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Cattle Grazing Distribution Patterns Related to Topography Across Diverse Rangeland Ecosystems of North America[☆]

E.J. Raynor[a,*], S.P. Gersie[b], M.B. Stephenson[c], P.E. Clark[d], S.A. Spiegal[e], R.K. Boughton[f], D.W. Bailey[g], A. Cibils[g], B.W. Smith[h], J.D. Derner[i], R.E. Estell[j], R.M. Nielson[k], D.J. Augustine[a]

[a] *Research Ecologist, US Department of Agriculture–Agricultural Research Service, Rangeland Resources and Systems Research Unit, Fort Collins, CO, 80526, USA*
[b] *Graduate Student, Colorado State University–Natural Resource Ecology Laboratory, Graduate Degree Program in Ecology, Fort Collins, CO, 80523, USA*
[c] *Assistant Professor, University of Nebraska–Lincoln, Panhandle Research and Extension Center, Scottsbluff, NE, 69361, USA*
[d] *Rangeland Scientist, US Department of Agriculture–Agricultural Research Service, Watershed Management Research Unit, Boise, ID, 83712, USA*
[e] *Research Rangeland Management Specialist, US Department of Agriculture–Agricultural Research Service, Range Management Research Unit, Las Cruces, NM, 88003, USA*
[f] *Assistant Professor, University of Florida, Range Cattle Research and Education Center, Wildlife Ecology and Conservation, Ona, FL, 33865, USA*
[g] *Professor, Department of Animal and Range Sciences, New Mexico State University, Las Cruces, NM, 88003, USA*
[h] *Postdoctoral Research Associate, Archbold Biological Station, Venus, FL, 33960, USA*
[i] *Supervisory Research Rangeland Management Specialist, US Department of Agriculture–Agricultural Research Service, Rangeland Resources and Systems Research Unit, Cheyenne, WY, 82009, USA*
[j] *Research Animal Scientist, US Department of Agriculture–Agricultural Research Services, Range Management Research Unit, Las Cruces, NM, 88003, USA*
[k] *Biometrician, Eagle Environmental, Inc., Santa Fe, NM, 87508, USA*

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Livestock distribution in extensive rangelands of North America can present management challenges to land managers. Understanding the role of topography on livestock distribution, within and across diverse rangeland ecosystems, could provide land managers valuable information for adaptive management of livestock to address both conservation and production goals from these ecosystems. Here, we examine the influence of topography on grazing distribution unevenness and intensity of use of beef cattle in seven rangeland ecosystems spanning arid, semiarid, and subtropical environments. We focused on grazing distribution during the late growing season (summer and autumn) periods when topographic variation in rangelands is more coupled to low and nonuniform availability of high-quality forage. Pasture size and water sources strongly influence grazing distribution across ecosystems. High unevenness of grazing occurred in pastures with extensive distances to water, low stock density, and more rugged topography. Conversely, more uniform grazing distribution occurred in smaller, well-watered pastures that support higher stock density (animals per unit area) and gentler terrain. Comparison of two topographic indices, topographic wetness index and topographic position class index, in terms of their ability to predict cattle grazing distribution, revealed that categorical topographic position classes were more effective. For most arid and semiarid rangelands, livestock grazing distributions showed affinities for lowlands and flat plains compared with open slopes and uplands. In contrast to drier rangelands, livestock grazing distributions exhibited preference for upland and sloped areas of subtropical pastures, as low-lying areas with water-inundation likely curtailed selection. Across these diverse rangeland ecosystems of North America, results provide benchmark information on livestock grazing distribution to formulate improvements in adaptive management and decision making and incorporate technological advancements in precision livestock management to integrate abiotic environmental information with spatial movements of livestock and temporal vegetation dynamics.

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* Correspondence: E.J. Raynor, USDA–ARS, Rangeland Resources and Systems Research Unit, Fort Collins, CO 80526, USA.
E-mail addresses: edward.raynor@usda.gov, edwardraynor@gmail.com (E.J. Raynor).

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Introduction

Livestock grazing distribution is driven by spatial patterns of resources that are both abiotic and biotic (Senft et al. 1985; Senft et al. 1987; Coughenour 1991) with primary abiotic factors including topography and distance to water (Howery et al. 1998; Bailey 2005; Bailey et al. 2015). Quantifying spatial heterogeneity is a central focus of landscape ecology (Turner 2005) with abiotic heterogeneity valuable for cross-site comparisons, as abiotic factors (e.g., slope, elevation) are stable across time (Bolliger et al. 2007). Abiotic factors such as topography also influence biotic variables including plant species composition (Abrams and Hulbert 1987; Milchunas et al. 1989; Schacht et al. 2000; Schmitz et al. 2002), plant production (Nippert et al. 2011; Stephenson et al. 2019), and forage nitrogen content (Risser 1988; Hook and Burke 2000; Ling et al. 2019), which may confound using only abiotic factors to model livestock grazing distribution. However, developing models with abiotic variables to identify foundational drivers of livestock grazing distribution provides options to evaluate grazing pressure variability across a landscape when biotic variables are not clearly measured or known and increases capacity to expand efforts with more complex models that add biotic variables. Cross-site efforts advance our understanding of grazing distributions across broad spatial and abiotic inferences (Wisdom et al. 2020).

Topography strongly influences livestock grazing distribution in rugged terrain, where areas of steeper slopes in areas distant from water are often underutilized (Mueggler 1965; Ganskopp and Vavra 1987; Bailey et al. 2015). However, less is known about the role of topography in more gently undulating terrain that characterizes many rangeland ecosystems of North America. Although studies of livestock grazing distribution have included slope and elevation in cattle distribution models (Bailey et al. 1996; Clark et al. 2014; Clark et al. 2016), the resulting model coefficients are specific to a given study pasture. Parameters such as slope can also be misleading. For example, a ridgeline and drainage may have the same slope but are clearly very different in their topographic position. Therefore, modeling efforts that use explanatory indices quantifying the landscape in more interpretable terms can potentially yield an increased understanding of grazing distribution (Wisdom et al. 2020). Two common indices are topographic wetness index (TWI) and topographic position classes (TPC). These indices can be calculated from readily available digital elevation models (Weiss 2001; Sorensen et al. 2006; De Reu et al. 2013). TWI quantifies topographic influences on hydrology and is a function of both the slope at a given point and the size of the upstream area potentially contributing to flow at that point (Beven and Kirkby 1979). TPC is a classification scheme developed by Weiss (2001), where the topographic position index (TPI) at two different neighborhood scales is used in conjunction with the slope to classify a landscape into topographic position classes.

Both TWI and TPC were used by Gersie et al. (2019) to model livestock grazing distribution during the growing season in the shortgrass steppe region of Colorado based on Global Positioning System (GPS) collar data collected from yearling steers. When used in combination with distance to fences and water sources, both indices were effective in predicting grazing distribution across the growing season, although TPC generally yielded more parsimonious models across diverse pastures (Gersie et al. 2019). Both indices predicted more variation in grazing distribution during the second half of the growing season when vegetation quality and quantity were more heterogeneous across the landscape due to variation in soil moisture availability and the rate of plant maturation and senescence. When adequate soil moisture is available for plant growth, grazers will seek these locations (i.e., low-lying wet areas vs. steep dry areas) and revisit them as long as plant nutritive value meets or exceeds their nutritional requirements (Ganskopp and Bohnert 2009).

Here, we examine the ability of TWI and TPC topographic indices to model variation in livestock grazing distribution across a diverse set of rangeland ecosystems in North America from humid environments of southern Florida to desert environments of southern New Mexico (from 1 325 to 217 mm of annual precipitation, respectively). None of the ecosystems contain mountainous terrain. We examined grazing distribution after the vegetation in each ecosystem had reached peak biomass and was senescing. We hypothesized that 1) high unevenness in grazing distribution would be associated with extensive pasture size and single water source availability, while evenness in grazing distribution would be observed in small, well-watered pastures; 2) low-lying, level areas across the rangeland ecosystems would exhibit higher levels of livestock grazing use due to accessible forage with little concomitant energy expenditure compared with locations with greater topographic relief (Dailey and Hobbs 1989; Bailey et al. 2001), and 3) TPC would produce more parsimonious models compared with TWI across the rangeland ecosystems (Gersie et al. 2019). This third hypothesis addresses the formulation of improvements in adaptive management and decision making for livestock grazing distribution that could incorporate technological advancements in precision livestock management overlain on precision abiotic environmental information for spatiotemporal synergies between livestock and vegetation dynamics.

