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Foraging behavior of Argentine Criollo and Angus cows grazing semi-desert rangelands in the Arid Gran Chaco region of Argentina☆

Oscar A. Herrera Conegliano[a,b,*], Lisandro J. Blanco[c], Santiago A. Utsumi[d], Andres F. Cibils[d], Maria G. Cendoya[e], Florencia Jaimes[e], Andres F. Moltoni[f], Patricia Ricci[g,h]

[a] *Instituto Nacional de Tecnología Agropecuaria (INTA), Estación Experimental Catamarca, Argentina*
[b] *Facultad de Ciencias Agrarias, Universidad Nacional de Catamarca, Argentina*
[c] *Instituto Nacional de Tecnología Agropecuaria (INTA), Estación Experimental, La Rioja, Argentina*
[d] *Department of Animal and Range Sciences, New Mexico State University, Las Cruces, NM, 88001, USA*
[e] *Facultad de Ciencias Agrarias, Universidad Nacional de Mar del Plata, Argentina*
[f] *Instituto Nacional de Tecnología Agropecuaria (INTA), Estación Experimental Castelar, Argentina*
[g] *Instituto Nacional de Tecnología Agropecuaria (INTA), Estación Experimental Balcarce, Argentina*
[h] *Consejo Nacional de Investigaciones Científicas y Técnicas, IPADS, Balcarce, Argentina*

A R T I C L E I N F O

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A B S T R A C T

We monitored grazing behavior and habitat selection of Argentine Criollo (AC), South American heritage cattle breed, and Angus (AA) cows during summer and winter of 2016 (wetter year) and 2017 (drier year) at a site in La Rioja, Argentina. In each year and season, five AC and five AA cows were fitted with GPS collars configured to log animal position at 10-min intervals for 40 days. Movement, activity, and vegetation use patterns of each breed were derived from the GPS data. In summer, AC cows traveled similar daily distances, explored smaller (wetter year) or slightly larger (drier year) areas of the pasture, tended to move along more sinuous path trajectories, and showed stronger selection of the vegetation unit with higher forage quality and lowest woody cover compared to AA counterparts. AC cows allocated similar (wetter year) or more time to graze (drier year), allocated roughly the same amount of time to travel, and spent similar (wetter year) or less time resting (drier year) than AA cows. In winter, foraging behavior differences between breeds were only observed in the drier year. AC cows traveled farther and spent less time resting than AA counterparts that year. When comparing summer vs. winter movement patterns of each breed, AC cows showed an apparent greater ability to adapt to changing forage conditions (foraging plasticity) compared to AA counterparts which appeared to exhibit more rigid foraging patterns. Criollo cattle could be a tool to increase the resilience of Arid Chaco beef systems in the face of climate change. The rangeland conservation implications of raising Criollo vs. British beef cattle require further investigation.

1. Introduction

Climate change is posing new challenges for graziers who raise livestock on desert and semi-desert rangelands worldwide (Polley et al., 2017; Godde et al., 2020). Increased variation in precipitation patterns and greater frequency of weather extremes including heat waves, wildfires, and drought (Sloat et al., 2018; Churchill et al., 2022; Wilcox et al., 2022), are accelerating the quest for novel adaptation strategies (Briske et al., 2015; Spiegal et al., 2020). Grazing remains the primary land use of arid ecosystems globally (Maestre et al., 2016), but the sustainability of desert animal agriculture is uncertain and increasingly depends on graziers' ability to select animal genetics that match grazing environments which are becoming more heterogeneous in space and time (Briske et al., 2021).

The use of locally adapted livestock breeds has been suggested as a cost-effective alternative to improve the resilience of rangeland-based animal agriculture enterprises (Spiegal et al., 2020). Previous studies conducted in the deserts of the southwestern United States, showed that compared to commercial beef cattle, heritage cows from northern Mexico (Raramuri Criollo) ranged farther from water, covered larger areas of extensive desert pastures, and exhibited a lower number of grazing hotspots during times of the year when herbaceous forage was

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* Corresponding author. INTA- Estación Experimental Catamarca, Ruta Provincial N° 33 km 4, (4705) Sumalao, Valle Viejo, Catamarca, Argentina.
E-mail address: herrera.ariel@inta.gob.ar (O.A. Herrera Conegliano).

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dormant and/or scarce (Peinetti et al., 2011; Spiegal et al., 2019; Nyamuryekung'e et al., 2022). An analysis of the economics of raising heritage cattle in this environment showed that in the Chihuahuan Desert, a rancher could obtain higher returns raising Criollo vs. commercial beef cows (Torell et al., this issue). Spiegal et al. (2020) therefore suggested that the use of heritage genetics could be a valuable tool to help ranchers adapt to increasing weather variability in the US Southwest. The efficacy of this approach, however, has not been tested in other arid and semi-arid ecosystems with different heritage cattle breeds or biotypes. Our primary goal was to determine whether a locally adapted heritage cattle breed, the Argentine Criollo (that differs in important ways from the Raramuri biotype), exhibited foraging traits similar to those of its North American relatives and whether use of this livestock genetics could be a viable climate adaptation strategy for ranchers in South America's Gran Chaco ecosystem.

The Gran Chaco region is one of the driest forest ecosystems of South America extending over northern Argentina, Paraguay, and southern Bolivia. In this region, cattle production based primarily on cow–calf operations is the main source of agricultural income and livelihood for many communities (Ferrando et al., 2001, 2006). A diversity of native grasses, seasonal forbs and browse species are main diet resources for cattle (Ferrando et al., 2001; Blanco et al., 2008). Despite the richness and abundance of forage species, previous studies have documented declines of up to 50% in the carrying capacity of rangelands across the Gran Chaco region (Blanco et al., 2005). The associated decline of native grasses and forbs, increasing shrub encroachment and associated patterns and risks for increasing soil erosion are among major concerns for rangeland management and conservation (Blanco et al., 2005).

Argentine Criollo (AC) cattle are direct descendants of cattle brought into the continent by the first Spanish explorers some 500 years ago (Armstrong et al., 2022). These animals evolved with little to no artificial selection pressure, giving rise to the current AC cattle that are known to thrive in high altitude steep mountain ranges, and arid grasslands of northwestern Argentina. This region that currently faces increasing variability of precipitation and temperature, and greater livestock numbers as a result of agricultural expansion and rural development (Namur et al., 2004; Ferrando et al., 2006). Argentine Criollo cows perform better than commercial beef cattle in Arid Chaco rangelands increasingly impacted by drought. Namur et al. (2004) showed that AC cows sustained higher pregnancy rates (93%) than Angus counterparts (36%) during drought. Interestingly, Angus cows in this study were the result of a decades-long cross-absorption breeding program of a local and rich genetic pool of cattle (Namur et al., 2004; Ferrando et al., 2006). Although beef production traits of Argentine Criollo cows have been extensively studied (Anderson et al. and references therein), no research addressing their foraging behavior and landscape use patterns relative to commercial beef cows has been conducted to date.

