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Seasonal Divergence of Landscape Use by Heritage and Conventional Cattle on Desert Rangeland☆

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ABSTRACT

Adopting livestock with heritage genetics may help to improve the sustainability of agriculture on rangelands with harsh, challenging conditions. In the Chihuahuan Desert, preliminary evidence suggests that heritage Raramuri Criollo exploit a greater variety of range resources than do conventional cattle. Accordingly, the use of Raramuri Criollo may help sustain vegetation and soils, as well as agricultural production. To explore these possibilities, we used Global Positioning System collars to track Angus × Hereford and Raramuri Criollo cows in a 1 535-ha pasture in southern New Mexico in June–December 2008. As predicted on the basis of past research, home range sizes of Raramuri Criollo exceeded those of Angus × Hereford during seasons with low forage availability—by 31.4 ± 6.5 ha during Pregreenup and 17.2 ± 6.5 ha during Drydown—but sizes converged during more productive seasons (Greenup 1, Greenup 2). Angus × Hereford allotted more daily time to resting, with the difference most pronounced during Drydown (71.1 ± 21.1 min day^{-1}). Angus × Hereford had twice as many hotspots of use (locations with multiple visits of long duration), with seasonal timing and location corresponding with distribution patterns known to impact desirable natural resources. Raramuri Criollo more strongly preferred the Bare/Forbs ecological state with seasonal timing that possibly signals an ability to use nutritious forbs on open ground despite summer heat. Results are consistent with conjectures that compared with conventional cattle, Raramuri Criollo have greater daily mobility and wider spatial distribution during dry seasons. Although not directly measured, results also suggest that the heritage breed has superior heat tolerance and lower impact on desirable natural resources. These findings provide evidence that Raramuri Criollo can support sustainable livestock production in the Chihuahuan Desert, but direct measurements of profitability and environmental effects are needed before adoption can be recommended widely.

Introduction

Livestock production and natural resource conservation are longstanding goals for rangelands, but achieving both simultaneously is an ongoing management challenge. Managing livestock distribution so that both animal and range productivity are sustained is desirable, but such distribution is often hampered by livestock behavior that results in uneven use of pastures. Manipulating fencing, water locations, and timing of use are common approaches to improving livestock distribution (Heitschmidt and Taylor, 1991; Owens et al., 1991). These manipulations, however, can be cost-prohibitive or inadequate in rangelands characterized by challenging conditions of large pasture sizes (Hunt et al., 2007), dense woody vegetation (Gutman et al., 2000), steep terrain (Bailey, 2004), or hot temperatures (Swain et al., 2007).

In rangelands with these challenging conditions from the Chihuahuan Desert to subtropical Florida to Mediterranean Israel, recognition is growing that using locally adapted breeds genetically predisposed to use resources in the context of local environmental variation can result in livestock distribution that is aligned with sustainable management goals (Sponenberg and Olson, 1992; Dumont et al., 2007; Estell et al., 2012; Shabtay, 2015; Scasta et al., 2016). In the Chihuahuan Desert, research is under way to investigate the distribution and landscape use of Raramuri Criollo (RC) cattle, a small-framed heritage breed that has undergone 500 years of adaptation to the harsh

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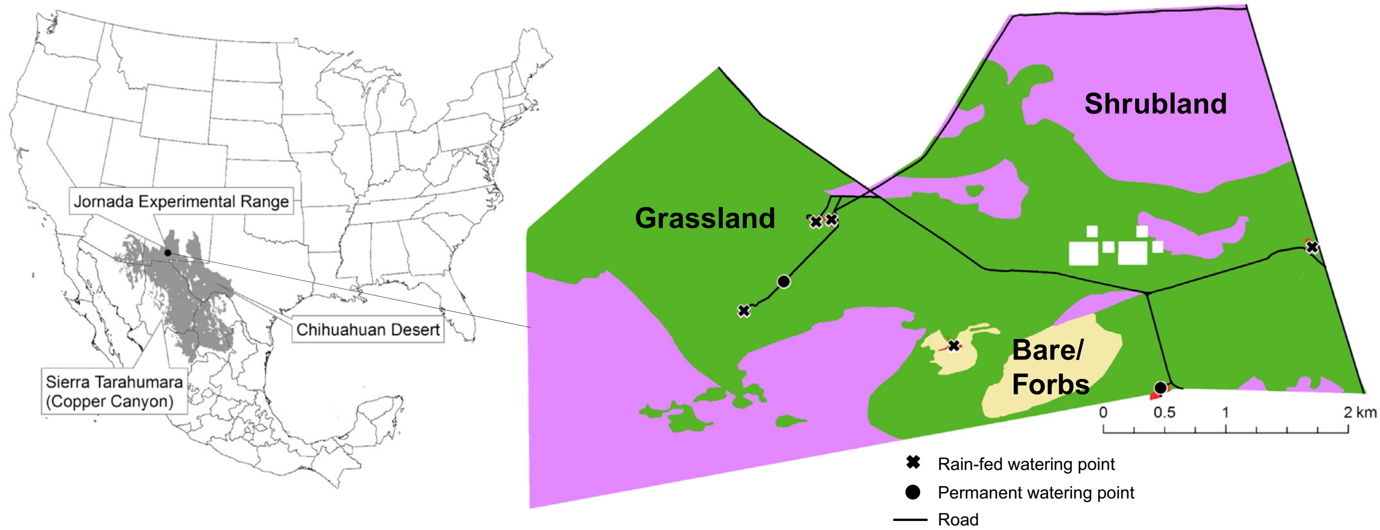

Figure 1. Geographic location and major features of the 1 535-ha study pasture at the Jornada Experimental Range in New Mexico. Left-hand map shows the general location of the Sierra Tarahumara, where heritage Raramuri Criollo have spent the past 500 yr with minimal crossbreeding. Right-hand map shows infrastructure and four generalized ecological states of the study pasture: Grassland, Shrubland, Bare/Forbs, and Watering Area (i.e., bare areas adjacent to watering points, colored red).

conditions of the Sierra Tarahumara in northern Mexico (Fig. 1) with minimal genetic influence of improved beef breeds (Anderson et al., 2015).

Preliminary evidence suggests that RC differ in important ways from the Angus breeds typically used in the Chihuahuan Desert (e.g., Brangus, Angus × Hereford [AH]). For instance, in the Sierra Tarahumara, RC have been observed to subsist mainly on woody plants, cacti (Ortega-Ochoa et al., 2008; Anderson et al., 2015), and forbs (Carswell, 2014) instead of mainly on grasses as is common for conventional breeds of the Chihuahuan Desert (Winder et al., 1996; Estell et al., 2012). Early-adopter producers have observed that the heritage cattle appear to travel across desert pastures more continually than conventional cattle, even in the heat of the summer (Carswell, 2014; Moreno, 2017). In addition, telemetry research during the course of 2005 showed that during months when forage was sparse and patchily distributed in a large Chihuahuan Desert pasture, RC distributed themselves more widely than AH, presumably seeking forage in distal portions of the pasture (Peinetti et al., 2011). Diet breadth, heat tolerance, and mothering style are possible behavioral explanations for observed breed differences in behavior and landscape use (Nyamuryekung'e et al., 2017; Nyamuryekung'e et al. in review).

To advance knowledge about whether and how the heritage breed differs from a breed used conventionally, we used Global Positioning System (GPS) collars to track RC and AH cows without calves during four phenologically defined seasons in June–December 2008 across a 1 535-ha pasture at the Jornada Experimental Range in southern New Mexico. The RC and AH herds grazed the pasture separately in successive 6-d trials within each season. We compared the herds in terms of home range sizes and spatial extents, daily activity budgets, hotspots of use, and preferences for ecological states while foraging. Tracking across multiple seasons was a priority because primary production, and livestock responses to it, vary greatly within and between years in arid lands (Thomey et al., 2011).

