during the second half of 2016 (map on left) and the predicted resource selection probability function based on the average of models from both steers as a function of topographic classes. For both steers, the model showed strong selection for lowlands and flat plains relative to the highlands of open slopes. See Table 1 for the definition of "other" topographic position, which was rare throughout the study area.

events, and often support lush vegetation consisting of C_3 grasses and sedges. The TPC model classified these incised channels (as well as the adjacent floodplains) as "lowlands." Surprisingly, however, the algorithm for calculating TWI did not consistently generate large TWI values for pixels containing these channels, because the TWI algorithm models water movement in such a manner that water flowing onto the floodplains does not reach the incised channel. In contrast, TPC and its use of neighborhood areas to classify a landscape were sensitive to influences of abrupt changes in elevation. For example, an extensive level area adjacent to a hill had portions near the hill classified as "lowlands" and portions farther away classified as "flat plains," while a human observer would likely classify the entire level area as the same topographic feature (shortgrass replicate 1).

Whether TWI or TPC provided more parsimonious predictions of cattle grazing distribution for shortgrass pastures varied by pasture and time of year, but TPC was consistently more parsimonious for pastures that included salt flats and associated incised stream channels. Thus, TPC may be a particularly useful approach for standardizing quantification of topographic variation across widely varying characteristics of semiarid rangelands. Currently, elevation and slope are commonly used for predicting livestock grazing distribution (e.g., Clark et al., 2014, 2016; Bailey et al., 2015), but the relevance and management inferences of these parameters are difficult to interpret beyond the specific study area or set of pastures. Thus, direct comparisons of variability in livestock grazing distribution across widely varying types of rangeland ecosystems and degrees of topographic variability are needed for modeling distribution in relation to relative measures of topography (such as TWI and TPC), which can be quantitatively derived in a repeatable manner from DEMs.

Cattle avoid grazing patches and even individual grass plants, especially bunchgrasses, which accumulate many reproductive culms (i.e., "wolf plants", Ganskopp et al., 1992; Romo et al., 1997), in which standing dead vegetation has accumulated (e.g., Willms et al., 1988; Ganskopp et al., 1993; Ganskopp and Bohnert, 2009). Although accumulation of standing dead vegetation in upland topographical positions is relatively limited in shortgrass steppe, its removal via dormant-season prescribed fire enhances cattle grazing distribution during the subsequent growing season (Augustine and Derner, 2014). In contrast, relatively high amounts of standing dead vegetation can occur in salt flat topographical locations (e.g., 88–181% absolute cover of standing dead vegetation during the growing season; see Table 3). Thus, conventional wisdom would suggest that cattle would preferentially select against these topographical areas. However, our results are inconsistent with this conventional wisdom. Cattle preferentially grazed in salt flats throughout the growing season in both years (see Fig. 6) in the pasture where the salt flat represented a

Table 5
Akaike information criterion (AIC) scores for salt flat pastures comparing the topographic wetness index (TWI) model with the topographic position class (TPC) model and TPC model including salt flat vegetation as a model variable. Lower AIC scores between the TWI and TPC model are shown in italics. The lowest AIC score among all three models is shown in bold. TPC models were always more parsimonious than TWI models. Including salt flat vegetation in the TPC model generally made the model more parsimonious; however, the effect of salt flat vegetation (preference vs. avoidance) varied among replicates. In analysis period 2 of both study years the TPC model with salt flat vegetation as a model coefficient was always the most parsimonious model.

Dataset	AIC											
	2014 analysis period 1			2014 analysis period 2			2016 analysis period 1			2016 analysis period 2		
Salt flat pastures	TWI	TPC	TPC w/ salt flat	TWI	TPC	TPC w/ salt flat	TWI	TPC	TPC w/ salt flat	TWI	TPC	TPC w/ salt flat
Replicate 1A	9750.2	*9722.5*	**9704.5**	9796.7	*9509.2*	**9180.4**	9612.3	***9581.7***	9582.7	9905.5	*9802.3*	**9773**
Replicate 1B	9895.9	*9866.2*	**9850**	9952.6	*9704.8*	**9371.8**	10092	***10063***	10064	10450	*10371*	**10339**
Replicate 2A	9611	***9418.2***	9419.4	9649.2	*9463.4*	**9448.4**	9817.5	*9691.7*	**9684.7**	9577.8	*9534.9*	**9529.9**
Replicate 2B	9703.9	***9542***	9543.6	9538.3	*9368.2*	**9340.6**	9646.9	*9536.5*	**9535.3**	9604.6	*9554.9*	**9553.6**
Replicate 3A	9866.1	*9656.5*	**9507.2**	6122.5	*5975.6*	**5935.7**	9958.1	*9830.2*	**9670.4**	9938.6	*9845.2*	**9520.6**
Replicate 3B	9802.5	*9630.7*	**9401.8**	9709.7	*9288.8*	**9265.8**	9946.1	*9833.5*	**9611**	9950.2	*9920.6*	**9603.4**