The objective of this two year study was to evaluate foraging behavior patterns of Argentine Criollo and Angus cows grazing Arid Chaco rangeland. We sought to determine whether desirable foraging traits observed in North American Criollo cows in the Chihuahuan Desert were also present in AC cows and whether AC cows showed a superior ability to adapt to varying environmental conditions of Arid Chaco rangeland.

2. Materials and methods

2.1. Study site

Our study was carried out at "Los Cerrillos" Experiment Station (Lat. 29°58′19,86''S, Long. 65°52′55.84''O) of the National Institute of Agricultural Technology (INTA) of La Rioja, Argentina. The experiment station is located 70 km from the city of Chamical, La Rioja, and comprises 8,263 hectares of typical semi-arid ecosystems of the Gran Chaco region (Morello et al., 1985). A pasture of 1,183 ha of native rangeland was used for this study (Fig. 1).

The dominant climate at this research site is semiarid to subtropical, with hot summers and mild winters. January (26 °C) and July (11 °C) are the warmest and coldest months of the year, respectively. The region also faces increasing annual and seasonal variability in precipitation regimes. For the last 40 years, the average annual precipitation varied between less than 200 mm in dry years and over 600 mm in wet years, with more than 80% of rainfall events occurring as summer monsoons between October and March (average precipitation 400 mm, Fig. 2).

Soils at the site are typical Aridisols and Entisols, exhibiting contrasting textures. The dominant vegetation unit is the xerophytic shrubland savanna characterized by native isolated trees dispersed over a shrub layer with herbaceous vegetation understory dominated by native grasses. The most dominant shrubs are *Larrea, mimozyganthus, Senna*, and *Capparis* sp. Dominant trees include *Aspidosperma* and *Prosopis* sp. The herbaceous understory is dominated by C4 perennial grasses, including *Trichloris, Chloris, Pappophorum, Aristida*, and *Setaria* sp. A supervised vegetation classification of a Landsat 5 TM multispectral imagery (30 × 30 m pixel), acquired on March 1, 2014, was conducted prior to placing animals in the research pasture. Seven vegetation units (VU) were determined in this analysis (Fig. 1).

Summer and winter sampling of the dominant VUs was carried out in February (wet season) and June (dry season) of 2016 and 2017, respectively. The sampling was carried out following methods described by Daubenmire (1959). Briefly, plant cover and density were measured on a 500 m transect established in each defined VU. A total of 50 readings were made in each transect, one reading every 10 m of the transect, using a 0.5 m^2 (1 m × 0.5 m) quadrat. One transect per VU was used totaling six 50 m transects in the study pasture. Transects were not permanent, however vegetation sampling in each season and year occurred in the same general locations of the pasture. Readings included vegetation cover (%), plant density (plants/ha) of dominant species, bare ground cover (%) and litter cover (%), respectively (Daubenmire, 1959). Botanical composition changes associated with distances to the only available watering hole were determined in VUs that were represented both in areas near and far from water. VUs representing less than 2% of the total study area were not discriminated and were excluded from analyses (Sawalhah et al., 2016).

Forage availability (grasses and broadleaf forbs) was estimated by clipping forage quadrats at ground level (Daubenmire 1959). Forage sampling was carried out in the transects used to evaluate plant cover and density of each VU. After completing cover and plant density estimates, all quadrats were clipped (50 per transect) and grass and broadleaf forbs were placed into separate bags and dried at 60 °C for 48 h to determine dry matter content per plant class. A total of 600 biomass samples (50 grass and 50 broadleaf samples for each of six VUs) were clipped and dried in each season (i.e. 1,200 biomass samples were processed in each of the two years of the study).

Five composite samples for grasses and five composite samples for broadleaf forbs per transect (squares 1–10, 11–20, 21–30, 31–40 and 41–50) collected in the first year of the study (2016) were ground using a Thomas Willey Model 4 mill with a 2 mm mesh. Ground samples were sent to the lab to be analyzed for content of crude protein (CP), neutral detergent fiber (NDF) and acid detergent fiber (ADF). The same procedures were used to collect and analyze summer and winter forages. Forage chemical analyses were therefore conducted on a total of 120 samples (60 for each of summer and winter of 2016). Due to budgetary constraints, no chemical analyses were conducted in 2017.

2.2. Animals and GPS data collection

Protocols for the use and handling of animals followed the institutional guidelines for animal care of INTA, Argentina (Comite Institucional para el cuidado y uso de animales de experimentación, CICUAE,). Rangeland-raised Argentine Criollo and Angus cows from herds locally developed at "Los Cerrillos" Experiment Station were used in this study.