Methods

Study Area

We evaluated the effects of TWI and TPC on cattle spatial behavior using resource selection probability functions (RSPF; Manly et al. 2002) and GPS collar tracking devices from seven different study sites distributed across the continental United States (Fig. 1, Table 1). These study sites contained a range of topographic diversity, but none were located in extremely rugged terrain (Table A.1). These sites also varied dramatically in annual precipitation (217−1 362 mm), vegetation types, pasture sizes (16−1 601 ha), and stocking densities (0.007−1.092 animals • ha^{-1}). As such, this variability represents an excellent opportunity to test robustness of RSPF models for TWI and TPC, but this comes at the cost of needing to control for confounding effects of pasture size and stocking density. At three sites, we studied a single pasture; at the remaining four sites, we studied multiple pastures ($n = 2-4$). Below, we describe each study site in turn, as ordered by increasing mean annual precipitation. Vegetation characteristics of each study site are described in supplemental data.

The Jornada Experimental Range (JER) encompasses northern Chihuahuan desert grasslands and shrublands owned and operated by the US Department of Agriculture (USDA)−Agricultural Research Service (ARS) in southern New Mexico (32°37′N, 106°45′W) (see Fig. 1). JER is a Long-Term Agroecosystem Research (LTAR) network site. Mean annual precipitation (1918−2008) is 217 mm (Spiegal et al. 2019). A single 1 535-ha pasture (Red Lake) varying in elevation from 1 315 to 1 342 m above sea level (asl; see Table 1) was used in this study. Within this pasture, five rain-fed, earthen tanks (i.e., dugouts) and two permanently filled water tanks were available to cattle in the study period (Spiegal et al. 2019).

The Central Plains Experimental Range (CPER) encompasses semiarid shortgrass steppe owned and operated by the USDA-ARS in northeastern Colorado (40°49′N, 104°46′W). CPER is a LTAR network site. We studied the same three pastures used by Gersie et al. (2019) that ranged in size from 130 to 152 ha with an elevation range from 1 597 to 1 690 m asl (see Table 1). Mean annual

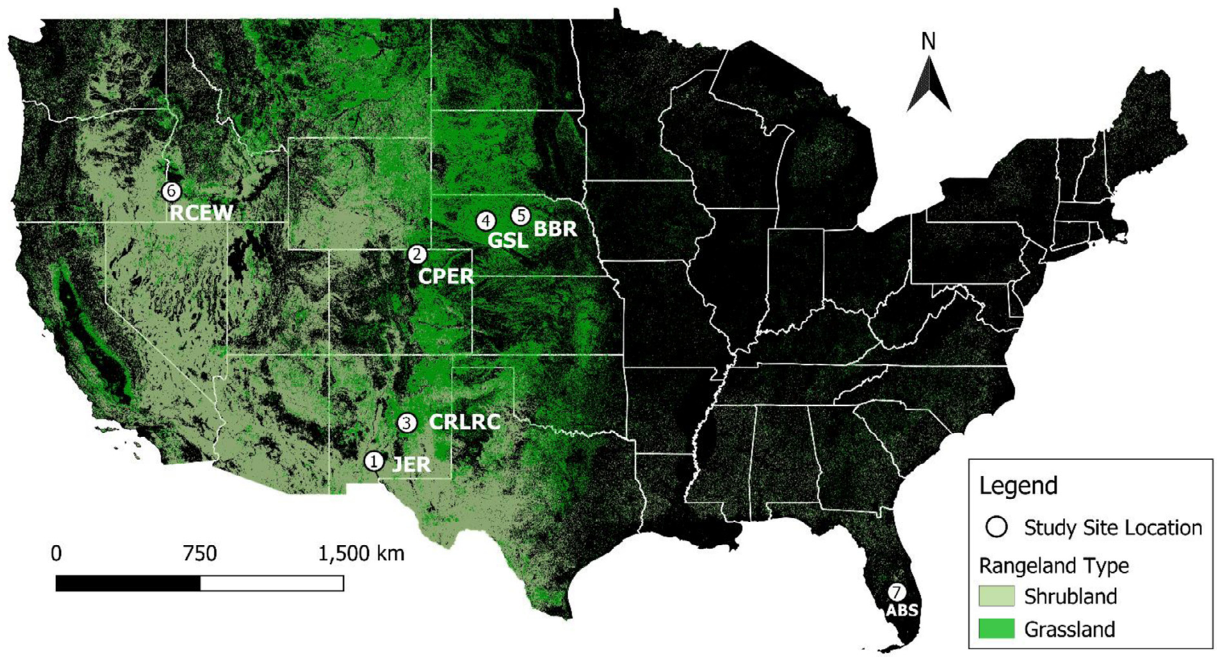

Fig. 1. Map of study locations and rangelands across the conterminous United States. 1) JER = Jornada Experimental Range, New Mexico, 2) CPER = Central Plains Experimental Range, Colorado, 3), CRLRC = Corona Range and Livestock Research Center, New Mexico, 4) GSL = Gudmendsen Sandhills Laboratory, Nebraska, 5) BBR = Barta Brothers Ranch, Nebraska, 6) RCEW = Reynolds Creek Experimental Watershed, Idaho, 7) ABS = Archbold Biological Station, Florida. Depiction of rangeland types was modified from Homer et al. (2012). Sites are numbered from lowest to highest annual precipitation.

Table 1
Topographic and environmental characteristics of pastures for each study location.

Site	Pasture	Area (ha)	TWI (mean, range)	Elevation, m (mean ± SD)	Slope, degrees(mean ± SD)	Distance to water, m(mean ± SD)
Jornada Experimental Range (JER)	Red Lake	1 535[1]	9.62 (4.71-25.36)	1 324 (7)	0.6 (0.5)	934 (513)
Central Plains Experimental Range (CPER)	5E	130	6.80 (2.09-14.78)	1 651 (5)	1.9 (1.9)	941 (407)
	24W	130	6.17 (3.47-12.30)	1 645 (7)	2.3 (1.2)	573 (234)
	31E	152	5.78 (2.78-15.75)	1 625 (9)	3.0 (1.5)	671 (267)
Corona Range and Livestock Research Center (CRLRC)	East Johnson	1 601	8.04 (3.60-21.02)	1 783 (20)	2.3 (1.5)	2346 (956)
Gudmundsen Sandhills Laboratory (GSL)	East Cow	260	5.99 (2.65-16.11)	1 076 (16)	6.6 (4.2)	645 (294)
	Heifer	463	5.88 (2.57-16.11)	1 080 (14)	6.45 (4.1)	760 (339)
Barta Brothers Ranch (BBR)	N1	65	6.11 (3.29-14.38)	791 (6)	5.4 (3.5)	354 (169)
	N6	60	7.29 (3.59-20.78)	780 (3)	3.4 (2.8)	285 (107)
	S3	51	6.03 (2.97-14.46)	779 (5)	5.7 (3.4)	277 (109)
	W4	47	6.83 (3.40-15.66)	787 (3)	4.4 (2.9)	270 (106)
Reynolds Creek Experimental Watershed (RCEW)	Breaks	176	6.57 (3.00-17.00)	1 567 (53)	10.5 (5.5)	185 (127)
Archbold Biological Station (ABS)	B	16	4.99 (2.72-12.68)	9 (0.2)	1.5 (2.6)	301 (116)
	G	16	4.92 (2.35-12.66)	9 (0.3)	1.4 (1.9)	317 (149)
	K	16	4.59 (2.25-10.91)	8 (0.1)	1.7 (2.1)	304 (152)

TWI indicates topographic wetness index; SD, standard deviation.
[1] 1 028 ha = final area of analyses.

precipitation (1939–2018) is 340 mm. Each pasture contained a single permanently filled water tank.

The Corona Range and Livestock Research Center (CRLRC) consists of semiarid shortgrass rangeland located in central New Mexico (34°15′N, 105°24′W). The study site is managed by New Mexico State University. Mean annual precipitation (1914–2006) is 370 mm, and elevation varies from 1 736 to 1 836 m asl. We studied the East Johnson pasture, which is 1 601 ha in size and encompasses undulating plains. A single drinking water source was available near the southwestern section of the pasture.

