



Movement, activity, and landscape use patterns of heritage and commercial beef cows grazing Chihuahuan Desert rangeland[☆]

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ABSTRACT

The objective of this study was to compare foraging behavior of mature Raramuri Criollo (RC, heritage breed) and Angus Hereford crossbred (AH, commercial breed) cows grazing Chihuahuan Desert rangeland during summer and winter in three consecutive years. Movement, activity, and spatial distribution variables were calculated from 10-min interval GPS positions of 5–11 randomly selected cows of each breed. Thirteen pasture pixel attributes were used to analyze grazing utilization and selection patterns of both breeds. Statistical mixed models were used to determine the effects of breed and season on all foraging response variables. Spatial regression analysis was used to examine resource utilization. Compared to AH, RC cows traveled farther at higher velocity rates, spent less time resting, more time grazing and traveling, explored larger areas as individuals, and exhibited lower herd cohesion. The RC herd explored more grazing patches (30-m pixel) overall and exhibited lower patch residence times in winter, a foraging strategy linked with lighter environmental footprint. During summer, similar pixel variables explained re-visitation rates of cows of both breeds. Both breeds avoided areas far from water, but RC cows showed higher avoidance of pixels farther out from a drinker during the dormant season. RC cows appeared to exhibit a keener ability to select patches with differing surface temperature, and greenness compared to AH counterparts. RC cows showed higher preference for pixels with high shrub density than AH counterparts in summer. During the dormant season, AH cows exhibited a strong preference for black grama patches, a species with high ecological value, and higher avoidance of patches with high density of other grasses. Differences in foraging behavior documented in this study support the hypothesis that RC cattle could impose a lighter footprint on desert rangeland relative to commonly raised commercial beef cattle.

1. Introduction

Ungulates play key roles in shaping ecosystem structure and function both directly, through herbivory-related impacts, and indirectly by altering plant-plant interactions, nutrient cycling rates, and fire regimes (Hobbs, 1996, 1999; Manier and Hobbs, 2007). In ranching systems of western North America, domestic ungulate herbivory has been

associated with environment deterioration in situations where stocking rates or spatial and temporal distribution of grazing pressure are poorly managed (Holechek et al., 2011). Spatial distribution of livestock herbivory is challenging to control because: 1) it is the result of a complex web of interacting animal and environmental factors that operate at multiple scales of space and time (Bailey et al., 1996; Hobbs, 1999; Launchbaugh and Howrey, 2005; Senft et al., 1987); and 2) corrective

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management strategies are frequently costly and difficult to implement (Knight et al., 2011; Walker, 1995).

Modifying spatial patterns of livestock herbivory on rangelands of western North America generally involves manipulating animal foraging behavior through fencing, water or supplement placement (Holechek et al., 2011), herding (Bailey et al., 2019), behavior conditioning techniques (Launchbaugh and Howery, 2005) and/or by selecting livestock species (Holechek et al., 2011), breeds (Peinetti et al., 2011; Spiegel et al., 2019), or individuals within a herd/flock (Bailey et al., 2015; Walker, 1995; Wesley et al., 2012) that exhibit desirable foraging patterns. Compared to improved commercial breeds, heritage livestock are often thought to exhibit foraging behavior traits that are better suited to achieve conservation goals on grazing lands (Pauler et al., 2019; Rook et al., 2004 and references therein). Although relatively few controlled experiments have documented this phenomenon (Rook et al., 2004) available evidence suggests that heritage livestock breeds could be a novel, and perhaps less costly, tool to address livestock spatial distribution challenges on some rangelands.

Raramuri Criollo, a heritage cattle biotype historically raised by the Tarahumara peoples in fairly isolated locations of the Copper Canyon of Chihuahua, Mexico, has shown intriguing landscape use patterns on desert rangelands of the southwestern United States (Anderson et al., 2015). These cattle have undergone semi-natural selection for close to four centuries which has allowed them to adapt to harsh environments where they do well with minimal modern-day animal husbandry inputs (Anderson et al., 2015). Studies conducted in the Chihuahuan Desert have shown that during times of the year when vegetation is dormant or scarce, Raramuri Criollo cows tend to distribute herbivory pressure across the landscape ranging significantly farther from the drinking water source (Peinetti et al., 2011) and creating fewer herbivory hotspots (Spiegel et al., 2019) compared to commercial beef cattle. This has led researchers to speculate that use of heritage genetics in desert ranching systems could address grazing distribution challenges and lead to more sustainable land stewardship practices (Spiegel et al., 2020). More broadly, heritage livestock breeds are viewed as a means of balancing animal agriculture and rangeland conservation to support rural livelihoods while continuing to meet local and global sustainable food demand in a rapidly changing world (Aharoni et al., 2013; Dolev et al., 2014; Estell et al., 2014; Pauler et al., 2019; Shabtay, 2015).

Previous studies comparing foraging behavior of Raramuri Criollo (RC) and Angus Hereford crossbreds (AH) mentioned above (Peinetti et al., 2011; Spiegel et al., 2019) were conducted during a single year and evaluated both breeds either grazing jointly in the same pasture (Peinetti et al., 2011) or grazing the same pasture separately in alternate fortnights (Spiegel et al., 2019). Results from both studies were highly consistent but experimental design limitations (i.e. not accounting for possible social interaction between breeds and/or limited replication in time) precluded making broader inferences about the conservation value of heritage beef cattle. Therefore, we designed a three-year study in which RC and AH cows grazed two adjacent pastures separately in a crossover design both in summer and winter to control for potential social interactions between breeds while adequately studying their foraging behavior in relation to seasonal and inter-annual variation in forage conditions.

The overall objective of this study was to compare foraging behaviors of RC vs. AH cows grazing extensive Chihuahuan Desert rangeland pastures. Based on previous findings reported by Peinetti et al. (2011) and Spiegel et al. (2019), we hypothesized that relative to AH, RC cows would exhibit movement, activity, and pasture use patterns that would collectively result in more desirable spatial distribution patterns of herbivory. We predicted that RC cows would travel farther (including travel distance from the drinker) at higher movement velocity rates, cover larger areas of the pastures, spend more time grazing and traveling and less time resting compared to their AH counterparts, and that such differences would be greater during the dormant season (prediction #1). We also predicted that RC cattle would spend less time on previously

grazed patches than AH cows, resulting in fewer hotspots of intense use particularly during the dormant season (prediction #2). Finally, we predicted that pixel selection patterns of both breeds would be affected by similar environment attributes in summer, when herbaceous forage is green, but not in winter, when herbaceous forage is dormant (prediction #3).

2. Materials and methods

2.1. Study site

The experiment was conducted at the Jornada Experimental Range (JER) located in southern New Mexico, USA (32° 37' N 106° 40' W) encompassing 78 266 ha of relatively flat terrain (1300 m–1600 m) within the northern Chihuahuan Desert. The climate of this site is typical of hot desert grassland with a mean annual precipitation of 247 mm, more than 50 percent of which occurs between July and September (Figure S 1, Suppl. Materials). Mean ambient temperature is highest in June and lowest in January, averaging 36 °C and 13.3 °C, respectively. Vegetation at JER is dominated by honey mesquite (*Prosopis glandulosa* Torrey) intermixed with perennial grasses dominated by black grama (*Bouteloua eriopoda*), dropseeds (*Sporobolus* spp.), and threeawns (*Aristida* spp.). Soap-tree yucca (*Yucca elata*) and broom snakeweed (*Gutierrezia sarothrae*) are common subdominants. Lowland grasslands are dominated by tobosa (*Pleuraphis mutica*) and burrograss (*Schleropogon brevifolius*) and occur on soils with high clay content (Havstad et al., 2000; Peinetti et al., 2011).

2.2. Study pastures

The study was conducted in two adjacent rangeland pastures (12A: 1190 ha and 12C: 1165 ha) during the growing and dormant seasons and replicated over three years (Aug 2015–Jan 2018). Each pasture had two watering points located on the farthest corners of the pasture with additional dirt tanks within each pasture (3 in 12A and 2 in 12C) covering underserved areas; the mean \pm SD and maximum distance to watering location was 949.93 \pm 495.22 m and 947.27 \pm 460.71 m and 2181.76 m and 2251.75 m for pastures 12A and 12C, respectively. Both pastures had permanent fencing and contained a network of roads; maximum distance to fence lines and roads was similar in both pastures (1519 m and 1260 m for pastures 12A and 12C, respectively). Both pastures had similar flat topography; their mean \pm SD and maximum elevation and slope were, respectively, 1324.69 \pm 7.10 m and 0.57 \pm 0.46° and 1348.48 m and 4.98°.

2.3. Animals and collars

All animal handling protocols were approved by the New Mexico State University Institutional Animal Care and Use Committee (protocol # 2015-021). Eleven to fourteen mature Raramuri Criollo (RC) or Angus Hereford crossbred (AH) cows weighing approximately 350 kg and 545 kg, respectively, were randomly selected in each deployment period from a herd that had been raised at the ranch (Table S 1, Suppl. Materials). Raramuri Criollo cattle were first introduced to the Jornada Experimental Range (JER) in 2005 (Anderson et al., 2015), whereas the AH herd had been raised at the JER for several decades. Therefore all cows used in this study were familiar with the research site. Study cows were nursing young calves (less than two weeks of age) during the growing season and were dry during the dormant season. Five to eleven cows of each herd were fitted with a Global Positioning System (GPS) collar (Lotek® 3300, Lotek Wireless, New Market ON, Canada) configured to record locations at 10-min intervals throughout each 4-week deployment period (Table S 1, Suppl. Materials).

2.4. Grazing management

Growing season experiments occurred during August–September 2015, 2016, and 2017 (summer), whereas dormant season experiments were conducted during January–February 2016, 2017, and 2018 (winter) (Figure S 1, Suppl. Materials). Cows of each breed grazed separately in adjacent pastures in a crossover design such that breeds switched pastures at the mid-point (end of week 2) of each sampling season ensuring both breeds were exposed to the same environment with no social interaction between breeds (Table S 1, Suppl. Mat.). Pastures were only populated during the 4-week experiment period in summer and winter and rested the remainder of the year. Hence the stocking rates were approximately 108 to 106 ha/AUM. Grazing intensity was judged to be light to conservative based on ocular estimates of key species utilization (Holechek and Galt 2000).