Anecdotal evidence and past research were the basis for four predictions about possible breed differences in landscape use during the study, with the first prediction pertaining to spatial extent. Peinetti et al. (2011) also compared the landscape use of RC and AH cows across a progression of seasons on a large pasture on the Jornada Experimental Range. The authors found that in the spring of 2005, when green forage was relatively plentiful and well distributed, the AH and RC herds exhibited similar spatial extents and spatial relationships to watering sites. Conversely, in the fall of 2005, when green forage was relatively scarce and patchily distributed, RC foraged across a larger spatial extent while AH had a smaller range that was closer to water. Accordingly, we predicted that during periods of relatively low forage production in our study, individual home range sizes and herd-level spatial extents of RC would be larger than those of AH, but during periods with more plentiful forage, home range sizes and spatial extents of the herds would converge.

Our second prediction was founded on anecdotal observations of early-adopter producers about the mobility of the heritage breed (Carswell, 2014; Moreno, 2017). Correspondingly, we predicted that the conventional cattle would spend more time resting each day while the heritage cattle would allot more time to moving across the pasture either foraging or walking.

Thirdly, we hypothesized that if in comparison with AH, RC did indeed cover a wider spatial extent in certain seasons and spend more daily time moving across the pasture—as hypothesized per the first two predictions—then RC would revisit particular locations less frequently and remain at those locations for less time. In our analysis, this would translate into fewer hotspots of use (i.e., locations with multiple visits of long duration). Understanding spatial and temporal distribution of hotspots in the Chihuahuan Desert is important because overuse of particular pasture locations is associated with social-ecological issues including perennial grass loss (Bestelmeyer et al., 2009), lateral soil redistribution (Nash et al., 2003), dust emissions (Baddock et al., 2011), and suboptimal utilization of the overall forage base (Holechek, 1992; Hunt et al., 2007).

Through our fourth prediction we explored the selection of ecological states by the cows while they were foraging. Given that RC subsist on woody plants, cacti, and forbs in their native Sierra Tarahumara (Ortega-Ochoa et al., 2008; Carswell, 2014; Anderson et al., 2015) and the contrasting tendency for Angus breeds to generally prefer grasses in the Chihuahuan Desert (Winder et al., 1996; Estell et al., 2012), we predicted that throughout most of the study, RC would concentrate foraging time on forb-dominated states and shrub-dominated states, whereas AH would concentrate foraging time on grass-dominated states. We sought to understand these patterns because preferential use of ecological states can affect supplemental feed requirements and the management of ecological state transitions—both of which influence the sustainability of agriculture on arid rangelands (Bestelmeyer et al., 2013).

We acknowledge that this was a 1-yr study and that replication of breed × season treatments will be required for a definitive comparison of heritage and conventional cattle in the Chihuahuan Desert. However, this study is valuable as it entailed monitoring RC and AH over multiple seasons and identifying livestock preferences for mapped ecological states (Steele et al., 2012), an aspect of livestock landscape use that has not yet, to our knowledge, been quantified. This is also the first study to use Time Local Convex Hulls (T-LoCoH) (Lyons et al., 2013) to construct home ranges and time-use maps to quantify livestock distribution. Further, we defined seasons for the study period using Normalized Difference Vegetation Index (NDVI) from satellite data (Browning et al., 2018). Ecological state mapping and the procedure for defining seasons are applicable to any pasture, so while our telemetry dataset spans only 1 yr, our use of reproducible approaches to characterize conditions improves chances for accurate comparisons between our livestock telemetry results and those from different locations in different years.

Methods

Location and Study Site

Livestock tracking was conducted in June − December 2008 at the US Department of Agriculture–Agricultural Research Service Jornada Experimental Range in the northern Chihuahuan Desert in New Mexico (central coordinates: 32.603°N, 106.776°W) (see Fig. 1). The Jornada is a 780-km^2 working ranch dedicated to ecological and agricultural research.

Soils and Vegetation

The Jornada is located in the Basin and Range Geologic Province and US Department of Agriculture Major Land Resource Area (MLRA) 42 (NRCS, 2005). Regional topography is characterized by north-south trending fault-block mountain ranges separated by desert basins and broad valleys that are flanked by alluvial fans, terraces, and bajadas with gentle to moderate slopes. Elevations range from 1 100 to 3 000 m depending on landscape position (Monger et al., 2006). Rangeland pastures are typically large (10^3 ha) and support a mosaic of ecological sites, divisions of the landscape that differ from other divisions with respect to geology, topography, and soils. Each ecological site has the potential to support a set of ecological states, patches of distinct vegetation covering ~10^0–10^2 ha (Bestelmeyer et al., 2011). Marked botanical and edaphic changes have occurred in the Chihuahuan Desert during the past 150 yr (Monger and Bestelmeyer, 2006), with significant state-transition processes including perennial grasslands transitioning to shrublands, palatable perennial grasses being replaced by less palatable perennial grasses, native grasses being replaced with exotic grasses, and the loss of vegetation due to severe soil scouring (Steele et al., 2012). Ecological Site Descriptions contain details about ecological sites, states, and state transitions in MLRA 42 (see edit.jornada.nmsu.edu).

On the Jornada, dominant grasses include dropseeds (*Sporobolus* spp.), tobosa *(Pleuraphis mutica),* and black grama *(Bouteloua eriopoda).* Dominant shrub species are honey mesquite *(Prosopis glandulosa),* creosote *(Larrea tridentata),* tarbush *(Flourensia cernua),* yucca (*Yucca* spp.), morman tea (*Ephedra* spp.), broom snakeweed *(Gutierrezia sarothrae),* and fourwing saltbush *(Atriplex canescens).* The ranch also supports several playas with alkali sacaton *(Sporobolus airoides),* tobosa, and annual gramas and dropseeds in the uplands and perennial forbs including hog potato *(Hoffmannseggia glauca)* and spreading alkaliweed *(Cressa truxillensis)* in the lowlands.

The study pasture is representative of the broad valleys (i.e., "basins") of the Basin and Range Geologic Province. Pasture elevations range from 1 309 to 1 397 m, with slopes ≤ 10 degrees. Pasture soils are mapped as the Berino-Bucklebar Association, Dona Ana-Reagan Association, Onite-Pajarito Association, Onite-Pintura Complex, Stellar Association, and Wink-Pintura Complex (Soil Survey Staff, 2013). Five ecological sites correspond to soils in the map units: Gypsiferous Playa, Clayey, Loamy, Sandy, and Deep Sand. Four generalized ecological states (*sensu* Williamson et al., 2011; Steele et al., 2012) occur in the pasture: Grassland, Shrubland, Bare/Forbs, and Watering Area (Table 1).

Climatic and Phenological Context

On the pasture, mean annual rainfall was 217 mm between 1918 and 2008, with ≈53% occurring from July to September as monsoonal storms originated from the Gulfs of Mexico and California (Fig. 2a). The study yr, 2008, was a relatively wet one: monthly rainfall totals in the rainy season of July, August, and September were higher than long-term monthly averages. 1918 − 2008 mean maximum monthly temperatures ranged from 13.5°C in January to 35.0°C in July. Monthly maximum temperatures during the study did not substantially differ from long-term averages (Fig. 2b).

In addition to being comparatively wet (Fig. 2a), the study yr 2008 was also "greener" than average. Maximum pasture-level MODIS-NDVI (Spruce et al., 2016) for 2000 − 2008, calculated by identifying the maximum NDVI value per pixel within each of the 9 yr and then calculating the average of the maxima, was 0.248. In comparison, for 2008, the same metric was higher at 0.294. Further, monthly pasture-level NDVI in the yr 2004-2008 (Fig. 2c) —quantified by calculating the average of MODIS-NDVI values of all pixels per month, and then calculating the monthly average among years—illustrates that July − November 2008 was higher in greenness than the other 4 yr.

Pasture Infrastructure

The study pasture was bounded by a perimeter fence and contained a network of roads (see Fig. 1). In addition, six small grazing exclosures were in the northeast zone of the pasture as part of a separate long-term experiment (see Fig. 1).