The Gudmundsen Sandhills Laboratory (GSL) is located in the western Nebraska Sandhills (42°07′N, 101°43′W) and is owned and operated by the University of Nebraska–Lincoln. Mean annual precipitation (1987–2002) is 468 mm, with elevation varying from 1 050 to 1 126 m asl. The terrain consists of large rolling grass-covered sand dunes with narrower interdunal valleys and flat

Table 2
Cattle attributes, stocking information, number of GPS collar datasets, and study period for each study location. Stocking density is based on mature cows per hectare. Full site names are listed in Table 1.

Site	Pasture name	Individuals per pasture	Stocking density (animals • ha^{-1})	GPS-collared individuals	GPS fix interval (min)	Study period	Physiological status	Breed
JER	Red Lake	11	0.007	6	5	12/4-12/15/2008	Mature cow, nonlactating	Angus × Hereford
CPER	5E, 24W, 31E	20-24	0.154-0.157	2	5	7/20-10/2/2014, 7/20-9/30/2016	Yearling steers	Angus cross
CRLRC	East Johnson	120-140	0.074-0.087	12-16	10	5/7–7/19/2010, 6/28-8/17/2012	Mature cow, lactating	Angus cross
GSL	East Cow	20	0.077	4	10	7/21-10/21/2015	Mature cow, lactating	Red Angus, Gelbvieh, and Simmental cross
GSL	Heifer	109	0.235	10	10	7/20-10/30/2015	Mature cow, lactating	Red Angus, Gelbvieh, and Simmental cross
BBR	N1, N6, S3, W4	45-71	0.950-1.092	3-5	10	7/22-9/6/2016, 7/18-8/31/2017	Mature cow, lactating	Black Angus
RCEW	Breaks	14	0.079	8	10	6/27-7/9/2001, 7/9-24/2002	Mature cow, lactating	Hereford, Angus, and Charolais cross
ABS	B, G, K	15	0.909-0.930	2-6	5	6/1-9/9/2017	Mature cow, lactating	Brahman, Angus, Hereford, and Cracker cross

GPS indicates Global Positioning System; JER, Jornada Experimental Range; CPER, Central Plains Experimental Range; CRLRC, Corona Range and Livestock Research Center; GSL, Gudmendsen Sandhills Laboratory; BBR, Barta Brothers Ranch; RCEW, Reynolds Creek Experimental Watershed; ABS, Archbold Biological Station.

plains. Here we studied the East Cow and Heifer pastures, which are 260 and 463 ha in size, respectively. Drinking water was available in two permanently filled water tanks in each pasture.

The Barta Brothers Ranch (BBR) is located in central Nebraska (42°14′N, 99°39′W) and is managed by the University of Nebraska—Lincoln. Mean annual precipitation (1960—2000) at the site is 576 mm. We studied four pastures that ranged in size from 47 to 64 ha with elevation varying from 770 to 815 m asl. The site consists of grass-covered dunes covered in a mix of warm- and cool-season grasses with scattered lowlands and subirrigated wetlands. A single drinking water source was available near the center of each pasture.

Reynolds Creek Experimental Watershed (RCEW) is a shrub-steppe site in the Great Basin rangelands of southwestern Idaho (43°6′N, 116°46′W). The RCEW is a LTAR network site. We studied one 176-ha pasture where the long-term mean annual precipitation (1965–1975, 2002–2014) is 588 mm (USDA-ARS Northwest Watershed Research Center 2017). Elevation varies from 1 461 to 1 667 m asl (Clark et al. 2018). The Breaks pasture encompasses the mid and lower slopes and narrow stream terraces, as well as riparian areas occurring on or near an east-facing hillslope. Cattle had access to three upland surface water sources and a perennial stream, Reynolds Creek.

The most mesic environment was the Buck Island Ranch, a division of Archbold Biological Station (ABS) in south-central Florida (27°10′N 81°21′W) and a LTAR network site. Mean annual precipitation (1932—2018) is 1 362 mm. The three ABS pastures (~16 ha) studied here are low lying with a mean pasture elevation of 9 m asl (range: 5—16 m asl). Drinking water was available in a permanently filled water tank in each pasture.

GPS Data

Study pastures were grazed for different time periods and with different numbers of cattle across sites (Table 2). For our analyses, we selected periods in the latter half of the grazing season when vegetation was largely senescing (i.e., the Drydown; Spiegal et al. 2019). We used GPS collars (e.g., Lotek 3300LR collars; Lotek Engineering, Newmarket, ON, Canada; Catlog-Gen 2, Perthold Engineering, LLC, USA) to measure cattle distribution. Each collar recorded positions at 5-min or 10-min intervals, depending on the study site (see Table 2). Study sites also varied on the number of cattle that were wearing collars. Collars at CPER 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 had previously been 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). As activity sensor data were not available for the other study sites, grazing locations were classified using a velocity-based method as follows. First, all positions 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 were removed, as these are heavily trampled areas with minimal available forage, so actual grazing here is improbable. Next, the remaining positions were classified as grazing when animal velocity was between 5 m and 105 m per 5 min^{-1}. We validated the efficacy of this velocity-threshold approach using data acquired in 2014 at the CPER using 10 GPS collars, which included the same activity sensors as those described by Augustine and Derner (2013). Data were classified into grazing and nongrazing behaviors according to the sensor and ground-truth methods described by these authors. This classification result was used as a standard to which to compare results derived using the velocity-threshold approach on the same data. About a mean of 35.8% (33.2—38.4 95% CI) of all GPS positions were classified as grazing using the methods of Augustine and Derner (2013), whereas 46.9% (45.4—48.4 95% CI) of all positions were classified as grazing using the velocity method. This contrast suggests that while the velocity method tended to misclassify in favor of grazing behavior, it still provided a reasonable estimate of where and when cattle are grazing each day. Additional site information on cattle herds and GPS collar deployment is available in Table 2.

Topographic Indices

We calculated topographic indices using a 10-m resolution because DEMs of this resolution are now widely available (e.g., entire North American continent). The topographic wetness index (TWI) for each 10-m pixel was calculated using the TauDEM extension

Table 3
Description of topographic classes used for modeling variation in grazing distribution. Modified from Gersie et al. (2019).

Topographic position class	TPI 50	TPI 500	Slope	TPI description	Example	Weisslandform
Lowlands	≤ −0.8	≤ −0.8	NA	Locally low, broadly low	Incised stream channel or canyon	3
Lowlands	−0.8 < × < 1.2	≤ −0.8	NA	Locally even, broadly low	Floodplain near channel; playa basin	2
Lowlands	≤ −0.8	−0.8 < × < 1.2	NA	Locally low, broadly even	Shallow valley	1
Flat plains	−0.8 < × < 1.2	−0.8 < × < 1.2	≤ 2	Locally even, broadly even, flat	Flat plains	5
Open slopes	−0.8 < × < 1.2	−0.8 < × < 1.2	≥ 2	Locally even, broadly even, sloped	No elevation extremes, sloped	6
Uplands	≥ 1.2	−0.8 < × < 1.2	NA	Locally high, broadly even	Ridge on hillside	8
Uplands	−0.8 < × < 1.2	≥ 1.2	NA	Locally even, broadly high	Slope on hillside	9
Uplands	≥ 1.2	≥ 1.2	NA	Locally high, broadly high	Hilltop, highest point in area	10
Lowlands	≥ 1.2	≤ −0.8	NA	Locally high, broadly low	Hill in valley, ridge in lowland	7
Uplands	≤ −0.8	≥ 1.2	NA	Locally low, broadly high	Drainage in hillside	4

TPI indicates topographic position index.

for ArcGIS (Tarboton 2005). TWI, which combines local upslope contributing area and slope, is commonly used to quantify topographic control on hydrological processes (Sorensen et al. 2006). Topographical wetness has also been found to be an important factor affecting ungulate movement and resource selection decisions (Augustine and Derner 2014; Monteith et al. 2018). We calculated the Topographic Position Index (TPI) for each pixel based on 1) a neighborhood radius of 50 m (TPI50) and 2) a neighborhood radius of 500 m (TPI500), which were generated using the Land Facet Corridor Designer extension developed by Jenness et al. (2013) for ArcGIS (v1.2.884; www.CorridorDesign.org). Next, we standardized each TPI raster by subtracting the mean, dividing by the standard deviation, and rounding up to a whole number (Weiss 2001).

Next, we used TPI50 and TPI500 in combination with the slope of each pixel to classify study site landscapes into four TPC or topographic position classes (see Table A.1). Weiss (2001) considered TPI values 1 standard deviation below the mean as low topographic features and TPI values 1 standard deviation above the mean as high topographic features. Weiss's method was designed for a region with rugged terrain, including mountaintops, which are absent from these study sites. Consequently, we adjusted the thresholds to 0.8 standard deviations and 1.2 standard deviations, respectively, to provide index calculations more appropriate for our study sites (Gersie et al. 2019). This shift in thresholds accentuates differences in low-lying topographic features and limits the over-classification of upper topographic features.