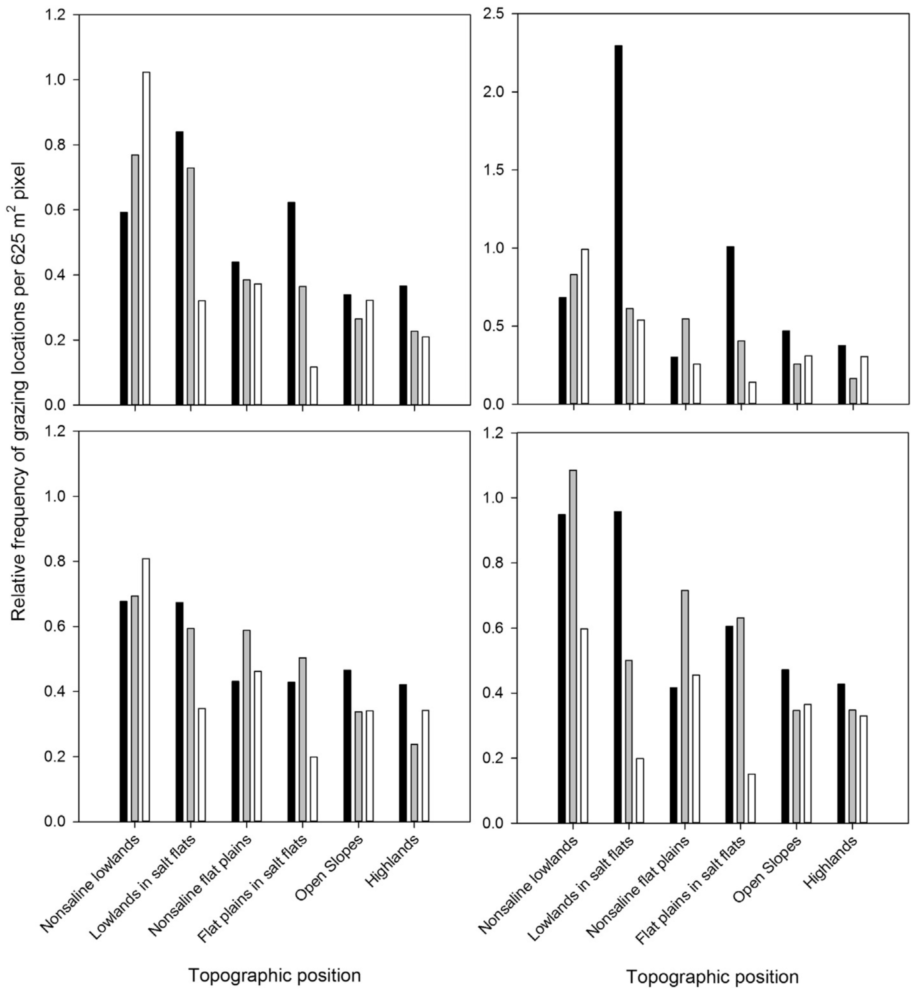

Figure 6. Predicted relative frequency of grazing locations per pixel in relation to topographic position classes and the presence/absence of salt flat vegetation in lowlands and flat plains in the shortgrass steppe of eastern Colorado during 2014 (upper panels) and 2016 (lower panels), separately for the first half of the growing season (left panels) and second half of the growing season (right panels). See Figure 1 for temporal patterns of vegetation greenness during these study periods. Each shade shows prediction values based on mean models fitted to two different steers for each of three pastures containing both shortgrass and salt flat vegetation.

small percentage (9% of area) of the pasture and contained a low amount (10%) of cover of the two saltgrasses, with corresponding substantial amounts of palatable C_3 and C_4 grasses (see Table 3). In contrast, however, cattle avoided salt flats relative to non — salt flat vegetation in equivalent topographic positions (see Fig. 6) in replicate 3 (see Fig. 7), where salt flat area comprised double the percent area of the pasture (20–22%) and substantially more cover (≥ 50%) of the two saltgrasses.