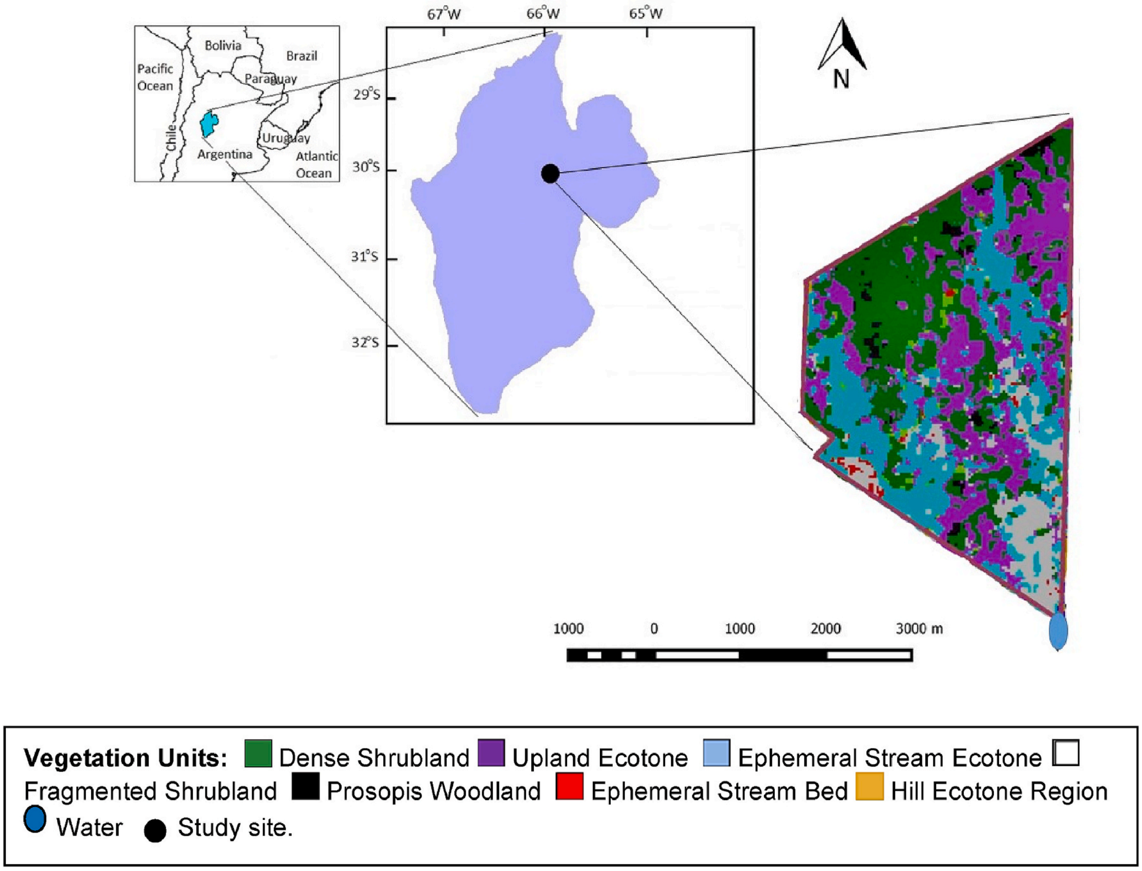

Fig. 1. Geographical location of Los Cerrillos INTA EEA La Rioja Experiment Station within the Arid Gran Chaco and pasture study site with main vegetation units (Lat 29° 58′19.86′′S, Long 65° 52′55.84′′W).

The Angus herd was developed during the 1970s by the absorption cross-breeding of Angus bulls on a former commercial crossbreed cow herd that included Argentine Criollo x Hereford and Argentine Criollo x Shorthorn crossbred genetics (Anderson et al., 1980). The Argentine Criollo cows were obtained from a purebred herd developed by the INTA Leales Experiment Station, in Tucuman, Argentina.

Five mature cows between 5 and 7 years old of each breed (10 cows total) were selected and used for focal observations of grazing behavior during the summer (wet) and winter (dry) season of 2016 (normal rainfall) and 2017 (dry year). The average live weight of the Argentine Criollo cows was 411 ± 22 kg (mean ± SE) with a range between 380 and 420 kg. The average live weight of the Angus cows was 443 ± 22 kg with a range between 400 and 440 kg. Calving dates were similar for the two breeds and occurred from November to mid-January for the two years of study. All study cows were managed equally. Cows were nursing calves of up to ~4-months of age during the summer (wet season) and were managed as dry (non-lactating) cows during winter (dry season). Weaning occurred when calves were ~5–6 months of age. However, actual weaning dates varied across years depending on the cows' body condition, the live weight of calves, severity of drought, and overall condition of the range.

Animals were tracked with cattle GPS collars configured to log positions at 10 min intervals. Collars weighed ~620 g, had memory capacity to store up to 4095 position records, and were powered by a 3.6 V rechargeable battery providing autonomy for 10 to 12 observation days (Gorandi et al., 2016). Cattle movements were monitored during windows of approximately 36 nonconsecutive days during each summer and winter. Summer monitoring was conducted from February 24 to April 4, 2016, and from February 22 to April 4, 2017, whereas winter monitoring occurred between June 10 and July 29, 2016, and between August 8 and September 16, 2017. Cows grazed jointly in the same study pasture along with 32 additional cows (½ Angus and ½ Argentine Criollo) that were used as put-and-take animals for adjustment of stocking rates. Cows remained in the study paddock for the 2 years of the study, starting on January 1 in 2016 and finishing on January 15 in 2018. Missing data due to collar failures are detailed in Table S1 (Suppl. Mat.). Collars that recorded less than 85% of expected GPS fixes in a day (i.e. $\leq$ 121) were excluded from analysis for that given day (Table S1, Suppl. Mat.) and days in which one or both breeds had less than three animals with complete GPS data sets were excluded from analysis (Table 1, Suppl. Mat.).

2.3. Animal movement, activity and vegetation interactions

Collar GPS data were retrieved, imported and projected into Q-GIS software (Quantum GIS Development Team, 2016) using a UTM system (WGS84, UTM, zone 20 south, EPSG 32720) for generation of shapefile datasets suitable for statistical analysis with R software (R Core Team, 2017). Daily cow tracks were processed with the adehabitatLT analytical package for R (Calenge, 2006) for calculation of distance traveled between locations and daily distance traveled (m/day).

Animal activity associated with each GPS location was classified as resting, traveling, or grazing, based on estimates of movement velocity between successive GPS fixes following Nyamuryekung'e et al. (2020). Consecutive GPS locations separated by $\leq$ 10 m were classified as resting, those separated by 200 m or more were classified as traveling, whereas consecutive fixes with distances between 10 and 200 m were classified as grazing.

Frequency of visits to the water trough and time spent at water per visit was determined using GPS track records. Frequency of visits was