Seven watering sites, in use for decades preceding and during the study, were distributed throughout the pasture. Two were fed by well or pipeline and were permanently filled (O's in Fig. 1). Five were earthen tanks (i.e., dugouts) that fill with water with sufficient rainfall (X's in Fig. 1). The bare areas surrounding the watering points were mapped as "Watering Areas" on the ecological state map (see Fig. 1). The five rain-fed tanks likely filled with water during August − November 2008; however, tank water content levels were not directly measured. Playas on the Jornada can also fill with sufficient rainfall (Monger et al., 2006). Playa water levels were not directly measured, but we did evaluate the 2008 Landsat image time series and detected wetter soils but no evidence of large areas of standing water.

The greatest distance to watering points in the study pasture was 2.45 km. Long-term research in rangelands of the Chihuahuan Desert shows that cattle use tends to be concentrated within 1.6 km from water, diminishes between 1.6 and 3.2 km, and tapers off significantly at distances beyond 3.2 km (Holechek, 1991).

Telemetry Data Collection and Quality Control

GPS collars were deployed in 10 trials from June to December 2008 (Table 2). To avoid the possibility of one breed influencing the behavior of the other (Bailey, 2004), breeds did not graze pasture together. Instead, they were alternated by trial, except for the seventh and eighth trials, when AH grazed consecutively.

Study animals were randomly selected from a pool of 18 RC and a pool of 11 AH. Traits that influence livestock behavior were standardized between breeds as closely as possible (Allred et al., 2011). Accordingly, all study animals were mature cows without calves that had at least 3 yr of experience grazing on the Jornada, in pastures with topography, infrastructure, and vegetation broadly similar to the study pasture. However, whereas the AH were born into the ranch's base herd, the RC had been imported from Mexico in 2005. RC were approximately

Table 1
Characteristics of the generalized ecological states on the five ecological sites in the study pasture.

Generalized state	Dominant plant species	Ecological sites	Area (ha)
Bare/Forbs	Bare ground with perennial forbs hog potato, spreading alkali weed. Limited annual grasses including Madagascar dropseed. Occasional annual forbs.	Gypsiferous Playa, Loamy	55
Grassland	Tobosa, black grama, alkali sacaton, mesa dropseed, spike dropseed, yucca, burrograss, threeawn, bush muhly. Patchy shrubs include honey mesquite, ephedra, and yucca.	Clayey, Loamy, Sandy	888
Shrubland	Honey mesquite, broom snakeweed, tarbush, fourwing salt bush. Sparse grasses include bush muhly, and mesa and spike dropseeds.	Loamy, Sandy, Deep Sand	589
Watering area	Mostly bare ground		4

6 − 8 yr of age, but the AH cows that were available for use and did not have a calf were approximately 4 yr of age. Cows 4 yr or older are commonly referred to as the "mature herd" in most cow-calf operations in the western United States. All study cows were "mature" when the study began. Cows available for use had average weights of 352 ± 40 kg (RC) and 474 ± 42 kg (AH). Weights within this range of variation were not associated with differences in activity patterns of three breeds of beef cows monitored with GPS collars in the Chihuahuan Desert (Russell et al., 2012).

At the start of each trial, 9, 10, or 11 Lotek Model 2200 and 3300 collars programmed to acquire geographic locations at 5-min intervals were fitted on a random subset of AH or RC cows (see Table 2), and animals were turned out into the pasture through a gate next to the southernmost permanent watering point (see Fig. 1). GPS data were stored on the collars and retrieved at the end of each trial. Mean position error of animal locations was 5 m, verified through stationary tests. We used the N4 software developed by Lotek to differentially correct GPS data retrieved from the collars. The software was configured to use 1-sec interval stationary GPS data from a National Geodetic Survey Continuous Operating Reference Station located nearby at New Mexico State University. Differential correction reduces the GPS error to ≤ 3 m (usually within 1 m).

Quality control of the differentially corrected GPS data comprised a routine of multiple steps. First, we omitted 40 of the 101 GPS datasets collected (see Table 2) from further consideration because they had a high proportion of fixes without dates or geographic location information. We mapped the remaining 61 datasets onto the pasture fence line using ArcGIS 10.1, extended the fence line by 10 m to accommodate minor GPS error, and omitted fixes outside of that line. We then calculated lengths and velocity rates between consecutive fixes, omitting the fixes that were recorded > 1 200 sec after the previous fix. Next, we screened out GPS fixes associated with improbable travel velocities (> 7.3 km h^{-1} speed based on calculation of velocity between fixes). This 7.3 km h^{-1} threshold was lower than the 12 km h^{-1} threshold

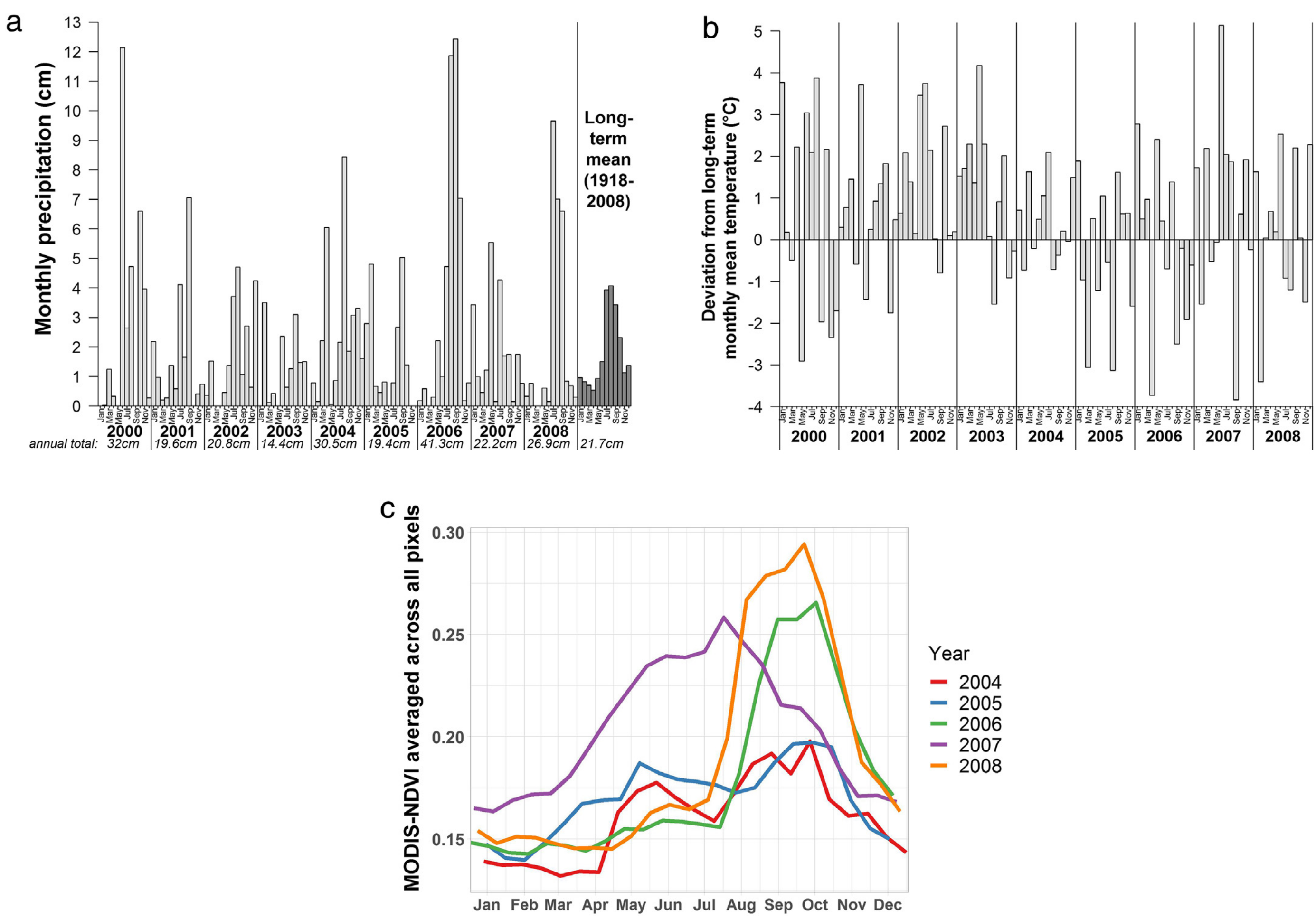

Figure 2. Long-term conditions in the study pasture. **a,** 1918 − 2008 monthly precipitation totals. **b,** 1918 − 2008 monthly ambient temperature (vertical lines denote 31 December). **c,** 2004 − 2008 pasture-level forage greenness measured with MODIS-NDVI.