2.5. Movement, activity and spatial distribution analyses

Distance traveled (km), movement velocity (m/min), and activity budget (h; hours spent resting, grazing, or traveling) were calculated from 10-min interval GPS fixes. Activity categories were calculated for each GPS coordinate using specific movement velocity ranges for resting (0–2.34 m/min), grazing (2.35–25 m/min), and traveling (25–500 m/min) based on previous classifications used by Augustine and Derner (2013) and Nyamuryekung'e et al. (2020). Activity budgets were calculated by assigning an activity to each GPS point and represented as a ratio within the day's total GPS count. The Lotek® 3300LR GPS collars utilized for this study were equipped with 2-axis accelerometers for motion detection. Use of motion indices has shown low to nil improvement in the accuracy of activity classification when both the motion sensor indices and GPS data were integrated in a classification algorithm compared to the use of GPS data alone (Augustine and Derner 2013; Continanza, 2019).

For each GPS coordinate, straight-line distances to the centroid of a collared cow's GPS point distribution on a given day, was calculated and averaged daily as a proxy for area explored (exploration radius):

$$R = \frac{\sum_{i=1}^k \left(\sqrt{(x - \bar{x}_k)^2 + (y - \bar{y}_k)^2} \right)_i}{k}$$

where x and y are easting and northing coordinates respectively whereas \bar{x}_k and \bar{y}_k are daily centroid coordinates and k is the total daily GPS coordinate count. The daily average exploration radius was again calculated for each cow with respect to its herd's daily centroid GPS point distribution as a means of assessing herd cohesion (social spacing) in grazing (Arnold and Maller, 1985). Average radius was considered a better metric for describing dispersal of clustered points in space than minimum convex polygon (MCP), a commonly used metric that only considers outlining points in the clustering and which assumes uniform use of space within the range (see MCP calculations in Table S 2, Suppl. Materials). Using a distance metric lowered our data description ability to a degree, but provided the advantage of less bias on over or under-estimating the spatial use as with most spatial analyses metrics such as the Kernel Density Estimator (KDE) (Kernohan et al., 1978). According to Downs (2008), KDE failed in analyzing point data that had sharp edges (Getz and Wilmers, 2004), was linearly arranged (Blundell et al., 2001), and/or contained areas inside the polygon with non-use (Row and Blouin-Demers, 2006). Finally, distance to the closest watering points within respective pastures for each GPS coordinate/animal/day was averaged to calculate daily average distance from water.

2.6. Habitat selection analysis

2.6.1. Pasture use patterns

Pasture use patterns were calculated using a subset of GPS positions

classified as grazing locations (see previous section). Rasterization of each GPS location was done to estimate total time spent in each 30-m pixel of the pasture (residence time; RT) by the group of collared animals. Pixel RT was used as a proxy for pixel grazing pressure. Additional processing of grazing GPS coordinates was conducted using SQL code language to correct autocorrelation among GPS data points and compute pixel re-visitation rate (RR) or number of same pixels selected on different days. The 24 h threshold used to define a re-visitation event was assumed to meet the time independence criterion (Swihart and Slade, 1985) as recommended in a previous study (Sawalhah et al., 2014). Using RT data, we determined the relative area of the pasture grazed by counting all the selected 30-m pixels within each pasture during the 2-week interval. Intensity of pixel use within a pasture per deployment was estimated using its pixel RT and calculating percentage of the pixels grazed once, twice, three times, four times, and five or more times. These analyses were conducted for the entire group of collared cows (a proxy for the herd) for every 2-week deployment period.

2.6.2. Pixel utilization and selection patterns

All mapping used for pixel selection analyses was conducted in ArcGIS (ESRI, 2018, ArcMap Desktop v. 10.6). Raster maps were developed representing Euclidean distances to the nearest water, road, and fence line within each pasture. Slope and elevation layers were derived from USGS 7.5 min topography maps. Landsat satellite images (30-m pixel) for moisture content (NDMI), and vegetation greenness (NDVI) were downloaded for each sampling period. Landscape thermal (LandTemp) maps for each sampling period were developed using infrared bands from Landsat-8 satellite images (30-m pixel) (Anderson et al., 2012).

Vegetation maps developed by Laliberte et al. (2007) using Quick Bird satellite imagery (0.70-m pixel resolution) based on November 4, 2004 data with classification of major species composition of our study area (shrubs, non-grasses, black grama, tobosa, and other-grasses) were also used. In this map, shrubs were detected using object-based classification and were subsequently masked during the classification of the understory (Laliberte et al., 2004). Non-grasses consisted mostly of forbs occupying bare ground spaces. Black-grama and tobosa occur in pure stands and were more spectrally distinct than other grasses such as dropseeds and threeawns that occurred in intermixed communities and were not easily identified with remote sensing (Laliberte et al., 2007). The resultant classification from a decision tree had an accuracy of 80 percent based on actual estimates from a paired field survey (Laliberte et al., 2007).

All raster maps were developed with a 30 × 30 m pixel resolution. The finer-resolution vegetation maps were up-scaled to 30-m pixels which resulted in an estimate of cover using a tabulate intersection function in ArcGIS (ESRI, 2018, ArcMap Desktop v. 10.6). Pixel attribute values were converted into a standardized z-score ($z = \frac{x - \mu}{\sigma}$) resulting in a single scale with a mean of 0 and with negative and positive z-score values. This allowed us to rescale all variables to the same units simplifying interpretation of results and enabling us to combine variable values that were unique to each deployment. Growing season NDVI, NDMI, and LandTemp for year1, year2 and year3 were all combined respectively by simply averaging their pixel score across years to represent growing season NDVI, NDMI, and LandTemp raster map respectively. The averaging was again computed for the dormant season (NDVI, NDMI, and LandTemp, Table S 3, Suppl. Materials).

Spatial regression analyses were conducted to identify pixel attributes that explained habitat selection patterns of each breed in both summer and winter separately. The standardized z-score values of pixel attributes were used for regression modeling. Explanatory (independent) variables included pixel topographic features (elevation and slope), greenness (NDVI), shrub density, black grama cover, and distance from water, roads, or fence lines. Response (dependent) variables were RR and RT of collared cows within each breed for the 2-week

period. Pixel RR and RT were averaged across herds in order to adjust for unequal number of collared individuals within the groupings (Table S 1, Suppl. Materials).

In addition to spatial regression modeling, we calculated Ivlev's electivity index ($E = \frac{(r-p)}{(r+p)}$, Jacobs, 1974) to determine preference ($E > 0$) or avoidance ($E < 0$) of pasture pixels using RR of each collared cow. Pixel RR was judged to be a suitable metric of pixel use because it captured the temporal dynamics of pixel selection. Electivity indices were calculated for each pixel attribute including topographic features (elevation and slope), NDMI, LandTemp, NDVI, plant species cover, and distance from water, roads, or fence lines. Ivlev's E was computed by first placing all pixel attribute standardized z-scores into categorical classes based on their nearest integer value (e.g. -1.23 , 2.78 , -3.48 classified into class -1 , 3 , and -3 , respectively). Final classification was limited to the range of -3 to 3 which resulted in a separation by one standard deviation across all classes with the -3 and 3 class range including all values ≥ -2.5 and ≤ 2.5 , respectively. Ivlev's E was calculated for each collared cow as the proportion of use (r ; re-visitaton rate RR) in pasture pixels with a given attribute class and the proportion of pixels with that attribute class available (p) within the pasture (Jacobs, 1974).

2.7. Statistical analyses

Daily movement (distance and velocity), activity budget (time spent resting, grazing and traveling), and spatial distribution (average distance from water, exploration radius by an individual cow, and exploration radius by individual cows relative to the herd (or herd cohesion), were averaged weekly for the four week period using the MEANS procedure in SAS 9.3 (SAS Institute, Cary, NC) and a weight statement was added on the computation of their least square means in the subsequent procedure. Grouping data in this way allowed us to account for unequal number of sampling days within weeks. All data were analyzed assuming a crossover design. Data were blocked by year (2015, 2016, and 2017), deployment (combination of year and season; S15, W16, S16, W17, S17, and W18), pasture (12A, 12C), and weekly time periods ($n = 4$). The MIXED procedure with a *covtest* statement in SAS 9.3 (SAS Institute, Cary, NC) was used to model the effects of breed (AH or RC) and season (summer, and winter) with their interaction as fixed effects for movement, activity budget and spatial distribution variables. The DDFM = Kenward-Roger option was selected for all variables analyzed. A "contrast statement" was added for each variable testing the effect of breed within season. Year-by-season-by-period, year-by-season-by-period-by-pasture, and cow nested within breed were considered random effects in this model.

Pasture use patterns (area of the pasture grazed) and pixel selection patterns (percentage of the pixels grazed once, twice, thrice, four, or five or more times) were analyzed using similar models. The temporal resolution of these data was a two-week period corresponding to the time collared animals were in each pasture per deployment. Data were blocked by year (2015, 2016, and 2017), pasture (12A, 12C), and the two-week time periods ($n = 2$). The MIXED procedure with a *covtest* statement in SAS 9.3 (SAS Institute, Cary, NC) was used to model the effects of breed (AH or RC) and season (summer and winter) with corresponding interaction effects on pixel selection and pixel use patterns for the herd. The DDFM = Kenward-Roger option was selected for all variables analyzed. Year-by-season-by-pasture, year-by-season-by-pasture-by-two-week period and breed nested within year-by-pasture were considered random effects in this model.

Spatial regression analyses were conducted using GeoDa (Anselin, 2005) to identify pixel attributes (see previous section) able to explain variation in RT and RR for each breed. Separate analyses were conducted for each breed and season (AH summer, RC summer, AH winter, RC winter) from an equal weight averaging of RT and RR across deployments. The suite of predictors included in our models were screened

for collinearity. The candidate predictor variables included distances from water, road, or fence line, topographic features (slope and elevation), plant species cover (shrubs, non-grasses, black grama, tobosa, and other-grasses), NDVI, NDMI, and LandTemp. Final predictor variables in our model included distances from water, road, or fence line, topographic features (slope and elevation), shrub and black grama cover, and NDVI. A weighted matrix was computed using a distance criterion in GeoDa (Anselin, 2005) and histograms of neighboring distribution were analyzed for normality. A 100 m buffering was chosen for the weighted matrix of all models. Model selection (spatial lag vs spatial error) was based on the spatial regression decision process proposed by Anselin et al. (2006); namely significance of Lagrange Multiplier (LM) and/or robust LM diagnostics.