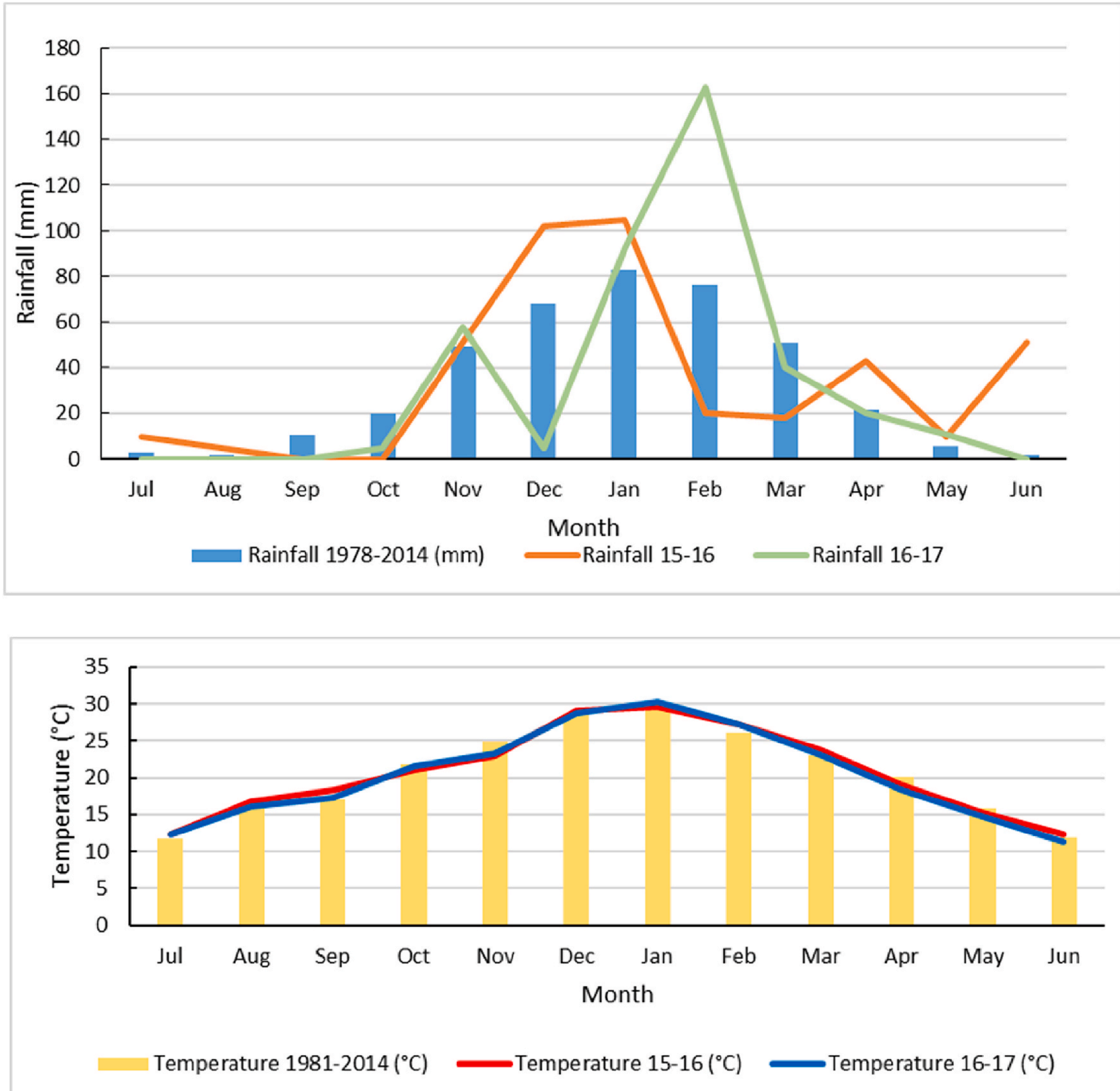

Fig. 2. Historical data series (1978–2017) and monthly average precipitation (mm), temperature (°C) for study years 2016 and 2017 at "*Los Cerrillos*" Experiment Station, INTA-EEA-La Rioja, Argentina.

calculated as the ratio between total water visits and the days of GPS monitoring (Sheehy, 2007). We only used data from cows whose GPS collars had collected a full day's worth of GPS fixes (at least 121 points). Visitation to water was determined by the interpolation of a cow GPS location and a predefined polygon of 300 × 33 m enclosing a small area around a water trough. A single water visitation event was assumed to occur when at least one GPS point in a given cow track fell inside this water trough polygon. Separate water visits that occurred during AM and PM hours of the same day were recorded as separate visits (Sheehy, 2007). The number of points in the area close to water during each visit was used to compute the time spent close to the drinker during each visit.

The area that each cow was able to explore daily was used as an indicator of the cows' ability to search and consume feed (Roach-o-Estrada, 2008). This area was calculated as the Minimum Convex Polygon (MCP, Wauters et al., 2006), a metric previously used to estimate the daily area grazed by free ranging cattle and deer (Perotto Baldivieso et al., 2012). GPS data were thinned to 2 h intervals fixes for MCP analysis (i.e. no more than 12 points per day) to reduce the likelihood of spatial autocorrelation among successive fixes (Perotto-Baldivieso et al., 2012).

The daily trajectory of the cow path was inspected by computing the sinuosity index. This index was previously proposed to assess animal selectivity for preferred patches and feeding sites (Bovet and Benhamou, 1988) and has been used to assess differences in foraging strategies among animals (Benhamou, 2004). The sinuosity index was calculated using JAVA software (Sawalhah et al., 2016), and was the ratio of the linear distance between the first and last point of a 24 h path and the sum of distances traveled between consecutive 10 min fixes over the 24 h period. Index values close to 0 indicate high sinuosity of grazing, whereas values close to 1 indicate a straight grazing path (Calenge, 2006).

Ivlev's E index was calculated to determine selection ($E > 0$), avoidance ($E < 0$), or indifference ($E = 0$) for vegetation units (VUs) by cows of both breeds in each season and year (Putfarken et al., 2008). E is calculated as $\frac{(r-p)}{(r+p)}$ where r is the proportion of time spent by a cow in a given VU and p is the proportion of the pasture covered by that VU.

2.4. Statistical analysis

Vegetation variables, including forage availability, CP, ADF and NDF, were analyzed using linear models considering the fixed effect of year, season, plant functional group (grass vs. forb) and all possible two- and three-way interactions. Transects laid within each distinct

Table 1
Comparison of the main vegetation units of the study site: physiognomic/floristic characteristics, availability and forage quality (average weighted by the proportion of broadleaf forbs and grasses).

	Fragmented shrubland	Dense shrubland	Upland Ecotone	Ephemeral stream ecotone
Area (ha)	138	398	306	284
Watering point distance (m)	<1000	>4500	3000–5000	<3000
Floristic/physiognomic characteristics				
Frequent plant species	Prosopis flexuosa, Aspidosperma quebracho-Blanco, Larrea divaricata, Xeroaloysia ovatifolia, Senna rigida, Cordobia argéntea, Bouteloua aristidoides, Partenium Sp. Croton Sp.	*Aspidosperma quebracho-blanco, Stetsone coryne Acacia furcatispina, Larrea cuneifolia, Mymoziganthus carinatus, Cordobia argéntea, Setaria pampeana*	*Aspidosperma quebracho-blanco, Larrea cuneifolia, Mimosyganthus carinatus, Licium ciliatum, Cordobia argentea, Setaria pampeana, Cottea pappophoroides*	*Aspidosperma quebracho-blanco, Prosopis flexuosa, Larrea divaricata, Trichomaria usillo, Cordobia argentea. Gouinia paraguayensis, Bouteloua aristidoides*
Woody aerial cover (%)	22	37	26	23
Herbaceous aerial cover (%)	3	11	7	10
Bare soil (%)	53	36	29	33
Forage availability (kg ha^{-1}): Grasses + broadleaf forbs = total				
Summer 2016	19 + 208 = 227*	221 + 166 = 387	141 + 444 = 585*	125 + 401 = 526*
Winter 2016	9 + 107 = 116	210 + 153 = 363	130 + 117 = 247	114 + 122 = 236
Summer 2017	10 + 195 = 205*	181 + 150 = 331	120 + 389 = 509*	105 + 371 = 476*
Winter 2017	6 + 97 = 103	170 + 123 = 293	107 + 96 = 203	87 + 102 = 189
Forage quality summer/winter (only 2016)				
Crude potein (%)	12,6/9,5	11,4/8,7	11,8/8,1	11,2/8,4
NDF (%)	55,8/64,1	59,8/68,2	59,2/68,9	58,7/67,4
ADF (%)	36,1/44,6	34,2/42,7	36,4/40,8	35,1/42,8

vegetation unit were assumed independent and used as replicates for analyses. However, our characterization and comparison of VUs cannot be extrapolated outside of our research pasture.