Table 2
2008 telemetry study design.

Trial	Breed	Dates in pasture	No. of cows in pasture	No. of GPS collars deployed	No. of usable collars[1]	Minimum no. of consecutive days captured by usable collars	Proportion of herd represented in analyses[2]	Dates used in analyses	Season
1	AH	11-18 Jun	11	10	8	6	36%	12-17 Jun	Pregreenup
2	RC	19 Jun-1 Jul	12	10	6	11	33%	20-25 Jun	
3	AH	3-15 Jul	9	9	6	11	44%	4-9 Jul	Greenup 1
4	RC	16-30 Jul	9	9	5	13	44%	17-22 Jul	
5	AH	31 Jul-12 Aug	11	10	5	11	—	—	Greenup 2
6	RC	13-27 Aug	15	11	4	13	27%	14-19 Aug	
7	AH	29 Aug-15 Sep	10	9	5	16	40%	30 Aug-4 Sep	
8	AH	5-12 Nov	11	11	10	6	36%	6-11 Nov	Drydown
9	RC	15 Nov-1 Dec	11	11	6	15	36%	16-21 Nov	
10	AH	4-15 Dec	11	11	6	10	—	—	

[1] Usable is defined in the text.
[2] Four usable collars per trial divided by number of cows in pasture.

used by Liao et al. (2017) for Boran cattle in southern Ethiopia, which often travel at a fairly rapid pace. The threshold we used is either at the top end of a walking gait or low end of a trot, and maintaining this velocity for 5 min is somewhat costly (Di Marco and Aello, 1998), making its occurrence uncommon, if not rare. Screening out fixes with long lag times and high path speeds resulted in a loss of 0.08% of remaining data points. Finally, we excluded records from the first and last days of tracking to omit pretrial handling and acclimation and post-trial handling periods.

After being subjected to quality control, the 10 trials differed with respect to the number of collars deemed to have yielded usable data, with the lowest count of 4 occurring for the sixth trial (see Table 2). In addition, the number of consecutive days captured telemetrically—beginning with the first full day of each trial—differed among usable collars, with the lowest number being 6 d (see Table 2). Accordingly, for statistical analyses, we used GPS data from only 4 collars per trial and 6 consecutive d per collar. The rationale for this approach was to "level the playing field" between the two breeds, as behavior and landscape use can change with increasing time spent in a pasture increases (Stuth, 1991), and interpretations of pasture use may change if different numbers of collars are considered for the different breeds. The proportion of the herd that was represented by collar data varied among trials in the analyses, from 27% to 44% (see Table 2).

The final GPS data subsets selected were evaluated to identify fixes with excessive position dilution of precision (PDOP) values. No data fixes exhibited values > 4.

Ultimately, each GPS dataset retained per cow comprised 1 717 − 1 728 fixes (6 d × 288 fixes day^{-1} = 1 728 fixes).

Defining Seasons on the Basis of Phenology

We sought to compare the landscape use of the breeds in similar forage conditions and also characterize forage conditions in a manner that would be reproducible to improve chances for accurate comparison of this livestock telemetry study with others. Accordingly, we identified seasons in 2008 in the study pasture using MODIS-NDVI from satellite data following methods in Browning et al. (2018), paired each AH trial with a consecutive RC trial with similar pasture-level MODIS-NDVI, and assigned each pair of trials to a season (see Table 2). We identified four seasons (Fig. 3): Pregreenup (1 Jan–6 Jul), Greenup (7 Jul–18 Sep), Peak Green (19 Sep–21 Oct), and Drydown (22 Oct–31 Dec). Of the 10

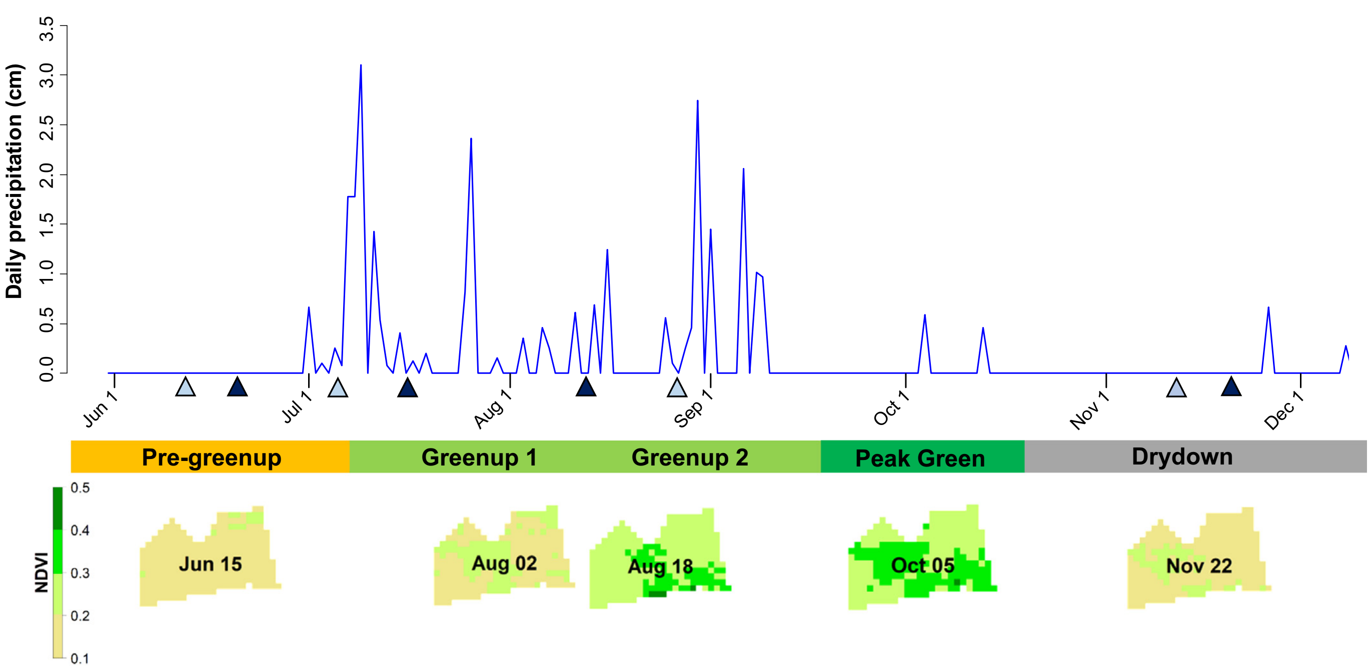

Figure 3. Daily rainfall *(blue line)* and phenologically defined seasons in June — December 2008 *(orange/green/gray bar)*. *Light blue triangles* denote the first day of Angus × Hereford, and *dark blue triangles* denote first day of Raramuri Criollo, trials used for further analysis. Two pairs of retained telemetry trials occurred during Greenup; we refer to them sequentially as Greenup 1 and 2. Raster maps depict MODIS-NDVI (250-m) on 2008 dates occurring during the seasonal stages.

sampling events, 4 were for RC and 6 were for AH. We removed two AH trials from further consideration (31 Jul—12 Aug, 4—15 Dec) because the NDVI during those trials was least similar to their temporally adjacent RC trials. No trials were conducted during Peak Green. Because two pairs of trials retained for further analysis occurred during Greenup, we recognized two phases of that season: Greenup 1 and Greenup 2 (see Fig. 3).

Per MODIS-NDVI maps (see Fig. 3), greenness was relatively limited and patchily distributed during Pregreenup (0.167 ± 0.019 on 15 Jun) and Drydown (0.188 ± 0.012 on 22 Nov) but more abundant and uniformly distributed during Greenup 1 (0.199 ± 0.023 on 2 Aug) and Greenup 2 (0.267 ± 0.044 on 18 Aug). Of the seasons when telemetry trials occurred, Greenup 2 had the highest pasture-level vegetation greenness.