We implemented classification for each pasture using the *raster* package (Hijmans et al. 2019) in R Studio (R Development Core Team 2020). See Table 3 for a description of the topographic position classification scheme. To use TWI and TPC in models of cattle grazing distribution within each pasture at each site, we resampled each 10-m resolution TWI and TPC map to a 25-m resolution (see explanation for selection of this spatial resolution under *Resource Selection Probability Analysis* subsection for further details). We used the nearest neighbor method in the ArcGIS Spatial Analyst resampling tool (ArcGIS v10.6.1; ESRI 2018) in our raster resampling procedure. Graphical examples of pasture-level TPC are available in Fig. 2.

Distance to Fence and Water

A 25-m resolution cell grid was first clipped to the boundaries of each study pasture. For each cell, the distance to surface water and distance to fencing (in meters) was calculated using the Euclidian distance tool in the ArcGIS spatial analyst toolbox (ArcGIS v10.6.1; ESRI 2018). To account for the tendency of beef cattle to travel and graze along fence lines (e.g., Augustine and Derner 2013), all pixels > 30 m from fences were set to a value of 30, thereby allowing us to model the influence of fences at a local (0–30 m) spatial scale. An exception was fence corners; fence corner pixels were removed if they were within 50 m of the corner or 100 m if the corner had a surface water source. Similarly, all pixels > 300 m from surface water sources were set to a value of 300, permitting us to model the local (75−300 m) influence of water on cattle behavior and clarifying our analysis focus on the influence of topography at larger scales (Augustine and Derner 2014). At JER and CRLRC, following the approach of Bailey et al. (2015) for the extensive pastures (> 1 000 ha), we doubled the buffer distance from a water source to 150 m as palatable vegetation is not available within this distance to water. Here, we also set all pixels > 600 m to water to a value of 600, allowing us to model the local (150−600 m) effect of water on grazing distribution at these comparatively, more extensive pastures. At the Breaks pasture at RCEW, we removed GPS locations within 12.5 m of each side of Reynolds Creek from our analysis to eliminate potential nongrazing locations likely associated with individuals drinking water.

Measures of Grazing Distribution Unevenness

Before evaluating unevenness of grazing distribution per pasture, a measure of relative grazing positions per pixel was calculated. Relative grazing positions per pixel is based on the actual number of grazing positions per pixel but relativized to be the number of grazing positions that would occur in that pixel if one distributed 1 000 positions across the pasture in the pattern shown by the actual data (Gersie et al. 2019). We employed three probability distribution-based metrics—coefficient of variation (CV), skewness, and excess skewness—for quantifying the magnitude of pasture-level unevenness of grazing distribution based on the relative number of grazing positions per pixel. The coefficient of variation shows how large the standard deviation of grazing positions per pixel is relative to the mean number of grazing positions per pixel. Skewness was used to describe the level of symmetry in grazing distribution within pastures based on the relative grazing positions per pixel. Our interpretation of a skewness value of 0, which follows Bulmer (1979), equates to a perfectly symmetric

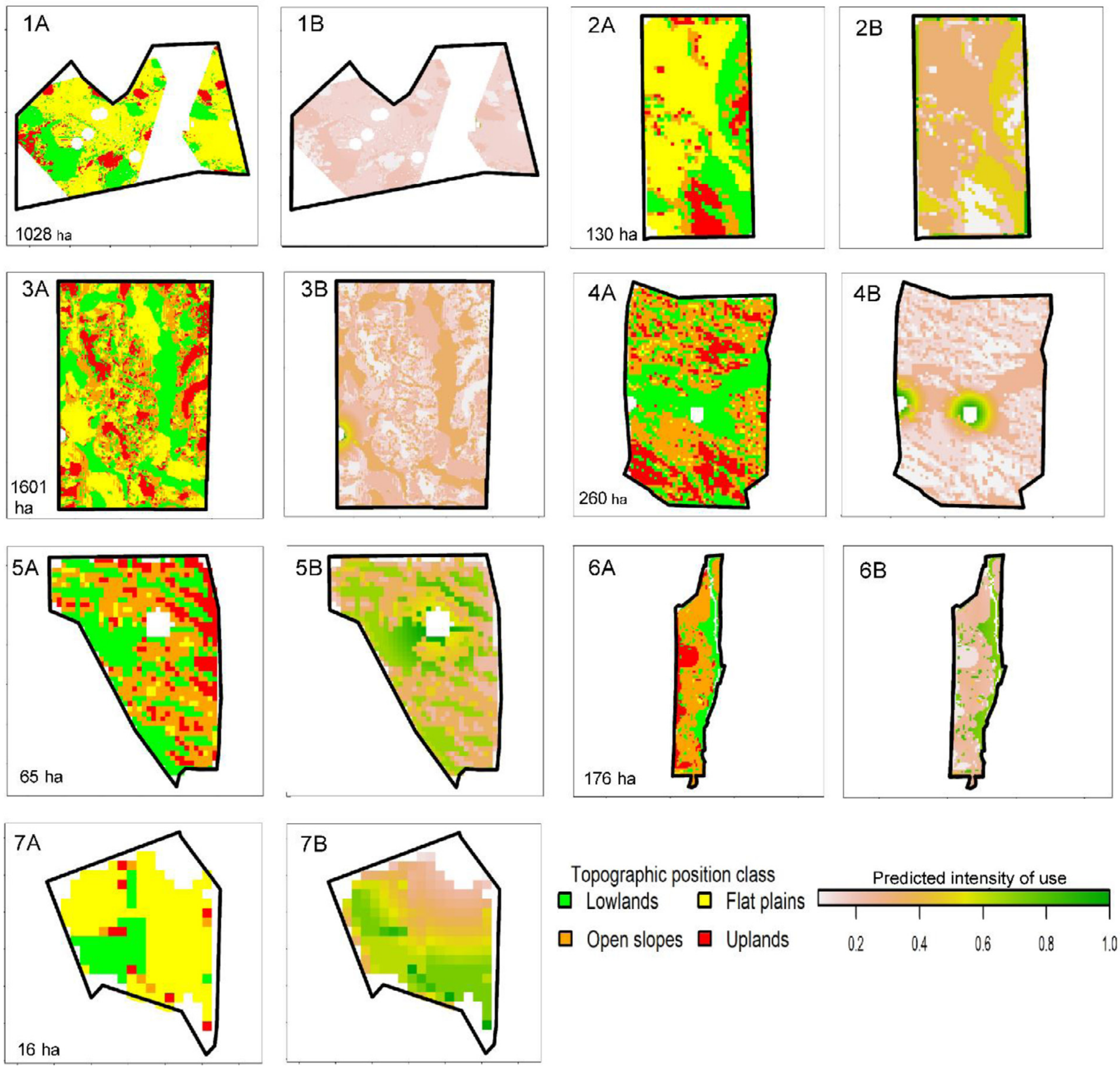

Fig. 2. Panels depicting four class topographic position class index (**A**) and resulting predicted intensity of use (**B**) for 1) Red Lake pasture at Jornada Experimental Range, New Mexico, 2) Pasture 5E at Central Plains Experimental Range, Colorado, 3) East Johnson pasture at Corona Range and Livestock Research Center, New Mexico, 4) East Cow pasture at Gudmundsen Sandhills Laboratory, Nebraska, 5) Pasture N1 at Barta Brothers Ranch, Nebraska, 6) Breaks pasture at Reynolds Creek Experimental Watershed, Idaho, and 7) G pasture at Archbold Biological Station, Florida. White pixels represent pixels removed from analyses due to bias from fence and water. Sites are ordered from panels 1 to 7 from lowest to highest mean annual precipitation.

distribution of grazing positions per pasture or that grazing intensity was uniform across a pasture. Skewness is based on the third moment about the mean and was computed following Groeneveld and Meeden (1984). Finally, we calculated excess kurtosis to illustrate the amount of probability occurring in the tails of the pasture-level grazing intensity distribution. Excess kurtosis is based on the fourth moment about the mean and was computed following Pearson (1916). A kurtosis value of 0 equates to a normal distribution. In contrast, larger values indicate increasing levels of magnitude of outliers in the data set. At each site, we calculated the mean and 95% confidence interval of each of three metrics using data pooled from all animal replicates across pastures and years.