To better deal with heterogeneous data resulting from sporadic GPS collar failures, animal response variables were analyzed using mixed linear models that considered both the occurrence of mixed effects and repeated measures over time (Pinheiro et al., 2013). Models considered the fixed effect for year, season and breed (and their possible two- and three-way interactions) and the random effect of animal and day, and selecting for best fitting models.

Prior to conducting analyses data were inspected for assumptions of normality and homogeneous variance. When assumptions were not met, appropriate transformations were used. Heterogeneity of variance was also modeled where necessary. An autoregressive correlation structure was used as the main model for repeated measures data. Comparisons and selection of adjusted models and their significance were conducted using the maximum likelihood ratio test (Pinheiro et al., 2013). Multiple comparisons for significant effects were made using protected pairwise contrasts, with a significance level declared at P = 0.05. All statistical analyses were carried out in R (R Core Team 2017) using the RStudio interface software (Version 0.99.903). Mixed model analyses were conducted using the nlme package for R (Pinheiro et al., 2013).

3. Results

Forage biomass in all VUs was greater both in summer vs. winter and in 2016 vs. 2017 (Table 1). Grasses had greater (P < 0.01) CP (10.90 vs. 8.37%) and lower (P < 0.01) NDF (69.30 vs. 77.16%) and ADF (35.94 vs. 42.30%) in summer than winter. Similarly, broadleaf forbs had greater (P < 0.01) CP (12.32 vs. 9.63%) and lower (P < 0.01) NDF (54.63 vs. 59.68%) and ADF (35.60 vs. 43.41%) in summer than winter. In 2016, forage quality of the Fragmented Shrubland was numerically greater than that of the Dense Shrubland, Upland Ecotone, and Ephemeral Stream Ecotone all of which yielded similar values of CP, NDF, and ADF.

Daily distance traveled was affected by a *breed * season* interaction (P < 0.01), showing greater walking distance by Argentine Criollo than Angus in winter (Table 2). Overall, the Argentine Criollo cows traveled greater (P = 0.05) distances in winter than summer, regardless (P = 0.12) of the year. Distance traveled was not different between breeds (P = 0.80) or seasons (P = 0.35) in 2016, but Argentine Criollo cows did travel greater distances (P = 0.01) than Angus in 2017 (Table 2). Furthermore, Argentine Criollo traveled greater (P < 0.01) daily distances in winter of 2017 than summer of 2017 and winter and summer of 2016. Regardless of the season, Angus cows always traveled similar daily distances, both in 2016 (P = 0.86) and 2017 (P = 0.81) (Table 2).

Daily area explored by cows (MCP) was affected by the *year * breed * season* triple interaction (P < 0.01). Argentine Criollo cows explored larger areas in winter vs. summer, both in 2016 (P < 0.01) and 2017 (P = 0.05), whereas Angus explored greater (P < 0.01) pasture areas in winter vs. summer of 2017, and had a similar (P = 0.42) MCP in winter and summer of 2016 (Table 2). The MCP was greater (P = 0.01) for Angus than Argentine Criollo during summer of 2016, but greater (P < 0.01) for Argentine Criollo than Angus during summer of 2017 (Table 2). There were no differences in MCP explored by Angus and Argentine Criollo, both during winter of 2016 (P = 0.08) and 2017 (P = 0.10) (Table 2).

Frequency of visits to the water trough in summer and winter was not different for AC cows in both 2016 (P = 0.18) and 217 (P = 0.24). Conversely, AA cows visited the drinker more frequently in summer than winter in both 2016 (P < 0.01) and 2017 (P = 0.04). Frequency of visits to water and time spent at the drinker was not different between breeds in either summer or winter of 2016 and 2017 (Table 2).

Path sinuosity was affected by a year * season * breed triple interaction (P = 0.01), with Argentine Criollo traveling a straighter path in summer of 2016 (P < 0.01) and a tendency (P = 0.06) to do the same in winter of 2017. Greater path sinuosity in summer vs. winter was detected for Argentine Criollo in 2016 (P < 0.01) and for Angus (P < 0.01) in 2017. Angus cows traveled straighter paths (P < 0.01) in summer of 2016 than in summer of 2017 (Table 2).

Breed- and season-related differences in daily time spent grazing were mostly observed in 2017 (Table 2). During 2017, Argentine Criollo

Table 2
Comparison of daily distance traveled (km), MCP of area explored (ha), path sinuosity index, frequency of visits to water and daily activity budget (proportion of time spent traveling, resting and foraging) for Angus (AA) and Argentine Criollo (AC) cows grazing arid rangelands of the Gran Chaco Region in the summer and winter of 2016 and 2017. Values in table are means ± SE.

	2016				2017			
	Summer		Winter		Summer		Winter	
	AA	AC	AA	AC	AA	AC	AA	AC
Animal movement								
Distance traveled (km)	5.7 ± 0.7^{Aa}	4.9 ± 0.6^{Aa}	5.5 ± 0.6^{Aa}	6.4 ± 0.5^{Aa}	5.9 ± 0.4^{Aa}	6.2 ± 0.3^{Aa}	6.1 ± 0.6^{Aa}	8.1 ± 0.5^{Bb}
Area explored (ha)	95.0 ± 23.4^{Aa}	43.3 ± 26.1^{Bb}	126.4 ± 18.5^{Aa}	116.0 ± 16.9^{Aa}	97.7 ± 18.9^{Bb}	119.5 ± 20.2^{Ba}	195.2 ± 25.9^{Aa}	208.8 ± 25.6^{Aa}
Path sinuosity index	0.29 ± 0.02^{Aa}	0.20 ± 0.02^{Ab}	0.31 ± 0.02^{Aa}	0.28 ± 0.01^{Ba}	0.20 ± 0.02^{Aa}	0.22 ± 0.02^{Aa}	0.32 ± 0.04^{Ba}	0.23 ± 0.03^{Aa}
Daily activity budget								
Traveling (%)	5.2 ± 1.2^{Aa}	3.6 ± 1.9^{Aa}	4.8 ± 1.3^{Aa}	4.9 ± 1.1^{Aa}	5.6 ± 1.1^{Aa}	3.0 ± 1.1^{Bb}	5.9 ± 1.2^{Aa}	5.9 ± 1.2^{Aa}
Resting (%)	53.4 ± 1.0^{Aa}	55.2 ± 1.0^{Aa}	54.6 ± 1.0^{Aa}	53.6 ± 1.0^{Aa}	52.1 ± 1.0^{Aa}	44.7 ± 1.0^{Bb}	51.5 ± 1.0^{Ab}	48.1 ± 1.0^{Aa}
Foraging (%)	39.5 ± 1.0^{Aa}	39.7 ± 1.0^{Aa}	38.7 ± 1.0^{Aa}	39.4 ± 1.0^{Aa}	40.4 ± 1.0^{Aa}	48.2 ± 1.0^{Bb}	44.4 ± 1.0^{Aa}	40.2 ± 1.0^{Aa}
Daily visits to water (%)	0.38 ± 0.18^{Aa}	0.45 ± 0.08^{Aa}	0.32 ± 0.04^{Aa}	0.47 ± 0.04^{Aa}	0.52 ± 0.03^{Aa}	0.69 ± 0.04^{Aa}	0.40 ± 0.05^{Aa}	0.33 ± 0.03^{Ba}
Time at water (min*visit^{-1})	18.0 ± 2.9^{Aa}	20.9 ± 6.5^{Aa}	6.1 ± 0.9^{Ba}	4.6 ± 1.1^{Aa}	18.2 ± 1.8^{Aa}	28.8 ± 7.2^{Aa}	4.4 ± 0.8^{Ba}	4.6 ± 0.9^{Aa}