Pixel attribute electivity indices of individual cows were analyzed using similar models for the all thirteen pasture variables. The temporal resolution for these data was again a two-week period corresponding to the time a collared animal was in each pasture per deployment. Data were blocked by deployment (combination of year and season; S15, W16, S16, W17, S17, and W18) and year (2015, 2016, and 2017). The MIXED procedure with a *covtest* and *nobound* statement in SAS 9.3 (SAS Institute, Cary, NC) was used to model the effects of breed (AH or RC), season (summer and winter), and the pixel attribute Z class (-3 , -2 , -1 , 0 , 1 , 2 , and 3) with their interactions on E values of individual cows. DDFM = Kenward-Roger option was selected for all variables analyzed. Year-by-season-by-breed, year-by-season-by-breed-by-Z class and cow nested within year-by-season-by-breed were considered random effects in this model. A "contrast statement" was added to test the effect of breed on E for each attribute per season. T-tests were conducted for each E cell mean (breed x season x class) to determine if indices were different from 0 so as to infer preference or avoidance for pixels with average, positive, or negative Z scores of a given attribute.

In addition, an average electivity value for each pixel was computed and mapped using ArcGIS (ESRI, 2018, ArcMap Desktop v. 10.6) to visualize areas of the pasture with corresponding mean electivity for each breed and season. Overall E for a single pixel was interpreted as reflecting grazing likelihood.

ANOVA assumptions were tested for all models to detect deviations from normality and presence of outliers. A log-transformation (\log transformation $f(x) = \ln(x+0.17)$) was used for all variables that failed to meet ANOVA assumptions. A log transformation was done before analysis and values were back transformed ($f(y) = (\ln^{-1}(y)) - 0.17$) after analysis. Because log transformation normalized the data, back transforming means following analysis corresponded to estimates of medians on the original scale following Ramsey and Schafer (2002). Means were compared via LSMEANS in SAS 9.3 (SAS Institute, Cary, NC) and differences were declared statistically detectable at $P \leq 0.05$.

3. Results

3.1. Movement, activity and spatial distribution

Compared to Angus Hereford crossbreds, Raramuri Criollo cows traveled greater distances each day ($P < 0.01$) at higher movement velocities ($P < 0.01$) during both summer and winter (Table 1). Raramuri Criollo cows spent less time resting and more time grazing and traveling ($P < 0.01$) than their AH counterparts regardless of season (Table 1). Compared to AH cows, RC exhibited on average a greater exploration radius both at the level of individual cows or when compared to the herd's centroid ($P < 0.01$) during both seasons (Table 2). During the growing season, both breeds traveled similar distances from water ($P = 0.35$) but in the dormant season, RC cows traveled farther from the drinker than AH cows ($P = 0.05$).

3.2. Habitat selection

Relative to AH, the RC group of collared cows (~herd) grazed more

Table 1

Movement and activity budgets of Angus Hereford crossbred (AH) and Raramuri Criollo (RC) cows while grazing Chihuahuan Desert rangeland in southern New Mexico during the growing (summer) and dormant (winter) seasons. A “contrast statement” for breed effect within season is included in the table (italic font).

Variables	Estimates				Standard Error ^a				P-Value ^b				
	Overall	Growing	Dormant	Overall	Overall	Grow	Dorm	Seas.	Overall	Grow	Dorm	Seas.	Seas. * Overall
Distance (km/day)^{c,d}	8.74	(6.24)	8.78	(6.54)				0.05				0.37	0.20
Angus X Hereford	8.55	(5.15)	8.55	(5.18)	0.04	0.06	0.06		<0.01	<0.01	<0.01		
Raramuri Criollo	8.98	(7.93)	8.93	(7.53)									
Velocity (m/min)	4.51		4.61					0.23				0.64	0.37
Angus X Hereford	3.70		3.73		0.17	0.25	0.23		<0.01	<0.01	<0.01		
Raramuri Criollo	5.42		5.29										
Resting (h/day)^d	14.33		15.39					0.33				<0.01	0.55
Angus X Hereford	15.75		15.30		0.28	0.41	0.37		<0.01	<0.01	<0.01		
Raramuri Criollo	13.96		13.34										
Grazing (h/day)^d	8.81		7.61					0.31				<0.01	0.35
Angus X Hereford	7.62		8.10		0.27	0.40	0.36		<0.01	<0.01	0.01		
Raramuri Criollo	8.79		9.52										
Traveling (h/day)^{c,d}	-1.59	(0.84)	-1.56	(0.99)				0.02				0.13	0.20
Angus X Hereford	-1.63	(0.61)	-1.64	(0.58)	0.01	0.02	0.02		<0.01	<.001	<0.01		
Raramuri Criollo	-1.51	(1.23)	-1.53	(1.11)									

^a Standard error for the main effects (breed and season) and a “contrast statement” for breed effect within season.

^b P Values for the main effects (breed and season), interaction term and a “contrast statement” for breed effect within season.

^c Values expressed as natural logarithm transformation used in analysis. Back-transformed ($f(y)=(\ln^{-1}(y))-0.17$) median estimates given in parenthesis.

^d Values were analyzed in units of m and percentage of the day but reporting units were in km and h/day.

Table 2

Exploration radius, herd cohesion, and distance traveled from the drinker by Angus Hereford crossbred (AH) and Raramuri Criollo (RC) cows while grazing Chihuahuan Desert rangeland in southern New Mexico during the growing (summer) and dormant (winter) seasons. A “contrast statement” for breed effect within season is included in the table (italic font).

Variables	Estimates				Standard Error ^a				P-Value ^b				
	Overall	Growing	Dormant	Overall	Overall	Grow	Dorm	Seas.	Overall	Grow	Dorm	Seas.	Seas. * Overall
Exploration Radius of Individual (km)^{c,d,e}	6.24	(0.52)	6.57	(0.72)				0.05				<0.01	0.25
Angus X Hereford	6.22	(0.51)	6.02	(0.42)	0.05	0.07	0.07		<0.01	<0.01	<0.01		
Raramuri Criollo	6.59	(0.73)	6.45	(0.64)									
Exploration Radius of Indiv. vs. Herd (km)^{c,d,e}	6.45	(0.64)	6.87	(0.97)				0.08				<0.01	<0.01
Angus X Hereford	6.34	(0.57)	6.21	(0.5)	0.05	0.07	0.07		<0.01	<0.01	<0.01		
Raramuri Criollo	6.98	(1.08)	6.69	(0.81)									
Distance from Water (km)^{c,e}	6.67	(0.79)	7.23	(1.38)				0.07				<0.01	0.51
Angus X Hereford	6.87	(0.97)	6.62	(0.75)	0.07	0.11	0.10		0.05	0.35	0.05		
Raramuri Criollo	7.02	(1.13)	6.72	(0.83)									

^a Standard error for the main effects (breed and season) and a “contrast statement” for breed effect within season.

^b P Values for the main effects (breed and season), interaction term and a “contrast statement” for breed effect within season.

^c Values expressed as natural logarithm transformation used in analysis. Back-transformed ($f(y)=(\ln^{-1}(y))-0.17$) median estimates given in parenthesis.

^d Radius measurements were based on average distance of each 10 min GPS location to a central point of either the individual cow or its herds central point at a daily time scale.

^e Values were analyzed in units of m but reporting units were in km.

patches (pixels) during the growing season ($P < 0.01$) and tended to do the same in winter ($P = 0.09$, Table 3). Pixel residence time of both herds was similar during the growing season (Table 3, Figure S 2, Suppl. Materials). However, during the dormant season, relative to AH, the RC herd tended to graze a greater number of pixels only once ($P = 0.07$), and fewer pixels twice ($P = 0.07$) or four times ($P = 0.05$, Table 3, Figure S 2, Suppl. Materials). In general, pasture use differences between herds (breeds) was highest in winter (Figure S 2, Suppl. Materials). Spatial lag models were used for all analyses. The suite of selected predictors explained roughly a third to half of the variation in pixel RR and RT. In general, models explained more of the variation in RR vs. RT

and summer vs. winter (Table 4). In summer, cows of both breeds tended to spend more time and return more often to pixels closer to water points or fence lines, to upland pixels (relatively higher elevation), and to greener sites with low shrub density ($P = 0.05$, Table 4). Overall, NDVI was the explanatory variable that exhibited strongest relationship with RR and RT followed by distance to water (Table 4). In winter, cows of both breeds spent more time grazing closer to fence lines, in swales (relatively lower elevation), on gentle slopes, or pixels which were greener (higher NDVI) and revisited these pixels more times. Winter pixel greenness showed a stronger relation with time spent grazing and revisit rates of RC vs. AH cows. Commercial cows (AH) spent more time

Table 3

Total and average pixel (grazing patch) use patterns of Angus Hereford crossbred (AH) and Raramuri Criollo (RC) groups of collared cows (~herds) while grazing Chihuahuan Desert rangeland in southern New Mexico during the growing (summer) and dormant (winter) seasons. Pixel use estimates used a subset of GPS locations while animals were presumed grazing. Residence time (RT) was computed for each pixel and was used as a proxy of grazing intensity for the entire herd. The time period used for analysis was 2 weeks.

Variables	Estimates			Standard Error ^a			P-Value ^b		
	Breed	Breed	Breed	Overall	Grow	Dorm	Overall	Grow	Dorm
	Overall	Growing	Dormant						
Total pixels grazed									
Angus X Hereford	1381.2	1127.1	1635.2	112.4	159.0	158.9	0.02	<0.01	0.09
Raramuri Criollo	1677.6	1422.0	1933.2						
Percentage of pixels grazed once									
Angus X Hereford	0.513	0.543	0.482	0.027	0.038	0.038	0.22	0.88	0.07
Raramuri Criollo	0.547	0.537	0.557						
Percentage of pixels grazed twice									
Angus X Hereford	0.217	0.202	0.232	0.008	0.011	0.011	0.09	0.23	0.07
Raramuri Criollo	0.199	0.188	0.210						
Percentage of pixels grazed three times									
Angus X Hereford	0.105	0.097	0.112	0.006	0.009	0.009	0.13	0.47	0.15
Raramuri Criollo	0.094	0.090	0.098						
Percentage of pixels grazed four times									
Angus X Hereford	0.063	0.056	0.070	0.006	0.008	0.008	0.12	0.86	0.05
Raramuri Criollo	0.053	0.054	0.052						
Percentage of pixels grazed > five times									
Angus X Hereford	0.103	0.103	0.104	0.015	0.022	0.022	0.84	0.21	0.33
Raramuri Criollo	0.107	0.131	0.082						

^a Standard error for the main effects (breed and season).