Although the breeds used the pasture in consecutive trials, we contend that breed was not confounded with season, because the seasons were sufficiently long to allow both breeds to graze the pasture during each season. Further, although the assignment of breeds into the pasture was systematic—with the AH trial preceding the RC trial in all seasons except for Greenup 2—the choice of breed in the first trial was randomized. In addition, we assumed that the use of the pasture by one breed did not materially affect forage availability for the next breed due to low stocking rates. The pasture was stocked at an order of magnitude lower than recommended rates for the ecological sites of the pasture (NRCS, 2014).

Constructing Home Ranges

We estimated home range of each individual using the Time Local Convex Hull (T-LoCoH) algorithm in R version 3.4.2 (Lyons et al., 2013). The algorithm constructs home ranges for tracked individuals by drawing convex hulls around nearest-neighbor point sets that are local in both space and time and then sorting and aggregating the temporally and spatially local hulls into utilization distributions (e.g., 95%). Home ranges were constructed following the method for parameter estimation described by Lyons et al. (2013) and the T-LoCoH package for R documentation (Lyons and Getz, 2018). We began by identifying parameters for local convex hulls to circumscribe point sets, in each of 32 samples retained for analysis (2 breeds $\times$ 4 cows $\times$ 4 seasons). This entailed selecting nearest neighbors based on the time-scaled distance value (TSD), which modifies Euclidean distance by the amount of separation in time. TSD includes a parameter s that determines the degree to which time influences the temporal and spatial "distance" between two points; as s becomes larger, the influence of time separation increases. We computed the s parameter based on the daily (24-h) foraging cycle, in recognition that foraging behavior tends to exhibit a daily pattern (Larson-Praplan et al., 2015). As such, two points that were a day apart could not be considered nearest neighbors, even if they were close together in space. To determine the number of neighboring points used to construct local hulls, we selected the "a" method, which intrinsically adapts to point density (Table A.1 contains "s" and "a" values for the 32 samples).

We selected T-LoCoH for home range estimation instead of other methods, such as Minimum Convex Polygon (Harris et al., 1990) or Kernel Density Estimation (Worton, 1989), because the algorithm was a good match for the characteristics of the telemetry data, as well as the foci of our study. Mapping the locations of each sampled individual's 6-d trial revealed a strong signature of linear movements, which hull-based home range estimation methods tend to preserve (Getz and Wilmers, 2004; Getz et al., 2007; Lyons et al., 2013). In addition, the locations were highly autocorrelated in time and space. We selected T-LoCoH because it 1) accounts for temporal overlap of path intersections by incorporating time separation in identification of nearest neighbors (Lyons et al., 2013), 2) addresses autocorrelation via explicitly accounting for the temporal nature of location data when constructing hulls (Fieberg et al., 2010; Van der Weyde et al., 2017), and 3) constructs home ranges at a fine spatiotemporal scale that is tightly linked to the data themselves, thus revealing a more probabilistic picture of space use when evaluating home range on a per-animal basis (Dougherty et al., 2017). Moreover, the study pasture had acute perimeter corners with ample cattle activity. The convex hulls computed by T-LoCoH tended to avoid "overshooting" estimates of pasture usage beyond sharp edges created by fence lines. To our knowledge, this is the first study using T-LoCoH for home range construction for domestic livestock.

Assessing Daily Activity Budgets

Daily activity budgets were quantified by assigning each GPS location to one of three behaviors and then calculating the average time each cow spent per day in each behavior. Movements of ≤ 5 m during a 5-min time interval were assumed to correspond with resting (< 1 m min^{-1}). Movements of ≥ 100 m during a 5-min time interval were assumed to correspond with walking (20 m min^{-1}). Movements ≥ 1 m min^{-1} and ≤ 20 m min^{-1} were assumed to correspond with foraging. Our rationale for using the same velocity thresholds for both breeds (*sensu* Peinetti et al., 2011) had two parts. First, research comparing GPS-based velocities of the two breeds conducted on the Jornada Experimental Range and the Teseachi Experimental Range in west-central Chihuahua, Mexico, found only minor differences in velocity/behavior relationships of the two breeds (Roacho Estrada, 2008). Second, a study conducted in the shortgrass steppe of Colorado that used 5-min GPS fixes, dual-axis activity sensors, and field observations to assess relationships between GPS-velocities and behavioral classes supports the thresholds used in this study (Augustine and Derner, 2013). That study used yearling steers with average weights between the weights of our RC and AH herds, lending further support for using the thresholds for both breeds in this study.

Modeling Breed Differences in Home Ranges and Daily Activity Budgets

We used 2-way analysis of variance (SAS/STAT 9.4 software) to evaluate breed differences in home range size (ha cow^{-1} 6-d trial^{-1}) and daily time spent resting, foraging, and walking (h cow^{-1} day^{-1}). For each response, we modeled breed, season, and their interaction as fixed effects and compared least squares means with protected Fisher's LSD. The data set comprised four collared cows per 6-d trial ($n = 4$ for each breed $\times$ season combination).

Mapping Cattle Distribution and Hotspots of Use

We used gridded time-use maps in the tlocoh.dev package in R version 3.4.2 (Lyons, 2018) to quantify herd-level distribution of each breed in the four seasons of the study. The process comprised creating a map for each of 32 cows (4 cows $\times$ 8 trials) and then creating 8 maps of the *average* distribution of the 4 sampled cows per trial.

We began by selecting a grid with 150 $\times$ 150 m grid cells. Then, in each of the 32 maps, we quantified the number of visits made by the cow to each cell and the average time spent per visit. A visit was defined as at least one occurrence in the grid cell separated by at least 12 h from the previous occurrence in that grid cell (i.e., whenever the individual was away from the grid cell for > 12 h, the next time she returned to the grid cell was counted in a separate visit). Average time spent per visit was calculated as the mean of the number of fixes per visit multiplied by the sampling interval of 5 min (we ultimately reported the time in hours). We used all fixes, not just those assumed to correspond with foraging, for this analysis.

Next we calculated herd-level visitation and duration at each cell by calculating the average of the cell values in the four maps generated per trial. This resulted in one gridded time-use map per breed per season. To visualize the spatial patterns of visitation and visit duration, we symbolized cells on the basis of where they fell on a two-dimensional scatterplot of the average number of visits and the average visit duration for each cell. Because the maps are based on averages, visitation is not presented as a discrete value but rather as ranging from 0 to 6.25. Likewise, duration represents the *average* time spent by the four cows during their visits to a given cell. Hotspots were defined as grid cells visited on average > 4 times for > 2 h per visit.

Identifying Preferences for Ecological States While Foraging

We used Ivlev's electivity index (E_i; Jacobs, 1974) to estimate selectivity of the breeds in relation to three generalized ecological states (*sensu* Putfarken et al., 2008). We calculated Ivlev's index per cow per state per 6-d trial as:

$$\mathbf{E_i} = (\mathbf{r_i} - \mathbf{p_i})/(\mathbf{r_i} + \mathbf{p_i}) \quad (1)$$

with r_i as the proportion of foraging time in ecological state i and p_i as the proportion of area covered by ecological state i. We then calculated the average of the four sampled cows per trial, resulting in one E_i index per ecological state per trial. We created bar charts to illustrate E_i, which ranged from −1 (complete avoidance) to 1 (perfect preference), with 0 indicating indifference (i.e., fraction of foraging time equaled the fraction of the area covered by the state).

States corresponding to areas directly adjacent to watering points (see Fig. 1) were excluded from the calculations because we conjectured that true foraging was not occurring in those areas, only rates of movement assumed to correspond to foraging.

We chose Ivlev's electivity index over other selectivity indices because it allows for a straightforward interpretation of preference, avoidance, and indifference in relation to respective vegetation types (Putfarken et al., 2008). We focused on selectivity of ecological states for two reasons: 1) understanding livestock use of states has important implications for sustainability of Chihuahuan Desert range ecosystems, ranching economics, and the interactions of these systems, and 2) nonvegetation factors known to generally influence cattle spatial distribution patterns, such as distance to and from drinking water and pasture topography, were deemed a priori to be unimportant in this relatively flat, well-watered pasture. Further, state mapping is reproducible in any pasture (Steele et al., 2012), and we investigated selectivity in relation to states to increase chances for accurate comparison between this and other livestock telemetry studies.