^{ABab} Mean values followed by different lowercase letters between breeds within a same year and season, or uppercase letters between seasons for the same breed and year differ significantly ($p \leq 0.05$; pairwise contrast test).

cows spent more time grazing in summer ($P < 0.01$) and less time grazing in winter ($P < 0.01$) than Angus counterparts (Table 2). There were no breed differences in time spent grazing during summer ($P = 0.90$) and winter ($P = 0.60$) of 2016 (Table 2). Angus cows spent similar time grazing, both in summer and winter of 2016 ($P = 0.61$) and 2017 ($P = 0.50$) (Table 2). Breed- or season-related differences in time spent traveling were also mostly observed in 2017. During this year, Argentine Criollo cows spent less time traveling than Angus counterparts in summer ($P < 0.01$), and more time traveling ($P < 0.01$) in winter than summer (Table 2). In 2016, both breeds spent similar time traveling in summer ($P = 0.11$) and winter ($P = 0.86$). Argentine Criollo cows spent similar time traveling ($P = 0.10$) in winter and summer of 2016. Travel time of Angus cows was similar in winter and summer of 2016 ($P = 0.71$) and 2017 ($P = 0.24$) (Table 2). Angus cows spent more time resting than Argentine Criollo in summer 2017 ($P < 0.01$) and winter 2016 ($P = 0.05$) (Table 2). The time spent resting by Argentine Criollo cows was similar for winter and summer of 2016 ($P = 0.41$) and greater for winter vs. summer of 2017 ($P = 0.02$) (Table 2). Angus cows allocated similar times to rest in both winter and summer of 2016 ($P = 0.53$) and 2017 ($P = 0.74$) (Table 2).

3.1. Selection of vegetation units

Argentine Criollo consistently showed greater selection for Fragmented Shrubland, in summer and winter of 2016 and 2017, while showing greater avoidance for Dense Shrubland, Hill Ecotone Region, Prosopis Woodland and Upland Ecotone in summer of 2016, and Prosopis Woodland in summer 2017. Angus cows on the other hand, exhibited a greater degree of indifference for vegetation units across seasons and years, with exception for greater selection of Dense Shrubland in winter 2016, Hill Ecotone Region in summer 2017, and Prosopis Woodland in winter 2017, and greater avoidance for Hill

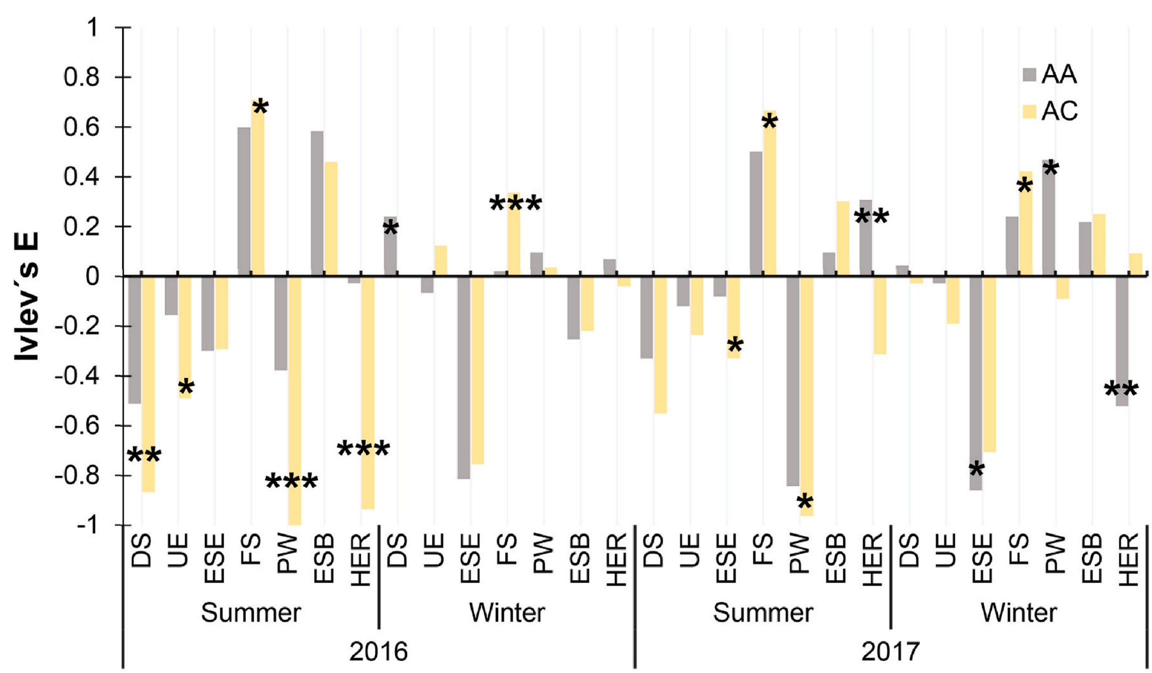

Fig. 3. Ivlev's Electivity index *E* for Aberdeen Angus (AA) and Argentine Criollo (AC) cows in relation to vegetation units (VU), calculated using only GPS locations associated with grazing activity on days where GPS data collection consisted of a minimum of 120 total fixes per breed. Days in which GPS data collection were insufficient were disregarded from analyses. The Ivlev's *E* varies from −1 (avoidance) to 1 (selection), with 0 indicating indifference. Dense Shrubland (DS), Upland Ecotone (UE), Ephemeral Stream Ecotone (ESE), Fragmented Shrubland (FS), Prosopis Woodland (PW), Ephemeral Stream Bed (ESB), Hill Ecotone Region (HER). Notes $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Ecotone Region and Ephemeral Stream Ecotone in winter 2017. Cows of both breeds exhibited greater selection for the Fragmented Shrubland vegetation unit in summer than winter (Fig. 3). Conversely, both breeds showed strong avoidance the Dense Shrubland and Prosopis Woodland in summer, but reduced avoidance for both these VUs in winter (Fig. 3) (see Fig. 4).