Resource Selection Probability Function Analysis

Following the approach of Augustine and Derner (2014) for modeling livestock distribution, we overlaid grazing positions for each collared animal onto the 25-m resolution multiband grid described earlier. We calculated the number of grazing locations per pixel for each GPS collared cow or steer. For each individual animal-pasture-year analysis, we fit generalized linear models (GLMs) predicting the number of cattle grazing positions per pixel (625 m^2) as a function of the predictor variables TWI, TPC, distance to water sources, and/or distance to the fences. The probability of cattle use was modeled as a continuous, count-based response variable in the GLM, which was parameterized using the *"glm.nb"* function in the "MASS" package in program R (Ripley et al. 2020). 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):

$$\ln(E[l_i/\text{total}]) = \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p \quad (1)$$

where, l_i is the number of GPS locations within sampling pixel i ($i = 1, 2, \ldots, n$), n is the number of pixels in study pasture, the total is the total number of GPS locations within the pasture study area, βo is an intercept term, β1, …, βp are unknown coefficients for the predictor variables X_1, ..., X_p, and E[*li*/total] represents the expected value.

Models that included topographic position class (TPC) as a predictor variable used "Flat Plains" as the reference class and coefficients for the other topographic position classes represent effect sizes relative to that of the "Flat Plains" class. Separate models were fit for each collared individual within each pasture. Model predictions were then calculated for grazing distribution as a function of TWI or TPC, given mean values for distance to fence and water source, and these model predictions were applied to each pixel of the study pastures. For all analyses, 25-m pixels were used to subdivide pastures because this resolution resulted in a distribution of grazing positions per pixel that approximated a negative binomial distribution, which allows the use of the modeling approach of Nielson and Sawyer (2013). Smaller cell sizes would increase the probability that a given cell contained no grazing positions, resulting in a zero-inflated distribution. The offset term converts 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 (RSPF; Manly et al. 2002). To validate RSPF models, we conducted k-fold cross-validation with 10 partitions to estimate the mean square error (MSE) of the predicted intensity of use with the "cv.glm" function in the *"boot"* package in program R (Canty and Ripley 2020). Relative frequencies are small on a per-pixel basis (typically varying from 0 to 0.002), so the relative frequencies were multiplied by 1 000 to express grazing distribution in units of the relative frequency of grazing positions per pixel per individual per 1 000 grazing positions (typically varying from 0 to 2.0) when reporting or presenting model predictions.

The herd at Red Lake (JER) in New Mexico predominantly grazed the western and eastern portions of this large pasture (1 535 ha), and grazing positions did not occur in the midsection. In this study, our goal was to predict grazing distribution within the area accessed by the cattle for grazing; therefore, we created separate home ranges for each grazed section of the pasture. Next, we aggregated the two resulting polygons (outcome: 1 028 ha; Fig. 2) and confined our subsequent analyses to these utilized portions of the pasture while controlling for the localized effect of water sources and fence lines on cattle grazing distribution. To estimate herd home range, we estimated a 95% fixed kernel home range with the plug-in estimator to determine bandwidth (Sheather and Jones 1991) using the package *"adehabitatHR"* in R (Calenge and Fortmann-Roe 2013; R Development Core Team 2020) and the herd's GPS collar data. For all other study locations, herds clearly accessed all portions of the pasture, and we, therefore, used the pasture fence lines to define the home range.

We used Akaike's Information Criterion (Akaike 1998) to evaluate whether RSPF models based on either TWI or TPC were more parsimonious or simpler in predicting topographic variation in grazing distribution for each individual animal-pasture-year data set ($n = 122$). We then used the topographic index that was most parsimonious in the majority of these models to predict grazing positions per pixel for each of the 122 data sets. Next, we calculated a selection ratio for each dataset, treating the animal as the primary sampling unit within each pasture or year (i.e., experimental units within spatial and temporal replicates). The selection ratio was based on Manly's design II, where the *availability* of each variable of interest is available to all animals, but the *use* is measured for each one (Manly et al. 2002). Using each individual animal-pasture-year data set's RSPF, we predicted grazing positions across the landscape (i.e., cell or pixel-level predictions), which sum to 1, and then summed the pixel-level predictions within each TPC. We calculated the selection ratio for each TPC by dividing the sum of predicted grazing positions per pixel for each TPC by the proportion of the pasture in each TPC. Last, we plotted these ratios for each TPC at each site by averaging overall individual-pasture-year replicates and calculating 90% confidence intervals based on all individual-pasture-year replicates from a site.

Analytical Strategy

First, we quantified grazing distribution unevenness by 1) filtering GPS collar datasets based on animal movement rate to remove the bulk of animal locations associated with nongrazing activity, 2) mapping variation in grazing distribution during the drydown period at the scale of 25×25 m pixels, and 3) quantifying variation in terms of the relative frequency of grazing positions per unit area, coefficient of variation, skewness, and kurtosis of the resulting pixel-level values. Second, we modeled grazing distribution at this scale in relation to TWI and TPC. Third, to determine herd affinity for different topographic positions, we calculated selection ratios for each TPC at each site using predicted grazing positions. Specifically, model coefficients from the 4-class TPC model for each individual-pasture-year data set were used to create a RSPF and subsequent selection ratios of the proportion of predicted grazing positions (use) of a TPC relative to its area (availability) within a pasture.

Results

Grazing Distribution Unevenness

Characteristics of the distribution of cattle grazing locations per pixel (625 m^2) across pastures at our seven rangeland study sites are presented in Fig. 3. The mean relative frequency of grazing positions per pixel (625 m^2) ranged from 0.04 ± 0.07 (mean ± SD) at CRLRC in New Mexico to a high of 4.51 ± 3.79 grazing positions per pixel at ABS in Florida. Relative to the mean, the standard deviation of relative frequency of grazing positions was greatest at JER-Red Lake playa pasture (CV: 308.76) and lowest at BBR pastures in Nebraska (59.9 ± 5.4 averaged over 2 yr; see Fig. 3). Based on skewness, grazing distribution in the Breaks pasture at RCEW in Idaho was the most uneven at 10.4 (16.4) (mean ± SD), and cattle at BBR exhibited the most even grazing distribution with a skewness of 1.4 (0.3). Kurtosis of relative grazing positions per pixel within pastures was nearest to a normal distribution in BBR pastures and farthest from a normal distribution in the Breaks pasture at RCEW.

Further evidence of evenness in grazing distribution at BBR is shown through the relationship between percent area of pasture with increasing relative frequency of grazing positions per 625 m^2 that follows a bell-shaped curve, indicating relatively even grazing distribution, whereas, at RCEW, large portions of the Breaks pasture received very low grazing frequency (e.g., 0–20% of the mean) and other portions received high grazing frequency (e.g., more than double the mean, or > 200%) (see Fig. B.1). See Figure B.1 for histograms illustrating the distribution of the relative frequency of cattle grazing locations per pixel (625 m^2) for each year and pasture at all seven rangeland sites.

Model Parsimony

Akaike information criterion (AIC) scores were used to identify the simplest of fitted models. To streamline the TPC metric, the 10 classes employed by Weiss (2001) were combined into 4 topographic position classes (see Table 3). A comparison of the resulting 4-class TPC model to the TWI model revealed that the 4-class TPC model was more parsimonious than the TWI model for 91 of the 122 datasets (75%; Fig. 4). Because we sought to model