We used 3-way analysis of variance (SAS/STAT 9.4 software) to evaluate breed and seasonal differences in E_i per ecological state. For each variable we modeled breed, season, ecological states, and their 2-way and 3-way interactions as fixed effects and compared least squares means with protected Fisher's LSD.

Results

Home Range Size and Herd-Level Spatial Extent

Home range sizes of RC were larger than those of AH during Pregreenup ($P < 0.0001$) and Drydown ($P = 0.0143$) (Table 3). Conversely, sizes converged during Greenup 1 and Greenup 2 (no trials occurred during the season Peak Green). After accounting for seasonal differences, the 6-d home range of RC exceeded that of AH by 15.50 ± 3.26 ha ($P < 0.0001$).

Table 3
Average home range size (ha) of conventional (AH) and heritage (RC) cattle in the study, with home ranges (95%) defined using Time Local Convex Hulls. Values represent the mean ± standard error of four collared cows per breed and season. For a given variable, means with the same letter are not different at α = 0.05; **bold font** denotes that the breeds differed significantly with the season.

	AH	RC
Pregreenup	**18.26 ± 4.62^{D}**	**49.69 ± 4.62^{A}**
Greenup 1	28.95 ± 4.62^{BCD}	39.73 ± 4.62^{AB}
Greenup 2	37.69 ± 4.62^{ABC}	40.25 ± 4.62^{AB}
Drydown	**24.36 ± 4.62^{CD}**	**41.60 ± 4.62^{AB}**

The RC herd visited a larger number of 150 × 150 m pixels in the pasture per season (Fig. 4). The greatest breed divergence was during Pregreenup (difference of 450 map pixels) and Drydown (565 map pixels). Smaller differences occurred during Greenup 1 (150 map pixels) and Greenup 2 (70 map pixels). RC visited more watering points than AH in every season (see Fig. 4).

Daily Activity Budgets

AH rested more each day in all seasons except Greenup 2, when there was no difference between the breeds (Table 4). There was no difference between daily foraging time in any season except Greenup 2, when AH daily foraging time was longer than that of RC. RC spent more time each day walking than AH during all seasons except Pregreenup. After accounting for seasonal differences, AH spent more time than RC resting each day (0.56 ± 0.18 h, $P = 0.0016$). RC spent comparatively more time walking overall (0.78 ± 0.11 h, $P < 0.0001$).

Hotspots

Over the four seasons, the AH herd had six hotspots (i.e., 150 × 150 m grid cells visited on average > 4 times for > 2 h) and the RC herd had three (see Fig. 4). During Pregreenup, RC had one hotspot at the permanent Watering Area ecological state in the west side of the pasture. AH had three on the permanent Watering Area near the pasture entrance and one on the Grassland ecological state in the southeast corner of the pasture (see Figs. 1 and 4). That Grassland area supported black grama, a palatable perennial grass valued for forage production and soil conservation (Steele et al., 2012). During Greenup 1, RC had a hotspot on the Bare/Forbs state and one at the rain-fed Watering Area adjacent to that state, while AH again had a hotspot near the permanent Watering Area by the pasture entrance. Neither breed had a hotspot during Greenup 2. During Drydown, AH demonstrated an increase in visitation and duration of visits at the Bare/Forbs state on or near the Gypsiferous Playa, with one hotspot at the nearby rain-fed Watering Area (see Figs. 1 and 4).

Ecological State Preferences While Foraging

Overall, compared with AH, RC preferred the Bare/Forbs state more strongly ($P < 0.0001$) and avoided the Shrubland state more strongly ($P < 0.0001$). Electivity in relation to the Grassland state was not significantly different between breeds ($P = 0.0934$).

Noteworthy seasonal differences occurred during Greenup 1 and 2 (Fig. 5), when RC strongly preferred the Bare/Forbs state yet AH strongly or weakly avoided it, and RC strongly avoided the Shrubland state yet AH lightly preferred or lightly avoided it.

Discussion

Home Range Sizes and Spatial Extents of Herds

Over the course of this 6-mo telemetry study, the spatial coverage of heritage RC and conventional AH diverged and converged on a seasonal basis. As we predicted, individual home range sizes and herd-level spatial extents of RC were larger than those of AH during periods of relatively low greenness and forage production (Pregreenup, Drydown), but home range sizes and spatial extents of the herds converged during periods with more green, plentiful forage (Greenup 1, Greenup 2).

These results correspond with a previous study conducted in 2005, when AH and RC covered a similar spatial extent during times of the year when green forage was relatively plentiful and well distributed, but the heritage RC covered comparatively more of the pasture when green forage was relatively scarce and patchily distributed (Peinetti et

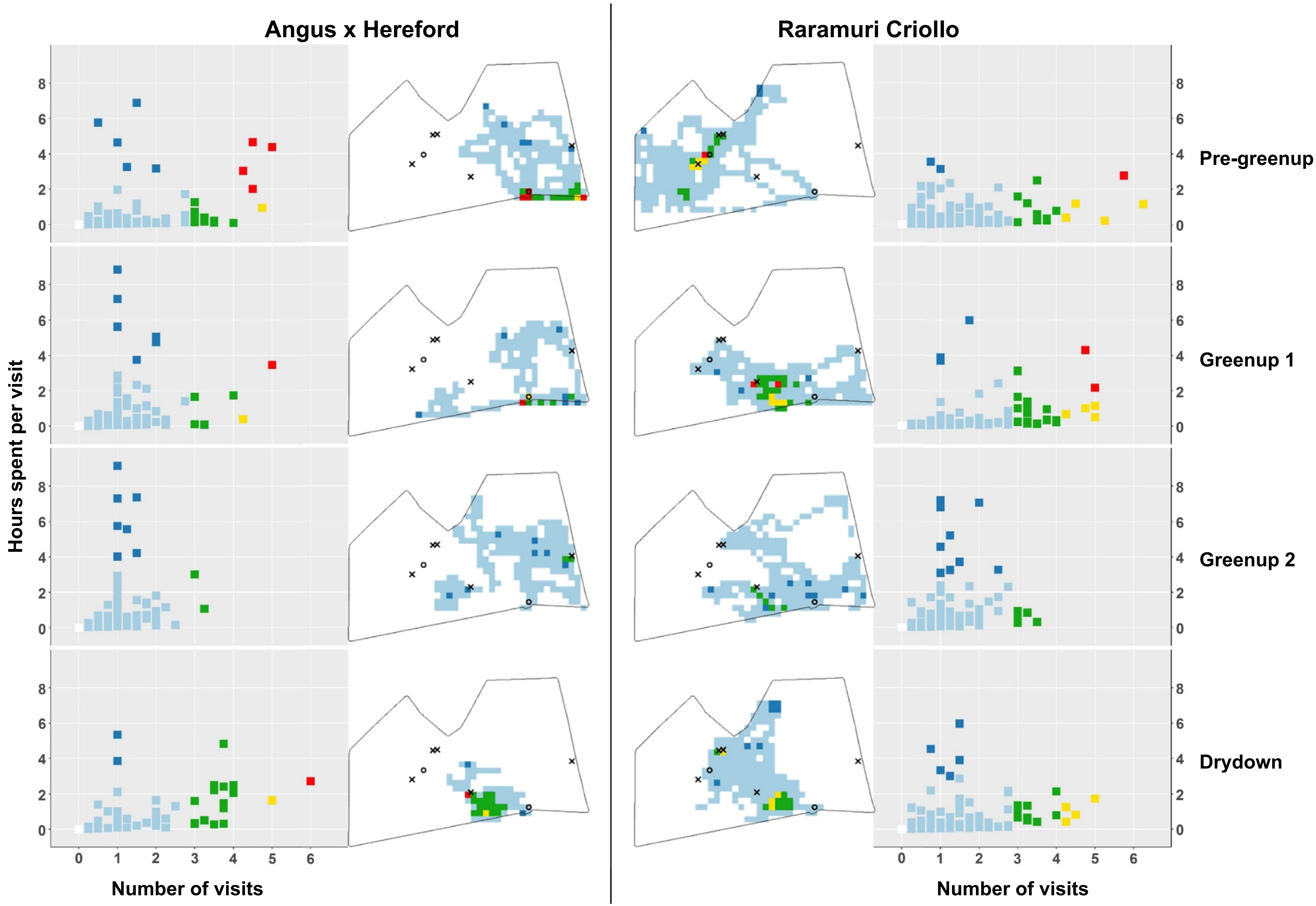

Figure 4. Cattle distribution quantified using the gridded time-use map function in the Time Local Convex Hulls program. Each grid cell represents 150 × 150 m; scatter plots are map legends. Values represent the average of four cows per season. Hotspots, colored *red*, are grid cells visited on average > 4 times for > 2 h per visit. X's represent rain-fed water points. O's represent permanent watering points.