4. Discussion

Argentine Criollo (AC) and Aberdeen Angus (AA) cows grazing Arid Chaco rangeland showed ecologically relevant differences in foraging patterns (see below) which varied depending on the season and year. In general, during plentiful times (e.g. summer of 2016) AC cows concentrated their grazing on smaller areas with higher forage quality, close to the water drinker, which they appeared to explore more intensely using more tortuous foraging paths than AA cows. In times of scarcity (e.g. winter of 2017), CA traveled roughly 30% farther than AA cows on any given day but explored similarly large areas of the grazing pasture. The most notable breed difference was observed when comparing summer vs. winter movement patterns of each breed; AC cows showed an apparent greater ability to adapt to changing forage conditions (foraging plasticity) compared to AA counterparts which appeared to exhibit more rigid foraging patterns (Fig. 4). Plasticity of foraging behavior is a trait that could be crucially important for climate adaptation of livestock-based livelihoods in arid and semiarid rangelands (Cibils et al., this issue).

Our results differed somewhat from those described for Raramuri Criollo vs. Angus x Hereford crossbred cows in the Chihuahuan Desert (Peinetti et al., 2011; Spiegal et al., 2019). Between-breed convergence of foraging patterns during growing seasons vs. dormant season divergence observed consistently in those studies were not as clear cut in our experiment. Argentine Criollo cows explored smaller areas of the grazing pasture compared to AA counterparts in the summer of 2016 (wet year), whereas the opposite occurred in summer of 2017 (drier year). Initial studies comparing Criollo and commercial beef breeds in the Chihuahuan Desert were conducted during a single year (Peinetti et al., 2011; Spiegal et al., 2019). By monitoring animals in two consecutive years with contrasting rainfall and forage availability, we were able to document the effect of year-to-year variation on breed-specific foraging patterns. Nonetheless, heritage vs. commercial breed differences in seasonal plasticity of foraging behaviors, especially those associated with forage search patterns, were similar across sites (Cibils et al., this issue).

During summer when forage availability and quality were not limiting, AC cows traveled similar daily distances, explored smaller (wetter year) or slightly larger (drier year) areas of the pasture, tended to move along more sinuous path trajectories (wetter year), and showed stronger selection of the VU with higher forage quality (FS) and lower woody cover compared to AA counterparts. During this season, AC cows allocated similar (wetter year) or more time to graze (drier year), allocated roughly the same amount of time to travel, and spent similar (wetter year) or less time resting (drier year) than AA cows. In winter, we only observed foraging behavior differences between breeds in the direr of the two years. Argentine Criollo cows traveled farther and spent less time resting than AA counterparts in winter of 2017.

Argentine Criollo cattle appeared to exhibit a greater ability, relative

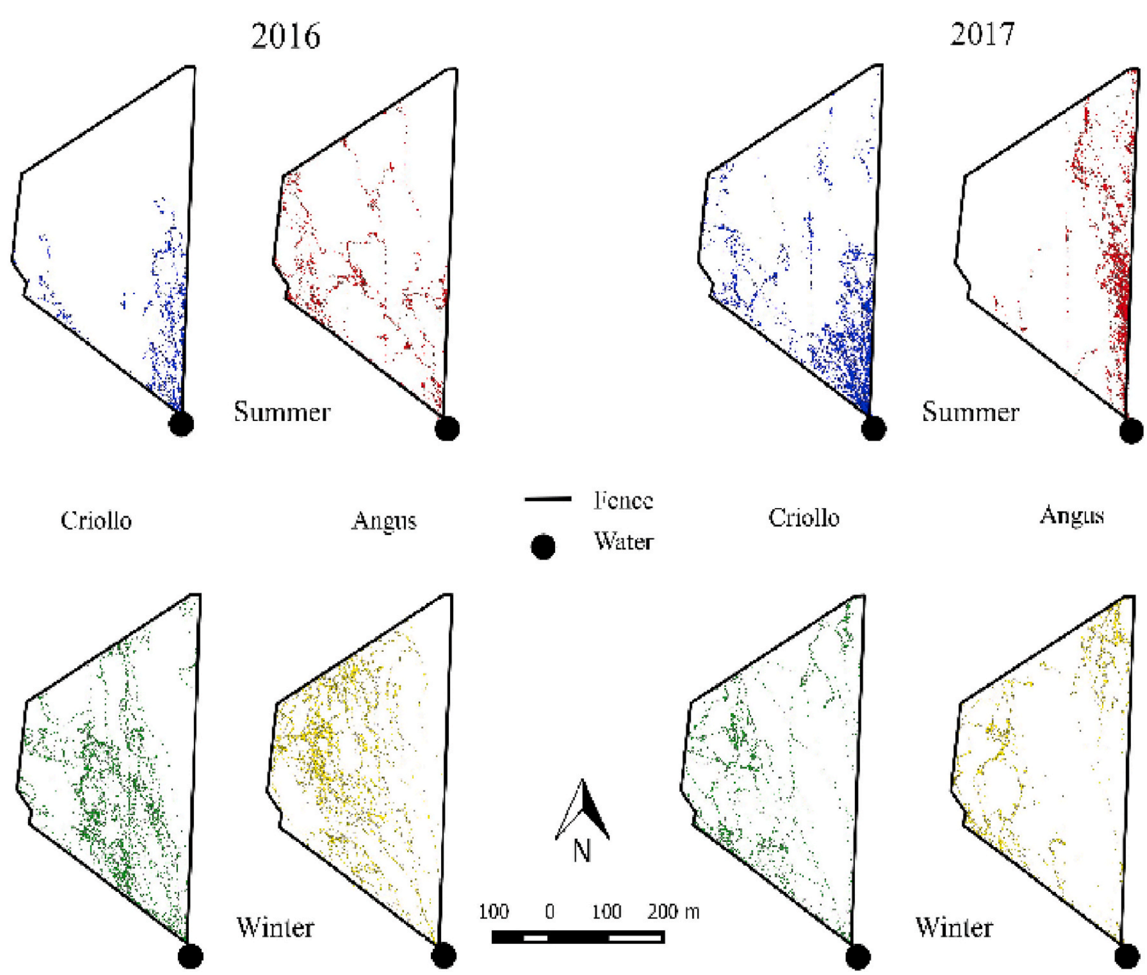

Fig. 4. Distribution of GPS locations of Aberdeen Angus (AA) and Argentine Criollo (AC) cows during summer and winter of 2016 and 2017.