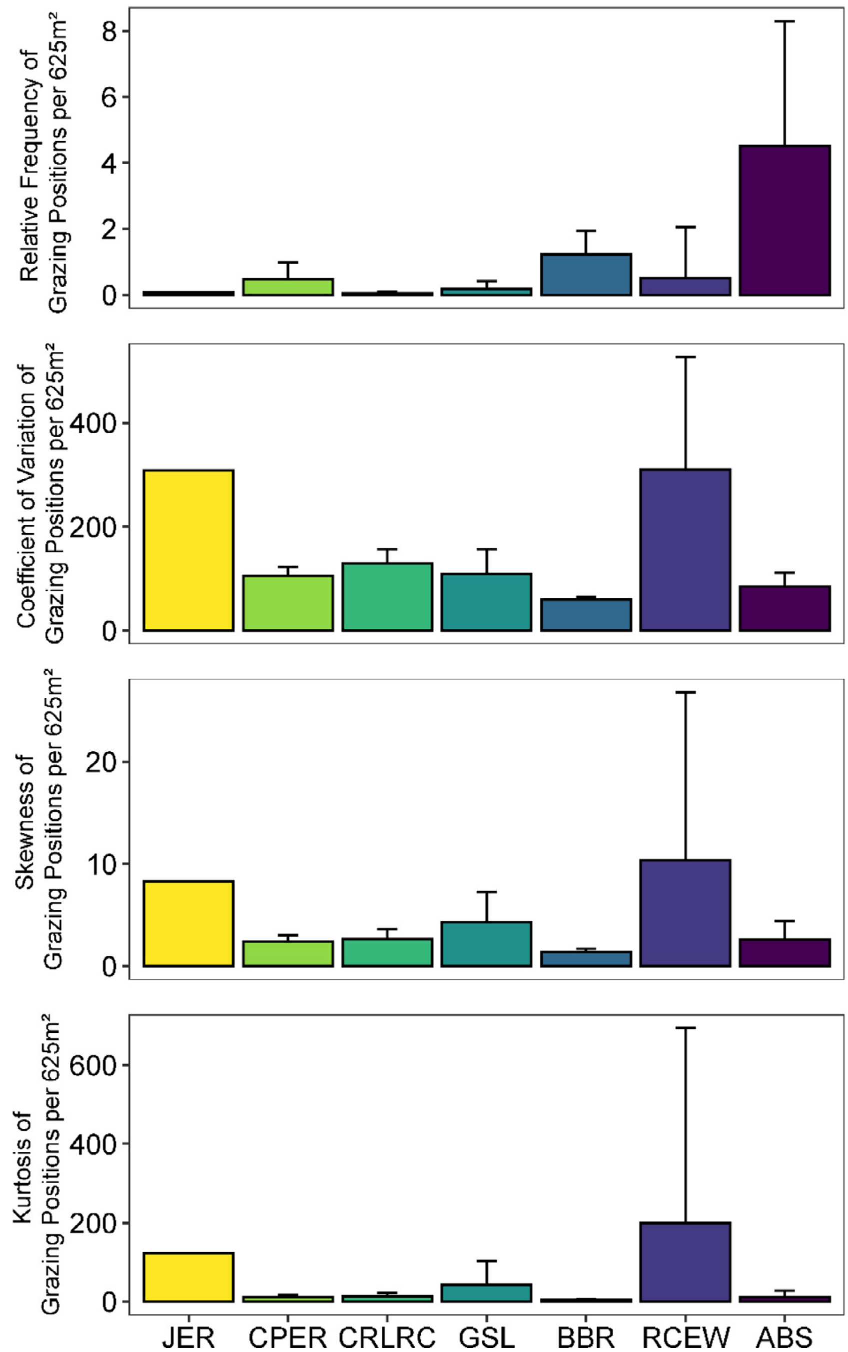

Fig. 3. Relative frequency of grazing positions per pixel (mean ± SD) and characteristics of the distribution of cattle grazing positions per pixel (625 m^2) across pastures at 7 rangeland study sites in North America. For the coefficient of variation, skewness, and kurtosis, error bars show the 95% confidence interval for the distribution characteristics based on spatial and/or temporal replicates at each study site. Values for Jornada (JER) are for one pasture in 1 yr. Note that the X-axis is oriented from lowest to highest annual precipitation.

grazing distribution relative to an abiotic driver in a simple and consistently interpretable way across sites, we chose to proceed with analyses using the TPC model coefficients for prediction at all study sites. We note there were considerable differences in the most parsimonious model predicting distribution among individual cattle at CPER and RCEW (see Fig. 4).

Predicted Grazing Intensity of Use

Models were fit for each collared animal at each study site, pasture, and year. At some sites, we observed little variability in coefficient estimates, but at other sites, coefficients for TWI varied by over 100% (Tables B.1 and B.2). Comparison of mean square error (MSE) values derived from *K*-fold cross-validation ($n = 10$ bins) for each TWI and TPC model for each individual-pasture-year data set showed TPC models had lower test error than TWI models for predicted intensity of use (mean difference of MSE ± SE: −0.73 ± 0.32; see Table B.3).

When compared across TPC, the predicted intensity of use varied with some classes being preferred, others not preferred, and some not differentiated (neither preference nor no preference). In general, the lowlands were grazed slightly more than flat plains, with more variation among datasets for flat plains. Open slopes were grazed slightly less than flat plains, and uplands were grazed

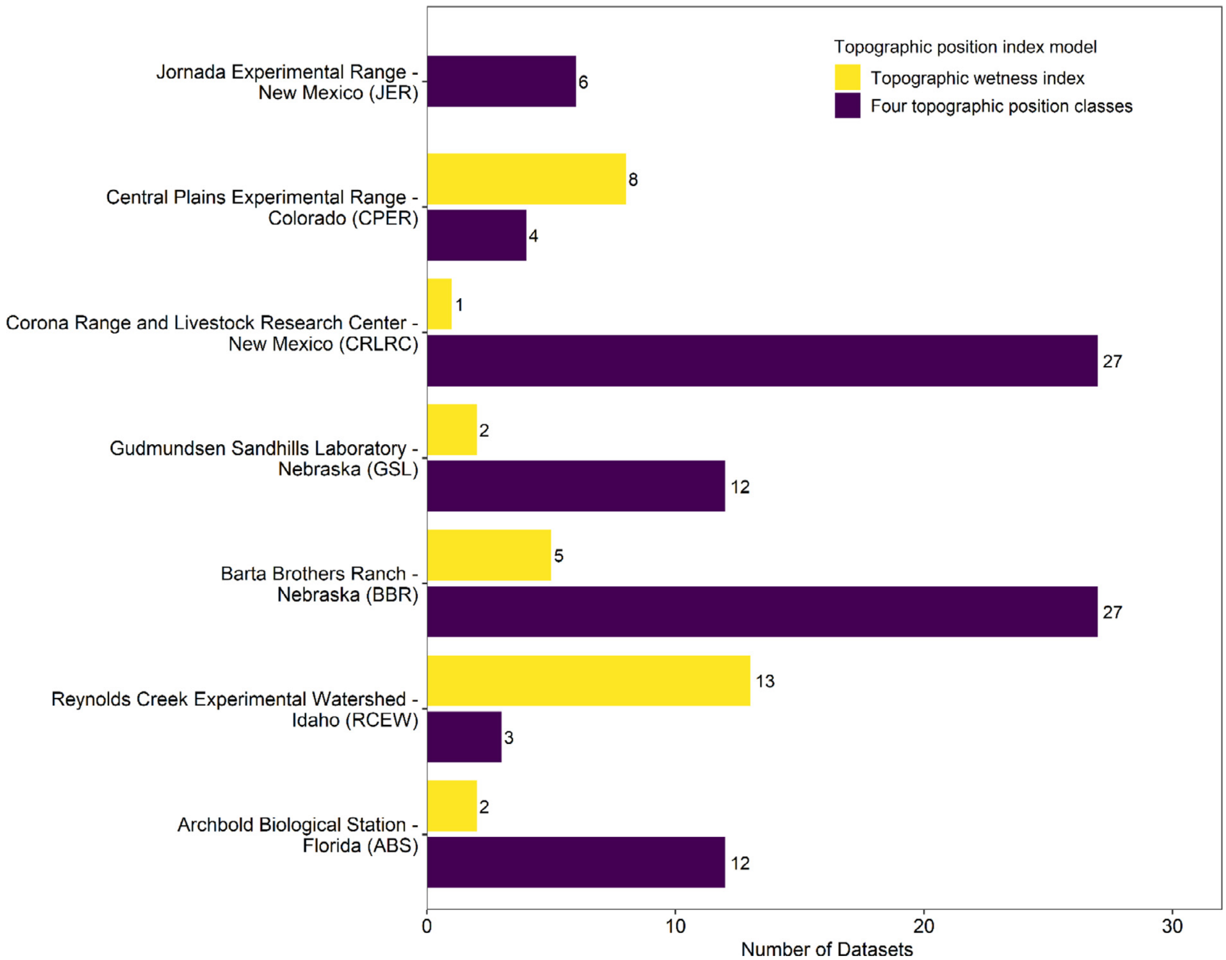

Fig. 4. Most parsimonious model (topographic wetness index or four-class topographic position class model) for each dataset at each study site. Number beside bar indicates the number of collared individuals. Model parsimony was compared using Akaike's Information Criterion (AIC); models with lowest AIC score were selected. Note that the Y-axis is oriented from lowest to highest annual precipitation.

the least at all sites with the exception of the mesic, subtropical site (ABS in Florida, Fig. 5), where that topographic position was the most preferred for grazing. Mapped examples of the pasture-level predicted intensity of use from RSPF models are shown in Fig. 6B, D.