^b P Values for the main effects (breed and season).

Table 4

Resource utilization function for 30*30 m pixel (grazed patch) use patterns of Angus Hereford crossbred (AH) and Raramuri Criollo (RC) herds while grazing Chihuahuan Desert rangeland in southern New Mexico during the growing (summer) and dormant (winter) seasons. Pixel use estimates used a subset of GPS locations while animals were presumed grazing. Pixel re-visitation rate (RR) was defined as presence of grazing GPS points that occurred on different days whereas pixel residence time (RT) was the overall GPS counts within a pixel. The time period used for analysis was the 2 weeks a single herd was within a single pasture (12A and 12C–1100 ha) over the 3 year deployment.

	Pixel Return Rate (RR)				Pixel Residence Time (RT)				
	Summer		Winter		Summer		Winter		
	AH	RC	AH	RC	AH	RC	AH	RC	
Model type	Spatial lag	Spatial lag	Spatial lag	Spatial lag	Spatial lag	Spatial lag	Spatial lag	Spatial lag	
R ² for model	0.434	0.468	0.316	0.346	0.409	0.420	0.320	0.340	
Coefficients									
Constant	0.028	0.077	* 0.189	* 0.074	* 0.000	0.003	* 0.007	* 0.002	
Distance from water	-0.129	* -0.088	* 0.016	-0.071	* -0.008	* -0.004	* 0.001	-0.003	
Distance from road	0.016	-0.014	-0.005	0.018	0.001	-0.001	0.000	0.001	
Distance from fence	-0.046	* -0.057	* -0.050	* -0.046	* -0.003	* -0.003	* -0.002	* -0.002	
Elevation	0.037	* 0.041	* -0.047	* -0.025	* 0.003	* 0.003	* -0.002	* -0.001	
Slope	-0.010	0.004	-0.024	* -0.031	* 0.000	0.000	-0.001	* -0.001	
Greenness, NDVI	0.155	* 0.151	* 0.058	* 0.149	* 0.010	* 0.008	* 0.003	* 0.006	
Shrub Density	-0.047	* -0.051	* 0.009	-0.027	* -0.003	* -0.002	* 0.000	-0.002	
Black Grama	-0.009	0.010	0.022	* -0.004	-0.001	0.000	0.001	* 0.000	
P-Value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	
Model SE	0.638	0.746	0.720	0.698	0.044	0.040	0.027	0.029	

^a Model included all the coefficients listed using a spatial regression software GeoDa.

*P Values < 0.05 for the predictors.

in pixels with greater black grama cover and revisited them more often than RC counterparts, who spent less time in shrub dominated pixels or pixels far from water; while revisiting these pixels less often than AH cows (Table 4).

Both breeds showed decreased preference for or increased avoidance of pixels located at increasing distances from the nearest drinker, but RC cows tended to show greater avoidance than AH for pixels located at average distances from water during winter (Fig. 1). No clear selection patterns were observed in relation to distance from roads for both breed or season (Fig. 1). Fence lines were associated with pixel selection only in winter when RC cows showed preference for pixels that were farthest from fences whereas AH cows showed increasing avoidance of pixels as

distance from fences increased (Fig. 1). In summer, both breeds exhibited stronger avoidance of pixels at higher relative elevations (Fig. 1) whereas in winter only AH showed strong avoidance for higher elevation patches (Fig. 1). RC cows showed no clear selection pattern for pixels on the basis of slope in either season, whereas, in summer AH cows showed increasing avoidance of pixels as slope increased (Fig. 1). Overall, distance to water was the factor that appeared to elicit the strongest pixel selection response while topographic features (elevation and slope) appeared to elicit the second strongest response, but with differences between breeds (Fig. 1).

Cows of both breeds avoided drier pixels (lower than average NDVI) and preferred pixels with greater moisture indices during summer when

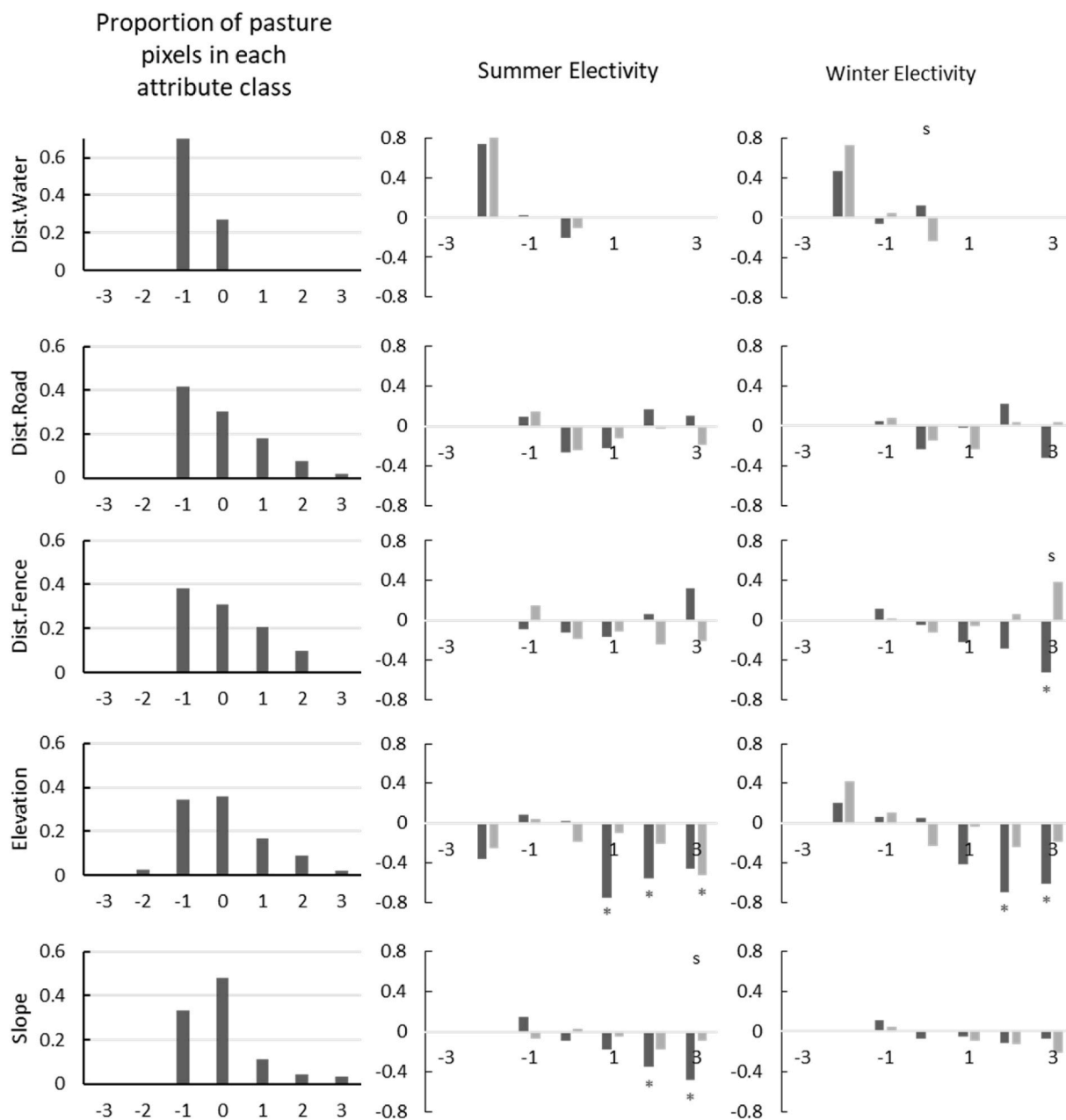


Fig. 1. Ivlev's electivity index for pixel attributes associated with pasture infrastructure (distance to water, roads, and fences) and topographic features (elevation and slope) calculated with presumed animal grazing locations derived from GPS coordinates. Horizontal axes show standardized z-score classification of attribute values (values closer to the mean have a z-score of 0; negative scores: attribute values smaller than the mean; positive scores: attribute values larger than the mean). First column shows distribution of pixel attribute value classes in the study pastures, with the vertical axis showing proportion values. Second and third columns show Ivlev's electivity (*E*) indices for each pixel attribute in summer and winter, respectively. Vertical axes show *E* values; positive indicates preference and negative indicates avoidance. Asterisks indicate significant *E* value ($P < 0.05$) (i.e. $E \neq 0$) for Angus Crossbred (dark grey) and Raramuri Criollo (light grey) cows. S- indicates significantly different *E* values ($P < 0.05$) between breeds for a given attribute class.

selection patterns were clearer (Fig. 2). During winter, the pattern reversed (and was less pronounced); both breeds showed moderate preference for drier pixels and avoided wetter ones (Fig. 2). In summer, both breeds selected pixels that were cooler than average (lower Land-Temp) and avoided pixels that were hotter than average (Fig. 2). In winter, surface temperature selection patterns were not as clear; only RC cows showed moderate preference for coolest or warmest pixels (Fig. 2). In summer, both breeds showed strong avoidance of and preference for patches with lower and higher than average greenness (pixel NDVI), respectively (Fig. 2). During winter, RC cows continued to avoid pixels with less than average greenness while preferring greener sites (Fig. 2). Conversely, AH cows showed no clear greenness selectivity patterns

while vegetation was dormant in winter (Fig. 2). Overall, surface temperature and vegetation greenness were the pixel attributes that appeared to respectively elicit strongest avoidance and preference responses in both breeds during summer. In winter, responses were mostly breed-dependent; RC cows appeared to exhibit a keener ability to select pixels with differing surface temperature and greenness compared to AH counterparts (Fig. 2).