We speculate that both the variability in the relative amount and spatial arrangement of salt flats within a pasture could affect their value as a grazing resource. The salt flat in replicate 1 was located in a pasture corner, where cattle naturally tend to drift and coalesce (Senft et al., 1985b). This may be another reason that cattle showed an unexpected preference for salt flats in this pasture. In replicate 2, the salt flat bisects the pasture and is near water sources, so cattle consistently travel through and graze in the salt flat. In contrast, in replicate 3, where cattle had the option of accessing portions of the pasture distant from water by traveling around rather than through the salt flat, they showed the strongest avoidance of salt flat vegetation.

We acknowledge that science-management partnerships with ranchers will be necessary to evaluate a diversity of topographical positions, amounts, and configurations across the shortgrass steppe rangeland ecosystem. In addition, subsequent evaluations will need to assess the influence of grazing management strategies, such as stocking density and length of grazing/rest period, on altering the influence of topography and salt flats on grazing distribution.

Implications

Variation in livestock grazing distribution is a key concern for sustainable management of rangeland ecosystems because consistent, intense grazing in particular locations within a landscape can potentially reduce or eliminate some palatable, productive forage species. Shortgrass steppe rangelands, however, are highly resistant to grazing pressure when properly managed with moderate stocking rates, such that the persistence of palatable, productive C_3 grasses (e.g., *Pascopyrum smithii*) is sustainable over many decades (e.g., Milchunas et al., 2008; Porensky et al., 2017; Augustine et al., 2017), despite the uneven grazing distribution patterns observed in this study. As stocking rates increase, declines in abundance of C_3 grasses in lowlands (e.g., Varnamkhasti et al., 1995; Porensky et al., 2017) are likely exacerbated by the grazing distribution patterns demonstrated here and can eventually lead to declines in total forage production (Irisarri et al., 2016).

Opportunities exist for ranchers and land managers to alter the amounts and configurations of topographical positions in pastures with creative fencing infrastructure, such as temporary electric fence or virtual fencing (e.g., Anderson, 2007). Flexibility associated with this temporary infrastructure or numerous geometric shapes and sizes through virtual fencing could provide ranchers and land managers endless possibilities in matching available topographic locations and associated plant communities to desired

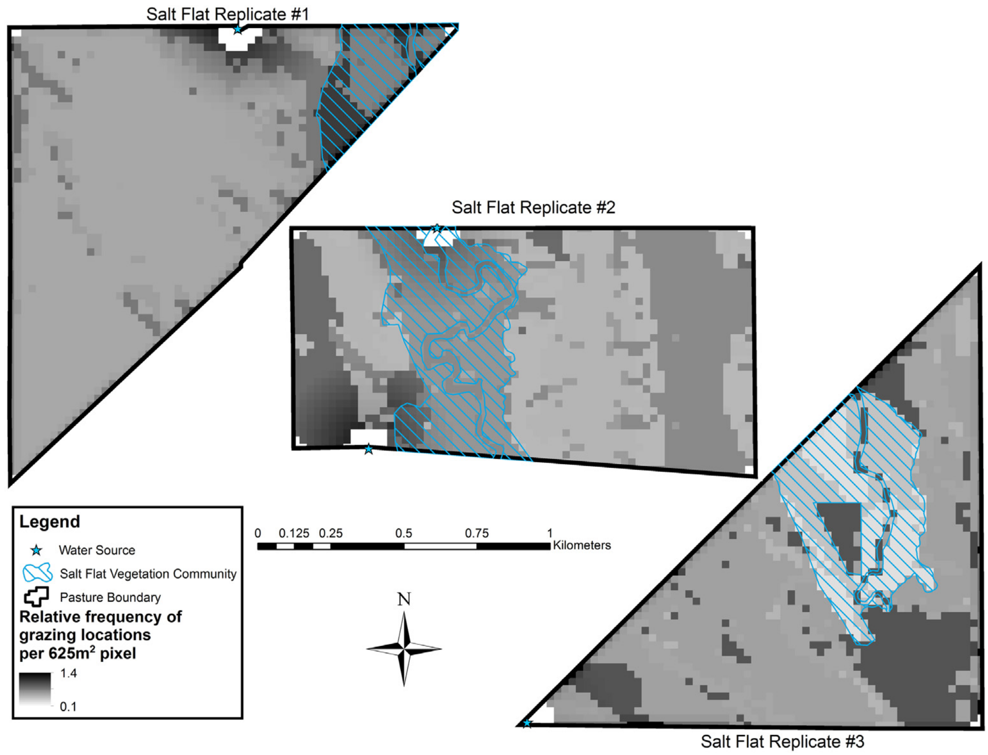

Figure 7. Predicted variation in the relative frequency of grazing locations for cattle in three pastures containing varying amounts of salt flat vegetation in eastern Colorado. See Table 3 for measures of the abundance of C_4 saltgrasses within the area mapped as a salt flat vegetation community in each replicate. Note the variation from strong selection of salt flat vegetation in replicate 1 to strong salt flat avoidance in replicate 3.

grazing distribution patterns at temporal scales of days to weeks to partial grazing seasons. Virtual fencing has been shown to provide ecological, lifestyle, and economic benefits to ranchers (Umstatter, 2011). Thus, adaptive temporal management strategies could be effectively combined with highly flexible spatial pasture configurations throughout the grazing season to achieve desired goals and provision of multiple ecosystem goods and services with positive environmental benefits.