Table 4
Daily activity budgets (h) of conventional (AH) and heritage (RC) cattle. Daily time was partitioned into behaviors on the basis of the rate of movement. Values represent the mean ± standard error of four collared cows per breed and season. For a given variable, means with the same letter are not different at $\alpha = 0.05$; **bold font** denotes that the breeds differed significantly within the season.

	Resting		Foraging		Walking	
	AH	RC	AH	RC	AH	RC
Pregreenup	**13.26 ± 0.25**^{A}	**12.55 ± 0.25**^{B}	9.28 ± 0.26^{E}	9.63 ± 0.26^{DE}	1.44 ± 0.15^{CDE}	1.82 ± 0.15^{BC}
Greenup 1	**12.17 ± 0.25**^{BC}	**11.26 ± 0.25**^{DE}	10.52 ± 0.26^{C}	10.23 ± 0.26^{CD}	**1.25 ± 0.15**^{E}	**2.45 ± 0.15**^{A}
Greenup 2	11.28 ± 0.25^{DE}	11.83 ± 0.25^{CD}	**11.28 ± 0.26**^{B}	**10.23 ± 0.26**^{CD}	**1.38 ± 0.15**^{DE}	**1.93 ± 0.15**^{B}
Drydown	**11.04 ± 0.25**^{E}	**9.85 ± 0.25**^{F}	12.27 ± 0.26^{A}	12.45 ± 0.26^{A}	**0.69 ± 0.15**^{F}	**1.69 ± 0.15**^{BCD}

al., 2011). Together, the studies support the notion that when forage conditions are poor in the Chihuahuan Desert, heritage RC cover more ground than conventional AH. It is reasonable to surmise that such landscape use could improve the sustainability of agriculture in arid landscapes, but additional studies on a variety of ranches and seasons are needed before that conclusion can be made.

Notably, findings of this study and those of Peinetti et al. (2011) concurred, even though they were conducted in different pastures (3 km apart), in different years, with different intra-annual timing of precipitation and green forage production (2005 and 2008 in Fig. 2b-c). Given the extreme variation in the interannual timing of rainfall and forage phenology in the Chihuahuan Desert, researchers comparing landscape use of cattle should consider defining seasons on the basis of phenology to enhance capacity to accurately compare across studies and facilitate meta-analyses (Browning et al., 2018).

Daily Activity Budgets

In light of anecdotal evidence from early adopters of the heritage breed, we predicted that compared with the conventional cattle, the heritage cattle would allocate more time to foraging or walking each day. Telemetry data supported this prediction, but interestingly much of the difference was due to time spent walking, not foraging. Notably, there was no difference between the breeds in daily foraging time except for during Greenup 2, when AH foraged for *longer* than RC each day. It is possible that this AH behavior was related to specialized knowledge of the environment learned by the AH study cows from their mothers (Zimmerman, 1980; Bailey et al., 2010). Before the 2008 study, both breeds had spent at least 3 yr on the Jornada. However, whereas the AH cows were born and raised on the ranch by mothers with experience grazing the ranch, the RC cows had been imported

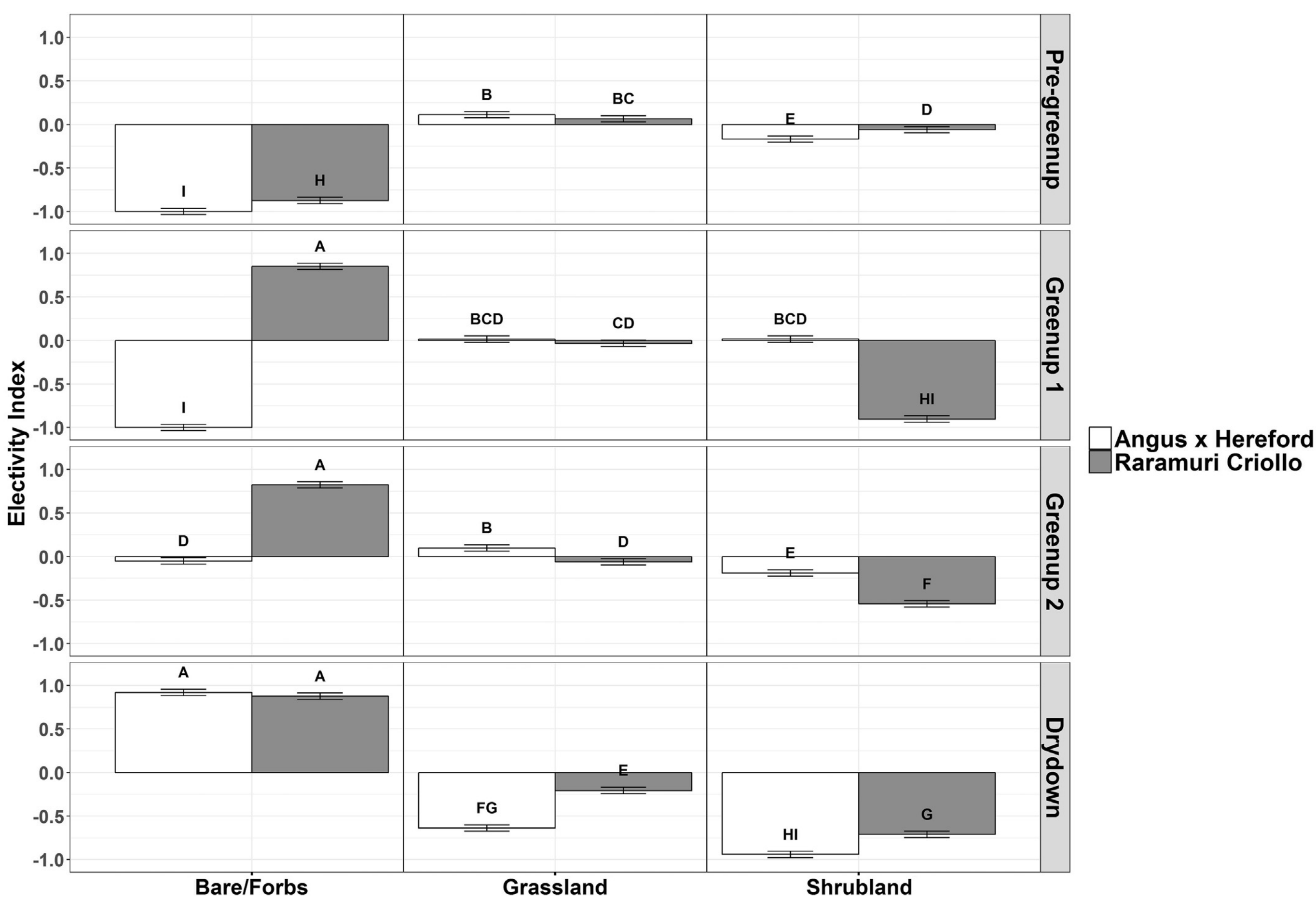

Figure 5. Ivlev's electivity index E_i in relation to three generalized ecological states in the study pasture, calculated for 4 collared cows per breed and season, using only GPS locations assumed to correspond with foraging. E_i ranges from −1 (complete avoidance) to 1 (perfect preference), with 0 indicating indifference (i.e., fraction of foraging time equals the fraction of the area covered by the state). Values represent the mean ± standard error of four collared cows per breed and season. Means with same letters are not different at $\alpha \le 0.05$.

from Mexico in 2005. It is possible that the boost in activity by the AH cows during Greenup 2 was triggered by a learned behavior not captured by the measurements in this study. Alternatively, it is possible that shifts in the array of plants or the digestibility of forage within Greenup 2 caused the breed difference in daily foraging time (Van Soest, 1994). Regardless, future comparative studies should use cattle born and raised on the ranch or individuals of the same age and class imported to the ranch at the same juncture.