In summer, both breeds preferred shrubbier pixels, but RC cows exhibited higher preference for areas with relatively higher shrub density than those selected by AH counterparts (Fig. 3). Similar overall selectivity patterns were observed in winter; during this season however, RC cows showed higher avoidance than AH of pixels with lowest

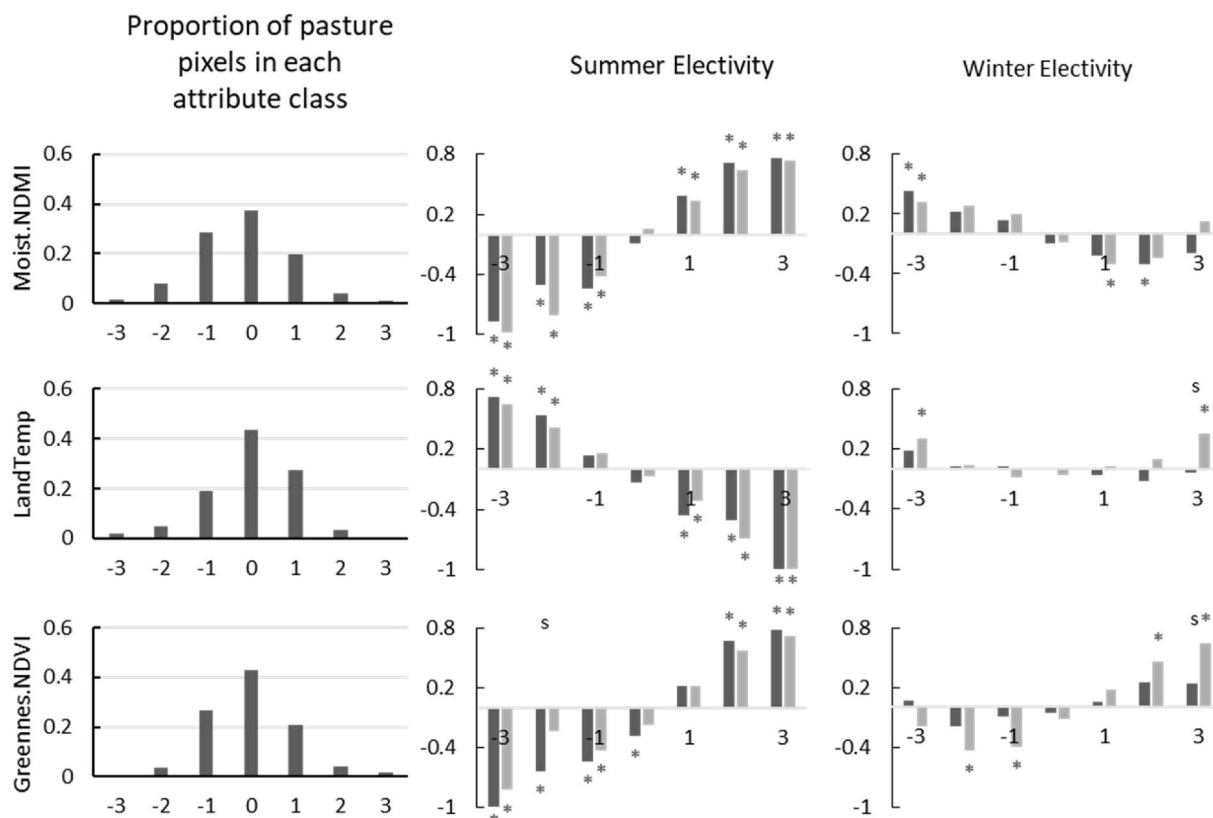


Fig. 2. Ivlev's electivity index for pixel attributes associated with pasture landscape thermal, moisture (NDMI) and vegetation greenness (NDVI calculated with presumed animal grazing locations derived from GPS coordinates). Horizontal axes show standardized z-score classification of attribute values (values closer to the mean have a z-score of 0; negative scores: attribute values smaller than the mean; positive scores: attribute values larger than the mean). First column shows distribution of pixel attribute value classes in the study pastures, with the vertical axis showing proportion values. Second and third columns show Ivlev's electivity (E) indices for each pixel attribute in summer and winter, respectively. Vertical axes show E values; positive indicates preference and negative indicates avoidance. Asterisks indicate significant E value ($P < 0.05$) (i.e. $E \neq 0$) for Angus Crossbred (dark grey) and Raramuri Criollo (light grey) cows. S- indicates significantly different E values ($P < 0.05$) between breeds for a given attribute class.

shrub densities (Fig. 3). Pixels with higher than average density of non-grass understory species were avoided by both breeds in both seasons (Fig. 3). Pasture pixels were not selected on the basis of black grama density by either breed in summer; whereas in winter, AH cows showed clear preference for pixels with greatest black grama density while RC cows were indifferent to these pixels (Fig. 3). In summer, both breeds avoided pixels with least densities of tobosa grass and only RC cows showed preference for sites with high densities of this grass (Fig. 3). Density of tobosa grass did not influence pixel selection patterns of either breed in winter (Fig. 3). Selection of pixels with other grasses decreased as cover of these grasses increased in both seasons; in winter however, avoidance of patches with high cover of other grasses was significantly lower in RC vs. AH cows. Overall, RC cows showed greater preference for pixels with high shrub density than AH counterparts in summer. During the dormant season, RC cows avoided areas with low shrub density while showing no selection for sites with black grama stands; AH cows showed strong preference for dense black grama stands and greater avoidance of pixels with high density of other grasses.

The grazing likelihood index revealed remarkable season differences between breeds. During summer both breeds appeared to prefer similar portions of the pasture (Fig. 4). During this season the grazing likelihood index for AH ranged from -0.28 to 0.27 for a pasture area including 8324 pixels, whereas index values for RC ranged from -0.21 to 0.24 for an area of 7509 pixels (Fig. 4). During winter, pixel preference, and hence spatial distribution, of breeds diverged significantly with narrower distribution of grazing likelihood indices than in summer; AH index values ranged between -0.14 and 0.13 for an area of 12 435 pixels, whereas RC index values ranged from -0.17 to 0.17 for an area of

14 730 pixels (Fig. 4).

4. Discussion

Our first prediction that RC cows would travel farther (including travel distance from the drinker) at higher movement velocity rates, cover larger areas of the research pastures, spend more time grazing and traveling and less time resting compared to their AH counterparts was largely supported by our data. Overall, our results confirmed findings of earlier studies comparing these two breeds (Peinetti et al., 2011; Spiegel et al., 2019). Raramuri Criollo cattle are possibly more selective foragers than their heavier and slower-moving Angus Hereford counterparts. We speculate that the foraging process is likely less costly for RC who due to their smaller frame and lighter weight have lower dry matter intake requirements which might allow them to prioritize meeting daily or weekly diet quality over gut-fill needs (Aharoni et al., 2013; Dolev et al., 2014; Rook et al., 2004). Further research comparing diets, dry matter intake, and energetics of these breeds is needed however.

Breeds exhibited differences in movement and activity patterns both in summer and winter except for distance traveled from the water source which only occurred in winter (RC > AH). In most instances, differences between breeds were greater in winter vs. summer (notably, difference in distance traveled from water tripled), a pattern that provides additional support for our first prediction and further confirms findings of previous studies (Peinetti et al., 2011; Spiegel et al., 2019). Cows of both breeds spent more time resting and less time grazing in winter vs. summer, which agrees with previous studies that documented seasonal dynamics of cattle activity at pasture (Ishiwata et al., 2008; Schoenbaum

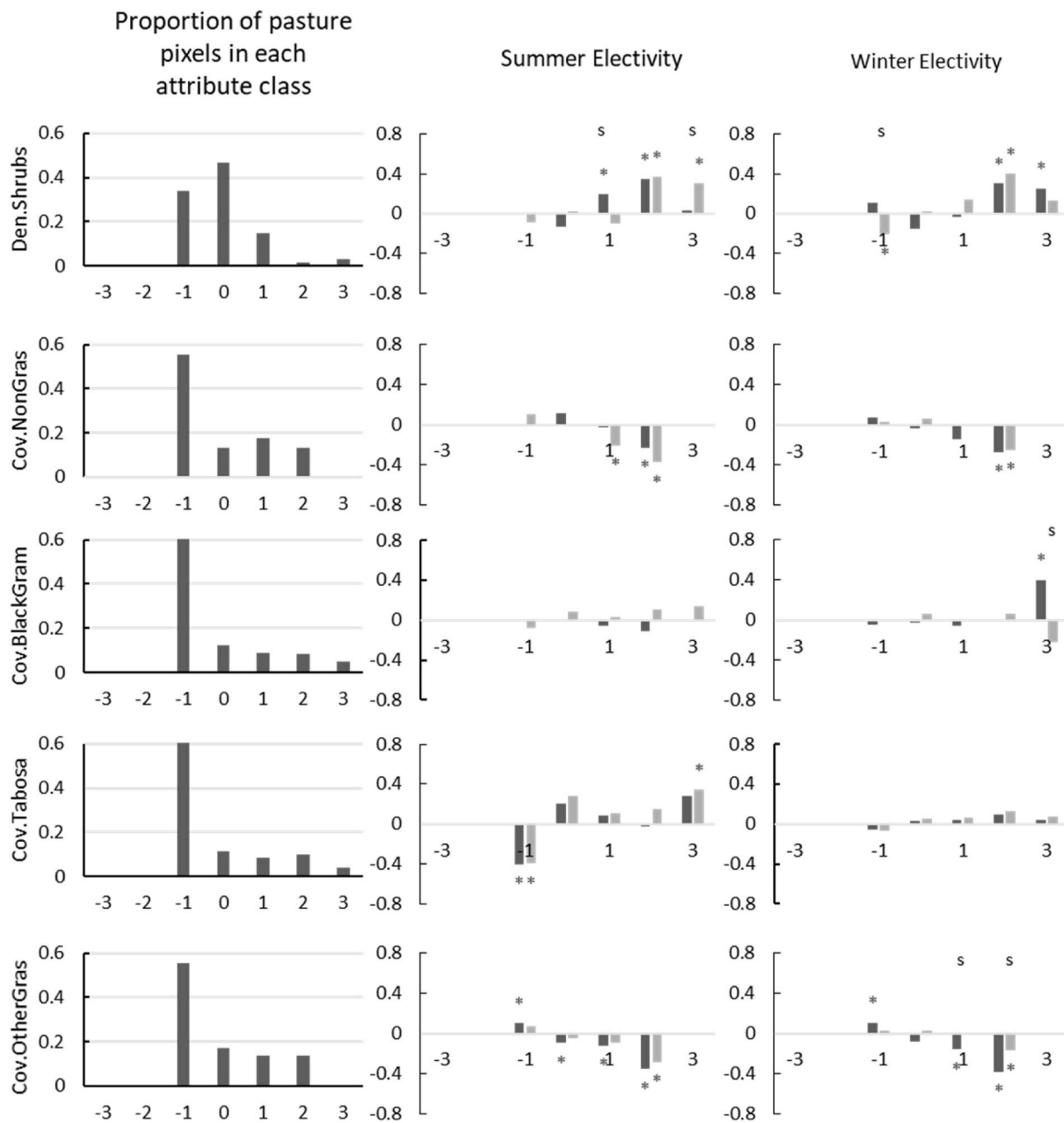


Fig. 3. Ivlev's electivity index for pixel (30 m) attributes associated with vegetation cover (shrubs, none grass, black grama, tobosa, and other grass species) calculated with presumed animal grazing locations derived from GPS coordinates. Horizontal axes show standardized z-score classification of attribute values (values closer to the mean have a z-score of 0; negative scores: attribute values smaller than the mean; positive scores: attribute values larger than the mean). First column shows distribution of pixel attribute value classes in the study pastures, with the vertical axis showing proportion values. Second and third columns show Ivlev's electivity (*E*) indices for each pixel attribute in summer and winter, respectively. Vertical axes show *E* values; positive indicates preference and negative indicates avoidance. Asterisks indicate significant *E* value ($P < 0.05$) (i.e. $E \neq 0$) for Angus Crossbred (dark grey) and Raramuri Criollo (light grey) cows. S- indicates significantly different *E* values ($P < 0.05$) between breeds for a given attribute class. dotted lines. S- signify significance ($P < 0.05$) in breed difference within the categorical classification of the pasture attribute.

et al., 2017; Spiegel et al., 2019) and may have reflected the likely decrease in diet digestibility and consequent increase in rumination time or, alternatively, may have been the result of changes in physiological state of cows. During the growing season, both breeds were lactating, a physiological state that is extremely taxing in terms of energy and nutrient requirements (NRC, 2016; Nyamuryekung'e et al., 2020; Provenza, 1995), whereas in winter cows were dry and had presumably not yet entered the last trimester of gestation.