Discussion

Understanding the degree to which livestock grazing distribution is linked to topography across a diverse set of North American rangeland ecosystems provides foundational benchmark information for land managers seeking to use other management actions to alter grazing distribution to achieve specific desired outcomes for multiple ecosystem services (e.g., soils, vegetation, livestock, wildlife habitat). Development of models predicting livestock grazing distribution based on topographic indices derived from readily available DEMs provides repeatable, consistent, and cost-effective predictions for land managers. Topographic position class maps of pastures, ranches, allotments, and rangeland landscapes could be used to guide decisions on a wide range of management actions, including modification of fencing and/or water infrastructure, prescribed patch burning (Allred et al. 2011; Augustine and Derner 2014), herding (Skovlin 1957; Bailey et al. 2008; Stephenson et al. 2017), and provision of supplements (Bohnert and Stephenson 2016). Furthermore, knowledge of the expected utilization of different topographic positions within a pasture in the absence of any management actions could enable more precise assessment of whether management is affecting grazing distribution in the desired way, regardless of whether the goal is to increase or decrease grazing intensity in specific parts of the landscape. Finally, knowledge of cattle real-time pasture use and topographic indices could be combined to inform the use of virtual fencing (Umstatter et al. 2015; Campbell et al. 2020) to manipulate grazing distribution.

Grazing Distribution Unevenness

Our analysis revealed a pattern of increasingly uneven grazing distributions as precipitation decreased from mesic environments to semiarid and arid rangeland ecosystems. Patterns of increasing unevenness from CV, kurtosis, and skewness results showcase this in a relatively consistent manner. All three grazing distribution metrics were lowest at the two sites (ABS and BBR) with small, well-watered pastures with low topographic relief and comparatively high stocking densities, indicating less preferential selection within study pastures. We note that patch-grazing (i.e., repeated use of productive swards) (Cid and Brizuela 1998) may be occurring here at scales smaller than a pixel. At CPER, where pastures are 2 × and 8 × larger than BBR and ABS, respectively, and contain more topographic relief, we documented increased CV in grazing distribution but still equivalently low skewness and kurtosis. The latter indicates all portions of the pastures received some level of use (i.e., no or few areas ungrazed), as well as a lack of intense grazing hotspots.

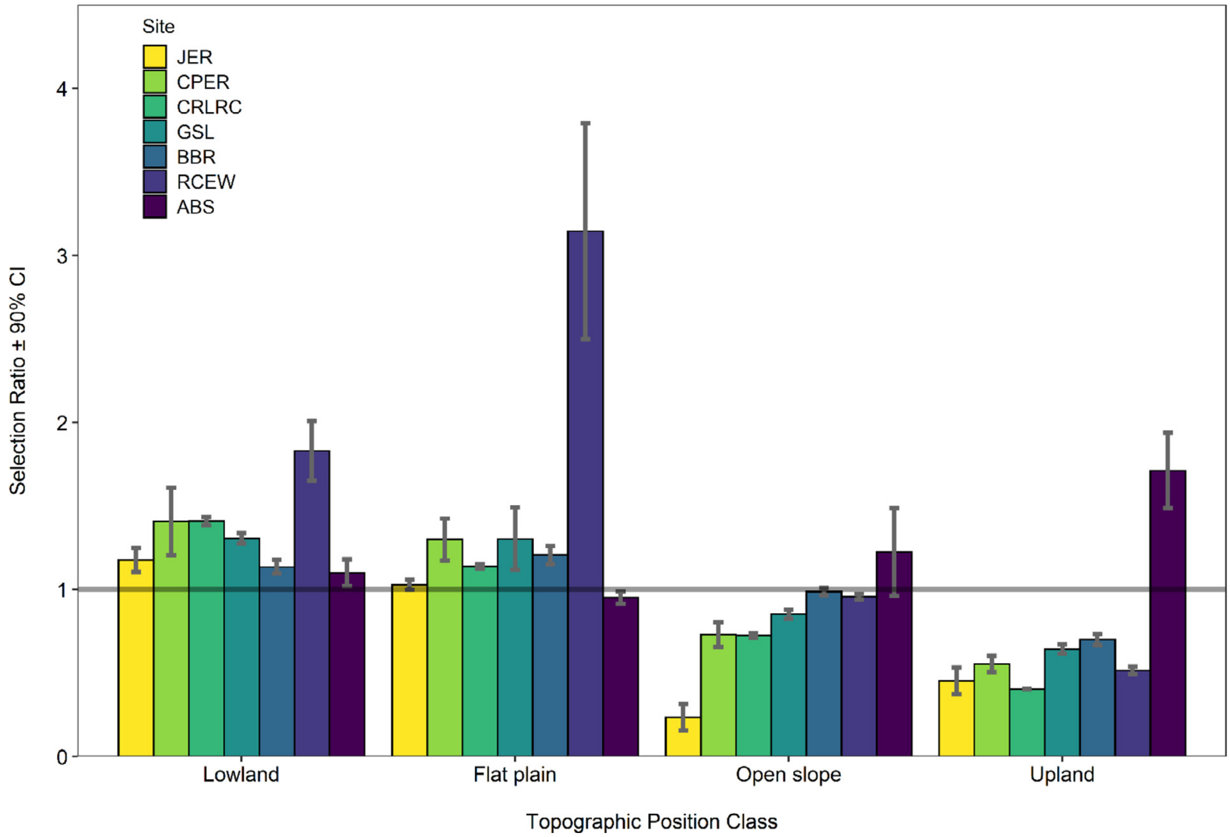

Fig. 5. Mean selection ratios for each of four topographic position classes within pastures at seven different rangeland sites in North America. Error bars show 90% confidence intervals based on variation among individual cattle across years and pasture. Note that apart from Archbold Biological Station (ABS), we found consistent avoidance of uplands and open slopes and preference for flat plains and/or lowlands across all study locations. The gray horizontal line indicates indifference (i.e., no preference or avoidance).

Interestingly, we also found a similar probability distribution of grazing intensity across the large pasture at CRLRC (> 1 600 ha) compared with the notably smaller pastures at CPER (130 ha). Both sites are characterized by shortgrass vegetation with gently undulating topography but much different distances that cattle travel from water sources, suggesting that pasture size may not have as strong an influence on grazing distribution when topographic variability is limited and the cattle are adapted (Bailey et al. 2015). Lactating cows at the CRLRC regularly traveled over 3.2 km from water during the summer, which exceeds expectations in the literature (Holechek 1988) and demonstrates the willingness of CRLRC cows to use areas far from water (Millward et al. 2020).

Across all study locations, JER and RCEW exhibited the most uneven grazing distribution, as reflected in the highest values for CV, skewness, and kurtosis. For JER, we posit the very low stocking density (0.007 animals • ha^{-1}) and large pasture size (1 535 ha) with extensive areas without palatable vegetation were responsible for the high level of grazing distribution unevenness. In contrast, at the RCEW site with a small but relatively more productive pasture that is well watered with a flowing creek and several water tanks, it was extreme topographic relief and concomitant relatively high use of lowlands and flat plains that led to the uneven grazing distribution. Evaluating the CV, skewness, and kurtosis of the distribution of relative grazing positions per pixel facilitates comparison of grazing distribution across sites and pastures in a manner that accounts for differences in the mean relative frequency.

Resource Selection Probability for Topographic Indices

TPC, constrained with distance to fence and distance to water sources, was a useful predictor of grazing distribution for most animals (75%) across this diverse set of rangeland ecosystems and with differing pasture sizes. Other than the extremely mesic ABS site, cattle grazed lowlands and flat plains more intensively than open slopes and uplands as predicted. Selection ratios derived from our RSPF analyses revealed the magnitude of preference for the different topographic position classes. Cattle grazed lowlands on average ~120% more intensively than uplands except at the ABS site, where upland habitats are preferred grazing sites compared with seasonally waterlogged patches (Pandey et al. 2009).