Hotspots

The conventional AH breed had twice as many hotspots as the heritage RC breed, which aligned with our third prediction. It is important to note that while AH had more hotspots overall, most of the hotspots for both breeds were located at or near artificial watering points. It is a longstanding observation that the arrangement of watering points is a key factor in livestock distribution in arid rangelands worldwide (Valentine, 1947; Holechek, 1991; Bailey, 2004; Pringle and Landsberg, 2004; Hunt et al., 2007), but this is the first study to illustrate watering points as hotspots of use for heritage RC. This finding suggests that RC may have similar watering requirements as AH, but direct measurements of drinking, including at rainfed tanks, are necessary to further explore this inference.

In addition to detecting the importance of watering points for both breeds, we also observed that the timing and location of AH hotspots corresponded with livestock landscape use patterns known to adversely impact playa surface soils and black grama, two natural resources of concern in the Chihuahuan Desert. The period of January–May is associated with the strongest winds in the Chihuahuan Desert and the highest probability of dust emissions from playas (Bergametti and Gillette, 2010). Because the study began in June, neither of the breeds were observed during that most sensitive time of year. However, dust emissions from the Gypsiferous Playa ecological site are known to increase after cattle trampling (Baddock et al., 2011). As dust emissions may result from cumulative trampling, an increase in visitation and duration of visits on or near the playa at calendar year end—as observed for AH in Drydown 2008—may intensify dust emissions during the sensitive period in the first half of the following year (Baddock et al., 2011). Black grama, moreover, is known to be most susceptible to grazing effects in the January — May period because defoliation coupled with wind erosion can create a harsh environment for subsequent growth (Bestelmeyer et al., 2013). AH had a hotspot of use on black grama in mid-June (Pre-greenup), soon after the windy season. The timing of concentrated use by AH of the black grama community during Pregreenup and the increase of use of the Bare/Forbs state during Drydown may signal a tendency for comparatively greater impact of AH on those resources, but at this point that idea is a hypothesis to be tested across multiple, entire calendar years. Direct measurements of wind, dust emissions, and black grama growth on a pasture grazed by both breeds would be necessary for definitive results.

Ecological State Preferences While Foraging

Our fourth prediction, that throughout most of the study RC would concentrate most of its foraging time in the Shrubland and Bare/Forbs states, whereas AH would concentrate most of its foraging time in the Grassland state, was only partially supported by study data. Statistically, RC did prefer the Bare/Forbs state more strongly overall. However, contrary to our prediction, RC avoided the Shrubland state more strongly than AH, and the preference by AH for Grassland was generally weak and did not differ significantly from that of RC.

Seasonal changes in phenology and associated fluctuations in forage quality likely contributed to the preferences of the breeds changing with the seasons. Moreover, ambient temperatures during different seasons may have further altered preferences of the two breeds. These complexities were not adequately captured by our prediction. Notably, breed differences in relation to the Bare/Forbs state were most pronounced during the relatively wet, green periods of Greenup 1 and 2, when RC strongly preferred the state and AH avoided it. Concurrently, AH demonstrated a weak preference for Shrubland during Greenup 1 and joined RC in strongly preferring the Bare/Forbs state only during Drydown. Though not directly measured, we surmise that the soils of the Bare/Forbs state were likely holding water during Greenup 1 and 2, rendering its perennial forbs greener and more nutritious; however, this nutrition would have been present in August, when ambient temperatures were hot. We infer that RC may have been able to capitalize on the higher nutrition available in the Bare/Forbs state during Greenup 1 and 2 due to heat tolerance, while AH may have needed to retreat to the Shrubland state for shade and was only able to preferentially forage in the Bare/Forbs state once temperatures had cooled during Drydown (contributing to the hotspot by AH on the Bare/Forbs state during Drydown). Although it is plausible that heat tolerance can affect diet selection (Nyamuryekung'e et al., 2017), direct measurements of dietary intake (e.g., Spiegal et al., 2018b) and heat stress (e.g., Hammond et al., 1996) are necessary before definitive conclusions can be drawn.

Together, the distribution maps and selectivity indices illustrate that cattle in arid environments can concentrate impacts on particular ecological states. Although stocking rates in the Chihuahuan Desert are typically low, individual management units can be large and topographically diverse (Havstad et al., 2006). The implicit assumption that grazing impacts are evenly distributed across the pasture is seldom valid in commercial practice (Bailey and Brown, 2011). This differential use could result in a situation in which stocking rates that are low for the entire pasture are effectively higher in certain areas of that pasture. The concentrated use of an ecological state could contribute to decreased resilience and increased potential for a transition to other states, which would not be predicted on the basis of pasture-wide stocking rate alone. We suggest future agroecological studies use predicted livestock movement patterns as part of the experimental design and direct measures of animal use to calculate effective stocking rates of particular ecological sites and states to better describe and understand influences of grazing on state transitions.

Implications

Results of this study corroborate preliminary evidence suggesting that heritage RC differ in important ways from the AH cattle used widely in the Chihuahuan Desert. In particular, results support conjectures about the heritage breed having a wider spatial distribution during drier seasons, greater daily mobility, superior heat tolerance, and lower impact on resources of concern. If the landscape use and behavioral patterns documented here are consistent in a wide range of conditions, stocking desert pastures with the heritage breed instead of conventional breeds may help producers more effectively advance the sustainability of agriculture by meeting dual goals of agricultural production and natural resource conservation. However, in order for producers to make fully informed choices, more information is necessary to assess whether the landscape use of the heritage breed would result in outcomes that are equally or more favorable than outcomes of "business as usual" cattle production (Spiegal et al., 2018a). This will require a new understanding of how livestock characteristics and use of spatiotemporally variable desert landscapes translate into a diversity of outcomes, including cattle weight gains, calving rates, supplemental feed costs, ranch solvency, soil health, and biodiversity. These outcomes must be assessed via direct measurements across multiple herds, years, operations, and pastures with different vegetation configurations. Enterprise budgets and other data streams informing understanding about barriers to adoption of heritage genetics should also be the focus of future research.

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Appendix A

Table A.1
T-LoCoH parameters *s* and *a*. See Table 2 for more on study design.

Season	Trial	Breed	Collar number	s	a
Pregreenup	1	AH	656	0.013328	300
	1	AH	658	0.010545	300
	1	AH	664	0.01324	300
	1	AH	666	0.013336	500
	2	RC	656	0.01018	500
	2	RC	658	0.012326	300
	2	RC	664	0.008234	400
	2	RC	666	0.008858	500
Greenup 1	3	AH	656	0.013018	500
	3	AH	658	0.012555	400
	3	AH	664	0.012913	500
	3	AH	666	0.012443	600
	4	RC	656	0.009651	300
	4	RC	658	0.005642	300
	4	RC	664	0.010226	400
	4	RC	666	0.004901	300
Greenup 2	6	RC	656	0.016038	500
	6	RC	658	0.012347	300
	6	RC	660	0.013111	500
	6	RC	666	0.011966	400
	7	AH	656	0.007019	300
	7	AH	658	0.009407	500
	7	AH	660	0.006237	300
	7	AH	666	0.008741	500
Drydown	8	AH	656	0.002593	400
	8	AH	658	0.002574	400
	8	AH	664	0.002742	300
	8	AH	666	0.002368	400
	9	RC	621	0.01515	400
	9	RC	622	0.010737	400
	9	RC	664	0.015154	500
	9	RC	666	0.011783	300

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