Herd cohesiveness (exploration radius in relation to the group of collared cows) was consistently higher in AH than RC (i.e. social

distance from peers was presumably greater for the Criollo cow herd) and was more dispersed in winter versus summer for both breeds. It is possible that irrespective of mothering style (Nyamuryekung'e et al., 2020), cows of both breeds tended to stay closer to peers shortly after calving. Alternatively, as potential competition for reduced food resources increased (winter > summer) cows in both herds may have tended to spread out in search of nutritious forages. The fact that RC cows consistently exhibited lower herd cohesiveness is a novel finding that warrants further investigation. Potential differences in herd social structure could be a previously overlooked factor partially responsible

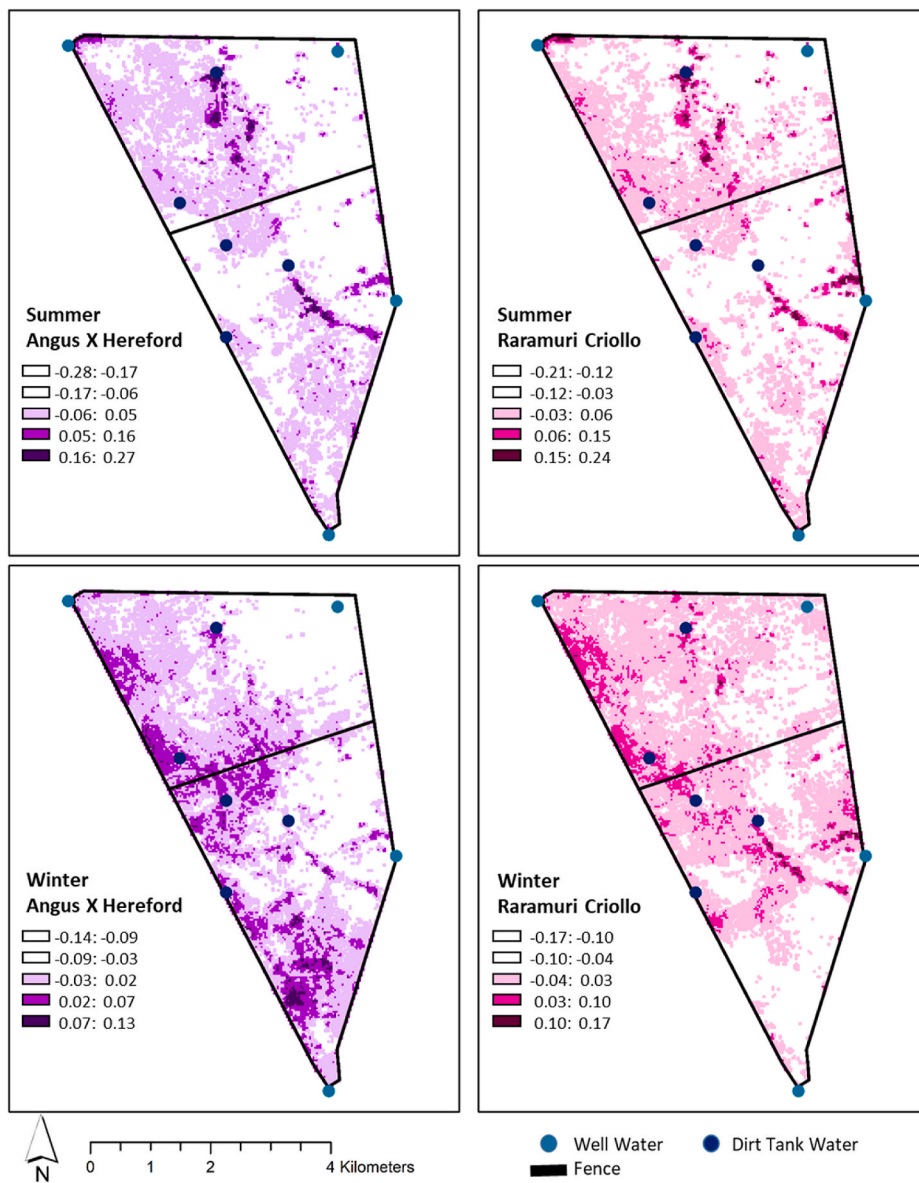


Fig. 4. Grazing likelihood index calculated from 13 Ivlev's electivity index for pixel (30 m) attributes associated with pasture infrastructure (distance to water, roads, and fences), topographic features (elevation and slope), landscape thermal (LandT), moisture (NDMI), vegetation greenness (NDVI) and lastly vegetation cover (shrubs, none grass, black grama, tobosa, and other grass species) calculated with presumed animal grazing locations derived from GPS coordinates using re-visitation rate interval. Ivlev's electivity (E) indices for each pixel attribute in summer and winter, were calculated with an overall average of all variables in their respective seasons. Classification on the maps was based on 5 equal distribution of the resultant E values (grazing likelihood) with in a panel; positive indicates preference and negative indicates avoidance. Only the third, fourth and fifth classification corresponding to mostly preference is visible on the map panels.

for contrasting spatial distribution patterns of heritage vs. commercial cattle observed in this and previous studies.

Our second prediction that RC cattle would revisit grazed patches less often than AH counterparts therefore creating fewer hotspots of intense use, particularly during the dormant season, was also supported by our data. In winter, the AH group of collared cows (~herd) collectively tended to graze fewer pixels overall, and tended to revisit grazed pixels more frequently compared to the RC herd, in agreement with what was reported in the Spiegel et al. (2019) study. In summer, no breed-related differences were observed. The Raramuri Criollo herd grazed more total pixels regardless of the season. These differences appear to support the hypothesis that RC cattle could have a lighter environmental footprint on desert rangelands due to their ability to better distribute their grazing pressure across the landscape. However, long term controlled grazing experiments are needed to test this hypothesis in a variety of rangeland environments.

Pixel selection analyses provided overall support for our third prediction. During summer, spatial regression models of pixel RR and RT for both breeds included the same suite of significant predictors. Pixel greenness (NDVI) appeared to weigh most heavily on pixel utilization patterns of both breeds, followed by distance to the closest watering

point. Both breeds tended to select greener pixels and avoid pixels far from drinkers. The influence of summer desert temperatures on animal water requirements (Roever et al., 2015) was likely responsible for the apparent reluctance of cows to travel far from water, a pattern of pasture utilization commonly observed in rangeland cattle (Holechek et al., 2011; Valentine, 1947). In winter, variation in pixel RR and RT of each breed was explained by a slightly different suite of predictors. Distance to drinking water and shrub density were significant predictors of RC but not AH pixel utilization patterns, whereas black grama cover predicted AH but not RC pixel RR and RT. Pixel greenness (NDVI) was a significant predictor of pixel use patterns of both breeds in winter, but the value of this parameter was 2.5 times larger in the RC vs. AH model, suggesting a somewhat stronger association between NDVI and pixel use in the heritage vs. commercial beef breed.

Commercial beef cows returned more often and spent more time in pixels with higher black grama cover compared to heritage breed counterparts. These findings agree with an earlier study by Spiegel et al. (2019) and support results of fecal metabarcoding analyses of diets of cows in this study (Estell et al., this issue). Estell et al. (this issue) found that winter diets of AH cows included significantly more black grama compared to diets of RC counterparts. Black grama is a critical forage

resource that plays an important role in protecting desert topsoil (Steele et al., 2012). Black grama is thought to have accounted for approximately 90% of vegetation cover on the Jornada in 1858 but by 1963, its cover had decreased to 23% (Buffington and Herbel, 1965). This decline is thought to be due to a number of management- and environment-related factors (Havstad et al., 2000). Holechek and Herbel (1982) considered this species to be the most important forage resource at this site partly because it maintains green stems (with high nutritional value) throughout winter. However, because vegetative reproduction via stolons and lateral spread is critical to the persistence of black grama stands at this site (Nelson, 1934), winter grazing could be detrimental to this species. Bestelmeyer et al. (2013) found that black grama cover was more adversely affected by winter vs. summer grazing compared to an ungrazed control at a site not far from our research pastures. We hypothesize that breed differences in winter use of black grama-dominated pixels (AH>RC) could result in significantly different environmental impacts of grazing commercial vs. heritage cattle at this site.

Electivity analyses provided additional insights into habitat selection patterns. Both breeds preferred to graze patches (pixels) that were closer than average to watering points and avoided pixels located farther from water. While this matched the general expectation for cattle grazing desert rangeland (Holechek et al., 2011; Valentine, 1947), the behavior of RC cows, which showed higher preference than AH for grazing patches located closer to the drinker during the dormant season, was contrary to our movement pattern findings (see above), and did not agree with previous studies (Peinetti et al., 2011; Spiegel et al., 2019). Previous analyses of spatial distribution of grazing of cattle monitored with GPS collars excluded locations within ~100 m of the drinker (Millward et al., 2020; Peinetti et al., 2011; Spiegel et al., 2019) which was not done in our study. It is possible that by including grazing points close to the drinker, many of which may have corresponded with cattle loafing rather than grazing, may have influenced our results.