Acknowledgments

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Appendix A

TWI model coefficients for each collared steer in the shortgrass pastures. Coefficient averages for each pasture are shown, as well as coefficient averages for all replicates (n = 3). Averages for all replicates taken together are shown in bold if significant at the 90% confidence level. In most cases, both steers in a pasture showed similar grazing distribution and therefore have similar model coefficients. Both steers in a pasture also shared similar model coefficients in the TPC model (not shown).

Dataset	2014 Analysis Period 1				2014 Analysis Period 2				2016 Analysis Period 1				2016 Analysis Period 2			
	Intercept	Fence Dist	H2O Dist	TWI	Intercept	Fence Dist	H2O Dist	TWI	Intercept	Fence Dist	H2O Dist	TWI	Intercept	Fence Dist	H2O Dist	TWI
Replicate 1A	-7.2143	-0.0229	-0.0030	0.1539	-8.1390	-0.0195	-0.0009	0.1848	-5.7552	-0.0131	-0.0060	0.0396	-8.8001	0.0000	0.0000	0.1653
Replicate 1B	-7.2658	-0.0194	-0.0030	0.1501	-8.2933	-0.0194	0.0000	0.1689	-5.5518	-0.0212	-0.0062	0.0515	-8.3775	0.0000	0.0000	0.1092
Replicate 1 Avg.	-7.2401	-0.0211	-0.0030	0.1520	-8.2161	-0.0194	-0.0005	0.1769	-5.6535	-0.0172	-0.0061	0.0455	-8.5888	0.0000	0.0000	0.1373
Replicate 2A	-7.5625	-0.0096	-0.0001	0.0450	-7.8549	-0.0140	-0.0003	0.1196	-7.3614	-0.0095	0.0000	0.0074	-8.1358	-0.0168	0.0000	0.1596
Replicate 2B	-7.3634	-0.0218	0.0000	0.0620	-7.9942	-0.0282	-0.0007	0.2150	-7.4225	-0.0217	0.0000	0.0712	-8.5989	-0.0023	0.0000	0.1677
Replicate 2 Avg.	-7.4629	-0.0157	-0.0001	0.0535	-7.9245	-0.0211	-0.0005	0.1673	-7.3919	-0.0156	0.0000	0.0393	-8.3673	-0.0095	0.0000	0.1637
Replicate 3A	-7.4433	-0.0026	-0.0038	0.1394	-7.9381	-0.0187	-0.0035	0.2659	-6.9089	-0.0083	-0.0024	0.0180	-8.8462	0.0000	0.0000	0.1785
Replicate 3B	-6.9517	-0.0084	-0.0044	0.1137	-8.2100	-0.0152	-0.0032	0.2762	-6.2767	-0.0173	-0.0033	-0.0041	-8.3455	-0.0028	-0.0011	0.1621
Replicate 3 Avg.	-7.1975	-0.0055	-0.0041	0.1266	-8.0740	-0.0170	-0.0033	0.2710	-6.5928	-0.0128	-0.0029	0.0069	-8.5959	-0.0014	-0.0005	0.1703
Mean	**-7.3002**	**-0.0141**	-0.0024	**0.1107**	**-8.0716**	**-0.0192**	-0.0014	**0.2051**	**-6.5461**	**-0.0152**	-0.0030	0.0306	**-8.5173**	-0.0036	-0.0002	**0.1571**
90 % CI	0.2403	0.0134	0.0035	0.0862	0.2458	0.0035	0.0028	0.0967	1.4669	0.0037	0.0052	0.0349	0.2191	0.0087	0.0005	0.0295
UCL	-7.0598	-0.0007	0.0011	0.1969	-7.8257	-0.0156	0.0013	0.3017	-5.0792	-0.0115	0.0022	0.0655	-8.2983	0.0050	0.0003	0.1865
LCL	-7.5405	-0.0275	-0.0059	0.0245	-8.3174	-0.0227	-0.0042	0.1084	-8.0130	-0.0189	-0.0082	-0.0043	-8.7364	-0.0123	-0.0007	0.1276

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