Topographic indices derived from DEMs are useful tools for describing a landscape, but methodological applications for livestock management have not been developed. Gersie et al. (2019) noted that both TWI and TPC had shortcomings in accurately reflecting the "ground truth" landscape for livestock management. For example, an incised stream channel cut through some of the CPER pastures, and this represented the lowest elevation in the local landscape. These incised streams were accurately described by the TPC method, but the TWI method failed to give the stream higher TWI values than the area around it (Gersie et al. 2019). This demonstrates that local knowledge of rangeland managers is needed to combine with predictions based on topographic indices for contextual interpretations. Both TPC and TWI represent improvements and are more interpretable than the more common method of using slope and elevation for predicting livestock distribution (e.g., Clark et al. 2014; Bailey et al. 2015; Clark et al. 2016). To date, limitations remain for the application of these topographic indices in mountainous terrain and landscapes due to the lack of their widespread adoption in cattle-grazing distribution studies.

Importance of Scale

Scale was an important factor in the TPC and TWI model predictions associated with livestock grazing behavior. For example,

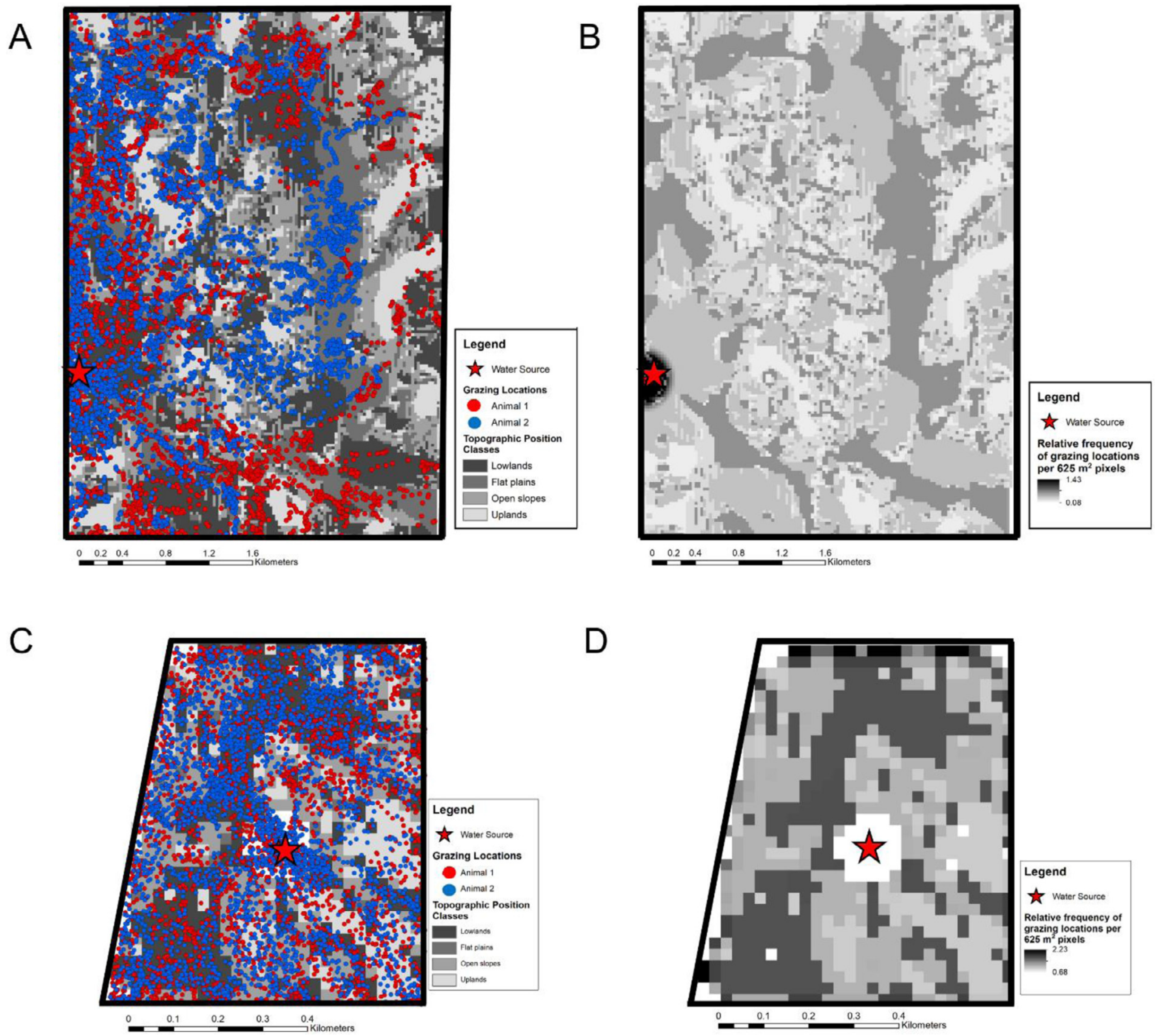

Fig. 6. Example of grazing position distribution for two individuals in a pasture at Corona Range and Livestock Research Center (CRLRC) encompassing shortgrass vegetation (A, B) and two individuals in a pasture at Barta Brothers Ranch (BBR) encompassing mixed-grass vegetation in (**C** and **D**). Actual grazing position distribution is depicted overlaid on topographic position classes for the CRLRC pasture (**A**) and the BBR pasture (**C**). The resulting predicted resource selection probability function in relation to topographic classes is shown for these two sites in (**B**) and (**D**).

for the largest pasture (1 601 ha, at CRLRC) in this study, distance to water source had a particularly strong effect on grazing distribution (see map in Fig. 6). This finding is likely due to the method used here of limiting distance to water from 150 to 600 m and therefore only accounting for local impacts of proximity to water. Although our modeling approach accounted for increased grazing time spent close to water, it did not account for a potential decrease in the use of areas distant from water. The latter is important where portions of the pasture are more than 1.6 km from water (Holechek 1988). Another issue with larger pastures is the increased chance that a given pixel will receive no grazing (see Figs. 2 and 3). Our modeling results confirm that the expected number of grazing positions per pixel increased as pasture size decreased. We would expect the number of grazing positions per pixel also to decrease as vegetation becomes patchier and stocking density decreases.

All of our study pastures contained a sufficient number of grazing positions to approximate a negative-binomial distribution when analyzed at the scale of 625 m^2 pixels. Extending our analyses to pasture sizes larger than included in this study (e.g., > 1 600 ha) could require additionally accounting for a larger proportion of pixels containing no grazing positions. Increasing the pixel size (to reduce the frequency of zero counts) or using modeling distributions that account for a high proportion of zeros (e.g., zero-inflated negative binomial distribution) may be needed for such efforts. Another issue to consider in large pastures is the home range of the livestock grazing animal (e.g., steer or cow). The time scale of the data influences home ranges. Pastures studied here were small enough that cattle could access the entire area, but many pastures/allotments are larger than 1 600 ha, suggesting that cattle may not access the total pasture area. In scenarios such as these, the study area could be restricted to the home ranges of the grazing animal using either 100% minimum convex polygon, 95% minimum convex polygon, or Kernel Density Estimators, as is done in many resource selection function studies (Nielson and Sawyer 2013).

Implications

Across seven sites representing a large environmental gradient for rangeland ecosystems in North America, we 1) quantified cattle grazing distribution unevenness at the pasture-level and 2) identified the topographic index, TPC, that most simply explains topographic features underlying grazing locations in pastures of varying sizes, vegetation type, and topographic complexity. For most arid and semiarid rangelands, livestock preferentially grazed lowlands and flat plains compared with open slopes and uplands. In mesic, subtropical rangeland, grazing livestock selected upland and sloped areas as low-lying areas with water-inundation curtailed selection. Across these diverse rangeland ecosystems of North America, results provide benchmark information on livestock grazing distribution to formulate improvements in adaptive management. Future work should carefully consider issues with scale, such as increasing the size of pixels used in the analysis, accurately describing the home ranges of animals when they do not access all areas in a pasture, and accounting for seasonal shifts in forage value and access. Modeling efforts could also be extended by including other abiotic variables such as soil type (Ramcharan et al. 2018) or biotic variables such as plant functional group cover and plant production (Jones et al. 2018; Robinson et al. 2019), where data are becoming more widely available and accurate. Conservation efforts regarding species of concern, where management often seeks to concentrate grazing into specific parts of the landscape without the construction of fencing that could impact wildlife (e.g., Hovick et al. 2014; Jakes et al. 2018; Geaumont and Graham 2020), could utilize knowledge of topographic effects to guide the use of prescribed fire, supplements, water distribution, or new technologies (e.g., virtual fence).

Declaration of Competing Interest

All authors acknowledge no conflict of interest is present in this manuscript.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2020.12.002.

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