Contrary to our expectations, we found breed-related differences in patch selection patterns in relation to roads, fences, and topography. Relative to AH, RC cows showed a tendency to prefer grazing patches far from fences (winter), located in small swales (both seasons) or on relatively steeper slopes (summer). Our road maps did not include cattle trails (Pringle and Landsberg, 2004) which could have potentially affected our assessment of the role of roads on RC and AH selectivity. Overall avoidance of grazing patches with higher or steeper landscape position by cows in both breeds (to different degrees) was somewhat expected (Bailey et al., 1996, 2001). Selection of grazing patches located in swales (lower elevation pixels) perhaps reflected preference for moister sites with more forage. Grazing patch selection by RC cows appeared less constrained by ranch infrastructure (roads and fences) and topographic features of grazing pastures, compared to their AH counterparts.

Selectivity patterns of grass-dominated pixels was similar for cows of both breeds in summer but not winter, partially supporting our third prediction. In summer, when tobosa was actively growing, cows of both breeds showed moderate preference for pixels dominated by this species. Not surprisingly, in winter both breeds showed similar weak to nil selection of tobosa-dominated pixels which likely offered very limited nutritional rewards; however, AH cows exhibited strong preference for pixels with high black grama cover and stronger avoidance of pixels dominated by other grasses (e.g. threeawns, dropseeds) during this season (winter). Raramuri Criollo cows mostly avoided grass-dominated pixels in winter, showing no preference for black grama-dominated patches and only moderate avoidance of pixels dominated by other grasses. This foraging pattern could have non-trivial implications on conservation of grazed Chihuahuan Desert rangelands (see discussion in previous paragraphs).

Both breeds preferred to graze in pixels with higher than average shrub cover but only RC cows showed higher preference for such patches in summer, again, only partially supporting our third prediction. Raramuri Criollo cows possibly included more browse in their diets in both

summer and winter. Estell et al. (this issue) reported higher proportion of honey mesquite in RC vs. AH diets. Both breeds also avoided pixels with high cover of non-grass plants, likely forbs, which are known to have a very narrow green-up window and are patchily distributed across our research pastures. These results differ somewhat from Spiegel et al. (2019) who reported that RC cows showed strong preference for bare soil/forb-dominated sites in summer at a site slightly north of our research pastures. Interestingly, shrub density was associated with lower patch residence time and re-visitation rates for both breeds in summer and for RC cows in winter (see previous paragraphs) suggesting that while preferred, shrub-dominated patches are perhaps less likely to become hotspots of intense use.

During summer, both breeds showed strong selection of pixels with greater than average moisture index (NDMI), lower than average land surface temperature (LandTemp) and greater than average greenness index (NDVI) and strong avoidance of pixels that were drier, hotter, or browner than average. Lower laying playa sites with greater moisture levels and high availability of green grass, especially tobosa (Havstad et al., 2000) likely explain summer preference for pixels with high NDMI and NDVI index values. Selection of pixels with cooler land surface temperature (low LandTemp) during summer were most likely associated with thermoregulation needs of cows in both breeds (Nyamuryekung'e et al., 2021). In winter we observed breed-related responses for all three pixel attributes; RC cows tended to graze pixels that were greener (higher NDVI) and somewhat warmer (higher LandTemp) than those selected by AH counterparts. Dormant season breed differences again appeared to highlight the superior ability of RC cows to adapt to conditions of low forage availability.

Average electivity values of grazing patches, which we used as a metric of grazing likelihood, confirmed findings reported by Peinetti et al. (2011) and Spiegel et al. (2019) that differences in landscape use patterns of commercial vs. heritage beef cattle are greatest during times of the year when forages are dormant. In winter, RC cows were likely to forage across larger areas of the pasture compared to their AH counterparts and to exhibit a more balanced patch selectivity pattern (i.e. exhibited intermediate electivity for a higher number of grazing patches). A comparison of summer vs. winter landscape use patterns of each breed suggests that heritage cattle exhibited a higher level of foraging behavior plasticity, a trait that has been observed in previous studies at this site as well as in studies conducted at sites in Mexico and Argentina (Cibils et al., this issue).

5. Conclusions

Matching animals to the landscape is of extreme importance in situations where the land is highly susceptible to degradation. Our study confirmed conclusions of Peinetti et al. (2011) and Spiegel et al. (2019) and revealed important foraging behavior differences between the heritage (RC) and commercial (AH) beef cattle breeds. Foraging behavior of Raramuri Criollo cows suggests that their footprint on desert rangeland is possibly lighter than that of improved commercial cattle. However, long term controlled grazing experiments are needed to test this hypothesis in a variety of rangeland environments. Further studies are also needed to determine the tradeoffs associated with raising heritage (RC) vs. commercial beef breeds on arid rangeland ranches (McIntosh et al., 2021; Speigal et al., 2020).

CRedit authorship contribution statement

Shelemia Nyamuryekung'e: Investigation, Data curation, Formal analysis, Writing – original draft. **Andres F. Cibils:** Conceptualization, Supervision, Writing – review & editing. **Richard E. Estell:** Conceptualization, Writing – review & editing, Resources. **Dawn VanLeeuwen:** Formal analysis, Writing – review & editing. **Sheri Spiegel:** Conceptualization, Writing – review & editing. **Caitriana Steele:** Software, Writing – review & editing. **Alfredo L. González:** Investigation,

Resources. **Matthew M. McIntosh:** Investigation, Writing – review & editing. **Qixu Gong:** Software. **Huiping Cao:** Software, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jaridenv.2021.104704>.

References

- Aharoni, Y., Dolev, A., Henkin, Z., Yehuda, Y., Ezra, A., Ungar, E.D., Shabtay, A., Brosh, A., 2013. Foraging behavior of two cattle breeds, a whole-year study: I. Heat production, activity, and energy costs. *J. Anim. Sci.* 91, 1381–1390.
- Anderson, D.M., Estell, R.E., Gonzalez, A.L., Cibils, A.F., Torell, L.A., 2015. Criollo Cattle: heritage genetics for arid landscapes. *Rangelands* 37, 62–67. <https://doi.org/10.1016/j.rala.2015.01.006>.
- Anderson, M.C., Allen, R.G., Morse, A., Kustas, W.P., 2012. Use of Landsat thermal imagery in monitoring evapotranspiration and managing water resources. *Remote Sens. Environ.* 122, 50–65. <https://doi.org/10.1016/j.rse.2011.08.025>.
- Arnold, G.W., Maller, R.A., 1985. An analysis of factors influencing spatial distribution in flocks of grazing sheep. *Appl. Anim. Behav. Sci.* 14 (2), 173–189.
- Anselin, L., 2005. Exploring Spatial Data with GeoDa™: a Workbook. University of Illinois at Urbana-Champaign. Center for Spatially Integrated Social Science, Urbana, IL, USA.
- Anselin, L., Syabri, L., Young, K., 2006. GeoDa: an introduction to spatial data analysis. *Geogr. Anal.* 3 (8), 5–22.
- Augustine, D.J., Derner, J.D., 2013. Assessing herbivore foraging behavior with GPS collars in a semiarid grassland. *Sensors* 13, 3711–3723. <https://doi.org/10.3390/s130303711>.
- Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M., Sims, P.L., 1996. Mechanisms that result in large herbivore grazing distribution patterns. *J. Range Manag.* 49, 386–400. <https://doi.org/10.2307/4002919>.
- Bailey, D.W., Kress, D.D., Anderson, D.C., Boss, D.L., Miller, E.T., 2001. Relationship between terrain use and performance of beef cows grazing foothill rangeland. *J. Anim. Sci.* 79, 1883–1891. <https://doi.org/10.2527/2001.7971883x>.
- Bailey, D.W., Lunt, S., Lipka, A., Thomas, M.G., Medrano, J.F., Cánovas, A., Rincon, G., Stephenson, M.B., Jensen, D., 2015. Genetic influences on cattle grazing distribution: association of genetic markers with terrain use in cattle. *Rangel. Ecol. Manag.* 68, 142–149. <https://doi.org/10.1016/j.rama.2015.02.001>.
- Bailey, D.W., Mosley, J.C., Estell, R.E., Cibils, A.F., Horney, M., Hendrickson, J.R., Walker, J.W., Launchbaugh, K.L., Burritt, E.A., 2019. Synthesis Paper: targeted livestock grazing: prescription for healthy rangelands. *Rangel. Ecol. Manag.* 72, 865–877. <https://doi.org/10.1016/j.rama.2019.06.003>.
- Bestelmeyer, B.T., Duniway, M.C., James, D.K., Burkett, L.M., Havstad, K.M., 2013. A test of critical thresholds and their indicators in a desertification-prone ecosystem: more resilience than we thought. *Ecol. Lett.* 16, 339–345.
- Blundell, G.M., Maier, J.A.K., Debevec, E.M., 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecol. Monogr.* 71, 469–489.
- Buffington, L.C., Herbel, C.H., 1965. Vegetation changes on a semi-desert grassland. *Ecol. Monogr.* 35, 139–164.
- Cibils et al. Foraging Behavior Plasticity of Criollo Cows Grazing Arid Rangelands in North and South America (this issue).
- Continanza, F.G., 2019. Influence of Animal-, Environment-, and Management-Related Factors on Grazing Behavior and Performance of Rangeland Beef Heifers. PhD Dissertation. New Mexico State University. ProQuest Dissertations Publishing.
- Dolev, A., Henkin, Z., Brosh, A., Yehuda, Y., Ungar, E.D., Shabtay, A., Aharoni, Y., 2014. Foraging behavior of two cattle breeds, a whole-year study: II. Spatial distribution by breed and season. *J. Anim. Sci.* 92, 758–766. <https://doi.org/10.2527/jas.2013-6996>.
- Downs, J.A., 2008. Network Analysis of Animal Space-Use Patterns. June 25, 2008. Florida State University. Retrieved from http://purl.flvc.org/fsu/fd/FSU_migr_etd-0680.
- Estell et al. (this issue) *J. Arid Environ.*
- Estell, R.E., Havstad, K.M., Cibils, A.F., Anderson, D.M., Schrader, T.S., 2014. The changing role of shrubs in rangeland-based livestock production systems: can shrubs increase our forage supply? *Rangelands* 36, 25–31. <https://doi.org/10.2111/Rangelands-D-13-00066.1>.
- Getz, W.M., Wilmers, C.C., 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography* 27, 489–505.
- Havstad, K.M., Kustas, W.P., Rango, A., Ritchie, J.C., Schmutz, T.J., 2000. Jornada Experimental Range: a unique arid land location for experiments to validate satellite systems. *Remote Sens. Environ.* 74, 13–25. [https://doi.org/10.1016/S0034-4257\(00\)00118-8](https://doi.org/10.1016/S0034-4257(00)00118-8).
- Hobbs, N.T., 1999. Responses of large herbivores to spatial heterogeneity in ecosystems. In: *Nutritional Ecology of Herbivores: Proceedings of the Vth International Symposium on the Nutrition of Herbivores*, vol. 101. American Society of Animal Science, pp. 97–129. Savory Apr 1999.
- Hobbs, N.T., 1996. Modification of ecosystems by ungulates. *J. Wildl. Manag.* 60, 695. <https://doi.org/10.2307/3802368>.
- Holechek, J.L., Herbel, C.H., 1982. Seasonal suitability grazing in the western United States. *Rangelands* 4 (6), 252–255.
- Holechek, J.L., Pieper, R.D., Herbel, C.H., 2011. Range Management: Principles and Practices, second ed. Prentice-Hall.
- Holechek, J.L., Galt, D., 2000. Grazing intensity guidelines. *Rangelands* 22, 11–14.
- Ishiwata, T., Uetake, K., Kilgour, R.J., Eguchi, Y., Tanaka, T., 2008. Comparison of time budget of behaviors between penned and ranged young cattle focused on general and oral behaviors. *Anim. Sci. J.* 79, 518–525. <https://doi.org/10.1111/j.1740-0929.2008.00558.x>.
- Jacobs, J., 1974. International association for ecology quantitative measurement of food selection: a modification of the forage ratio and Ivlev's selectivity index. *Oecologia* 14, 413–417. <https://doi.org/10.1007/BF00384581>.
- Kernohan, B.J., Gitzen, R.A., Mills, J.J., 1978. Chapter 5: analysis of animal space use and movements. In: *Radio Tracking and Animal Populations*. Academic Press, pp. 125–166. Jan 1, 2001.
- Knight, K.B., Toombs, T.P., Derner, J.D., 2011. Cross-fencing on private US rangelands: financial costs and producer risks. *Rangelands* 33, 41–44. <https://doi.org/10.2111/1551-501X-33.2.41>.
- Laliberte, A.S., Fredrickson, E.L., Rango, A., 2007. Combining decision trees with hierarchical Object-oriented image analysis for mapping arid rangelands. *Photogramm. Eng. Rem. Sens.* 73, 197–207. <https://doi.org/10.14358/PERS.73.2.197>.
- Laliberte, A.S., Rango, A., Havstad, K.M., Paris, J.F., Beck, R.F., McNeely, R., Gonzalez, A.L., 2004. Object-oriented image analysis for mapping shrub encroachment from 1937 to 2003 in southern New Mexico. *Remote Sens. Environ.* 93, 198–210. <https://doi.org/10.1016/j.rse.2004.07.011>.
- Launchbaugh, K.L., Howery, L.D., 2005. Understanding landscape use patterns of livestock as a consequence of foraging behaviour. *Rangel. Ecol. Manag.* 58, 99–108.
- Manier, D.J., Hobbs, N.T., 2007. Large herbivores in sagebrush steppe ecosystems: livestock and wild ungulates influence structure and function. *Oecologia* 152, 739–750. <https://doi.org/10.1007/s00442-007-0689-z>.
- McIntosh, M.M., Cibils, A.F., Estell, R.E., Nyamuryekung'e, S., Gonzalez, A.L., Gong, Q., Cao, H., Spiegel, S.A., Soto-Navarro, S.A., Blair, A.D., 2021. Weight gain, grazing behavior and carcass quality of desert grass-fed Raramuri criollo vs. Crossbred steers. *Livest. Sci.* 249, 104511. <https://doi.org/10.1016/j.livsci.2021.104511>.
- Millward, M.F., Bailey, D.W., Cibils, A.F., Holechek, J.L., 2020. A GPS-based evaluation of factors commonly used to adjust cattle stocking rates on both extensive and mountainous rangelands. *Rangelands* 42 (3), 63–71.
- Nelson, E.W., 1934. The Influence of Precipitation and Grazing upon Black Grama Grass Range. USDA, Washington, DC, p. 31.
- NRC, 2016. Nutrient Requirements of Beef Cattle. Natl. Acad. Press.
- Nyamuryekung'e, S., Cibils, A., Estell, R.E., McIntosh, M., Gonzalez, A.L., VanLeeuwen, D., Spiegel, S.A., Anderson, M., 2021. Foraging behavior and body temperature of heritage vs. commercial beef cows in relation to desert ambient heat. *J. Arid Environ.* 193, 104565. <https://doi.org/10.1016/j.jaridenv.2021.104565>.
- Nyamuryekung'e, S., Cibils, A.F., Estell, R.E., VanLeeuwen, D., Steele, C., Estrada, O.R., Almeida, F.A.R., González, A.L., Spiegel, S., 2020. Do young calves influence movement patterns of nursing Raramuri criollo cows on rangeland? *Rangel. Ecol. Manag.* 73, 84–92. <https://doi.org/10.1016/j.rama.2019.08.015>.
- Pauler, C.M., Isselstein, J., Braunbeck, T., Schneider, M.K., 2019. Influence of Highland and production-oriented cattle breeds on pasture vegetation: a pairwise assessment across broad environmental gradients. *Agric. Ecosyst. Environ.* 284, 106585. <https://doi.org/10.1016/j.agee.2019.106585>.
- Peinetti, H.R., Fredrickson, E.L., Peters, D.P.C., Cibils, A.F., Roacho-Estrada, J.O., Laliberte, A.S., 2011. Foraging behavior of heritage versus recently introduced herbivores on desert landscapes of the American Southwest. *Ecosphere* 2. <https://doi.org/10.1890/ES11-00021.1> art57.
- Pringle, H.J., Landsberg, J., 2004. Predicting the distribution of livestock grazing pressure in rangelands. *Austral Ecol.* 29, 31–39.
- Provenza, F.D., 1995. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. *J. Range Manag.* 48, 2. <https://doi.org/10.2307/4002498>.
- Ramsey, F.L., Schafer, D.W., 2002. *The Statistical Sleuth—A Course in Methods of Data Analysis*, second ed. Thomson Learning, Inc., Stamford.

- Roever, C.L., DelCurto, T., Rowland, M., Vavra, M., Wisdom, M., 2015. Cattle grazing in semiarid forestlands: habitat selection during periods of drought. *Anim. Sci. J.* 93 (6), 3212–3225.
- Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., WallisDeVries, M.F., Parente, G., Mills, J., 2004. Matching type of livestock to desired biodiversity outcomes in pastures - a review. *Biol. Conserv.* 119, 137–150. <https://doi.org/10.1016/j.biocon.2003.11.010>.
- Row, J.R., Blouin-Demers, G., 2006. Kernels are not accurate estimators of home-range size for herpetofauna. *Copeia* 4, 797–802.
- Sawalhah, M.N., Cibils, A.F., Hu, C., Cao, H., Holechek, J.L., 2014. Animal-driven rotational grazing patterns on seasonally grazed New Mexico rangeland. *Rangel. Ecol. Manag.* 67, 710–714. <https://doi.org/10.2111/REM-D-14-00047.1>.
- Schoenbaum, I., Kigel, J., Ungar, E.D., Dolev, A., Henkin, Z., 2017. Spatial and temporal activity of cattle grazing in Mediterranean oak woodland. *Appl. Anim. Behav. Sci.* 187, 45–53. <https://doi.org/10.1016/j.applanim.2016.11.015>.
- Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E., Swift, D.M., 1987. Large herbivore foraging and ecological hierarchies: landscape ecology can enhance traditional foraging theory. *Bioscience* 37 (11), 789–799. <https://doi.org/10.2307/1310545>.
- Shabtay, A., 2015. Adaptive traits of indigenous cattle breeds: the Mediterranean Baladi as a case study. *Meat Sci.* 109, 27–39. <https://doi.org/10.1016/j.meatsci.2015.05.014>.
- Spiegel, S., Cibils, A.F., Bestelmeyer, B.T., Steiner, J.L., Estell, R.E., Archer, D.W., Auvermann, B.W., Bestelmeyer, S.V., Boucheron, L.E., Cao, H., Cox, A.R., Devlin, D., Duff, G.C., Ehlers, K.K., Elias, E.H., Gifford, C.A., Gonzalez, A.L., Holland, J.P., Jennings, J.S., Marshall, A.M., McCracken, D.I., McIntosh, M.M., Miller, R., Musumba, M., Paulin, R., Place, S.E., Redd, M., Rotz, C.A., Tolle, C., Waterhouse, A., 2020. Beef production in the southwestern United States: strategies toward sustainability. *Front. Sustain. Food Syst.* 4, 114.
- Spiegel, S., Estell, R.E., Cibils, A.F., James, D.K., Peinetti, H.R., Browning, D.M., Romig, K.B., Gonzalez, A.L., Lyons, A.J., Bestelmeyer, B.T., 2019. Seasonal divergence of landscape use by heritage and conventional cattle on desert rangeland. *Rangel. Ecol. Manag.* 72, 590–601. <https://doi.org/10.1016/j.rama.2019.02.008>.
- Steele, C.M., Bestelmeyer, B.T., Burkett, L.M., Smith, P.L., Yanoff, S., 2012. Spatially explicit representation of state-and-transition models. *Rangel. Ecol. Manag.* 65, 213–222.
- Swihart, R.K., Slade, N.A., 1985. Testing for independence of observations in animal movements. *Ecology* 66, 1176–1184. <https://doi.org/10.2307/1939170>.
- Valentine, K.A., 1947. Distance from water as a factor in grazing capacity of rangeland. *J. For.* 45, 749–754.
- Walker, J.W., 1995. Viewpoint: grazing management and research now and in the next millennium. *J. Rangel. Ecol. Manag.* 48, 350. <https://doi.org/10.2307/4002488>.
- Wesley, R.L., Cibils, A.F., Mulliniks, J.T., Pollak, E.R., Petersen, M.K., Fredrickson, E.L., 2012. An assessment of behavioural syndromes in rangeland-raised beef cattle. *Appl. Anim. Behav. Sci.* 139, 183–194. <https://doi.org/10.1016/j.applanim.2012.04.005>.