to AA, to cope with declining forage resources in winter as well as during the drier year of the study. Adjustment of the area grazed each day (MCP, dry year > wet year; winter > summer), which has been documented previously in beef cows on rangeland (Sawalhah et al., 2016), as well as breed-differences in time spent resting (AA > AC) and grazing (AC > AA) could be associated with breed-specific diet selection patterns. Criollo cows have been shown to include a different and, in some cases, broader array of rangeland plants in their diet relative to commercial beef cows (Miñón et al., 1991; Ortega-Ochoa et al., 2008; Anderson et al., 2015, Estell et al. this issue). Angus cattle, on the other hand, were primarily developed for temperate grazing environments characterized by humid cold weather and rich availability of highly nutritious forages, C3 grasses in particular. When placed in arid rangelands this breed appears to cope with declining availability and nutritive value of forages by increasing rumination and digestion of a somewhat narrow menu of forages which translates into more time spent resting vs. grazing, as observed in winter 2017. However, further research investigating Criollo vs. Angus diets is needed to test the hypothesis that differences in foraging patterns observed in this study are partly associated with the diets selected by each breed.

Contrary to our expectations, AA cows ranged further from the water drinker than CA counterparts in summer, particularly in 2016. We had anticipated the opposite results based on what Peinetti et al. (2011) and Spiegal et al. (2019) reported for Raramuri Criollo cows in the Chihuahuan Desert of New Mexico. Our study design did not allow us to independently assess how distance from the drinker vs. animal preference for VUs with different herbaceous plant life forms (forbs vs. grasses), forage availability and quality, and availability of shade (woody plant cover) affected foraging patterns. Despite this, we believe that the summer grazing patterns we observed were likely not related to greater dependence on drinking water of CA vs. AA cows. Frequency of visits to the drinker as well as time spent close to water were not statistically different between breeds. Furthermore, metabolic water requirement of AC cows was likely less than that of AA counterparts for a number of reasons. Drinking water needs of lactating beef cows in summer are a function of water quality (which was the same for both breeds), body weight, milk production, and body heat load (Kellems and Church, 2010; Brew et al., 2011). AC cows at our site were on average 30 kg lighter than their AA counterparts and likely had slightly lower baseline metabolic water requirements. Ongoing studies at this site, suggest that milk production of lactating AC cows is only 50% of that measured in AA counterparts at similar stages of lactation (R. Avila, pers. comm.). Thus, AA cows likely had twice the lactation-related drinking water requirements of AC cows. Thermoregulation during hot weather can also increase demand for water considerably. Raramuri Criollo cattle are known to dissipate body heat load at faster rates than British beef cattle (Nyamuryekung'e et al., 2021a) a phenomenon that is thought to be driven in part by differences in subcutaneous fat deposition (Criollo < British beef breeds). Given what is known about AC carcass fat content (AC<Hereford, Anderson et al., 2015), it is very likely that dissipation of body heat was also greater in AC than AA and that, therefore, thermoregulation water needs of AC were less than those of AA counterparts. Still, experiments measuring water intake of Criollo and commercial beef cows on rangeland are currently lacking and should be prioritized in future breed comparison studies.

Physiological stage of cows (nursing vs. dry) likely contributed to summer vs. winter activity differences of cows of both breeds. At our site, calving occurred from mid-November to mid-January (early summer), therefore cows were in early to mid-lactation during our summer monitoring periods. Nursing beef cows on rangeland are known to graze smaller areas and travel shorter daily distances compared to non-lactating peers (Black Rubio et al., 2008) which was apparently the case when comparing summer (nursing) vs. winter (dry) movement metrics (MCP, especially) of cows at our site. Our study was not designed to determine the influence of AC and AA cow-calf pair behavior on summer foraging patterns of the dams. Nonetheless, the movement patterns we observed differed from those reported by Nyamuryekung'e et al. (2021b) who studied summer foraging behavior of Raramuri Criollo and Angus x Hereford cow-calf pairs in New Mexico. They reported that breeds exhibited different mothering styles which were apparently partly responsible for differences in summer foraging behavior. Criollo cows, with fewer apparent movement restrictions imposed by calves, traveled further and grazed areas of the pasture that were three times larger than those explored by their British crossbred peers. Averaged across summers, these two movement metrics were similar for AA and AC cows in our study. Whether AC calves behave similarly to their North American relatives that follow their dams at all times (Nyamuryekung'e et al., 2020; Nyamuryekung'e et al., 2021a) is unknown, but any influence of nursing calves on their dam's movement patterns was likely similar for both breeds at our site.

Both breeds showed seasonal and year-to year variations in their daily activity budgets. Cows dedicated about 10 h per day to foraging activities (i.e. searching, biting and chewing feed) and appeared to do so at the expense of time allocated to travel and rest likely in response to changes in forage availability and environmental conditions. Body size and nutritional requirements are known to influence foraging activities in situations where forage quantity and quality interact to influence feed intake patterns (Laca, 2009). In contrast with earlier studies conducted in the northern hemisphere (Roacho-Estrada et al. this issue; Sheehy, 2007), breed-specific foraging behavior in this study was apparently unrelated to differences in body size, frame score, or other traits related to body size. Argentine Criollo and Angus had body weights (411 ± 21,69 vs. 443 ± 23,52 kg, respectively) and frame scores (4–5; Beef Improvement Federation, 1986) which are associated with lower maintenance requirements and better adaptation to arid zones (Pauler et al., 2020). However, each breed apparently used divergent foraging strategies across both space and time. Angus cattle appear to have attempted to maximize the intake of bulk diets regardless of season and annual fluctuations in availability and nutritive value of forages (Díaz Falú et al., 2014). Conversely, the similarly sized Argentine Criollo cows appeared to selectively consume food items of greater nutritive value. They consistently selected feeding sites dominated by more nutritious forages (e.g. Fragmented Shrubland) but with plant architectures known to reduce bite size and mass compared to bulk grass canopies. Consequently, Argentine Criollo cattle may have had to increase foraging time, especially in the summer of the drier year, to feed on forages requiring a greater number of small bites. Further mechanistic research addressing foraging strategies of Criollo and commercial beef cows on rangeland is needed.

Argentine Criollo cattle showed greater preference than AA cows for the fragmented shrubland VU in summer and winter of both years of the study. Although Angus cows showed lesser preference for this VU, particularly in winter, electivity index values during the summer monitoring period were the highest recorded for this breed ($E \sim 0.6$). Fragmented shrubland ranked last in summer and winter forage biomass yield in both years but ranked first in summer and winter forage nutritional value in 2016 (no chemical analyses of vegetation were conducted in 2017). Fragmented shrubland (FS) was the smallest of VUs, was also the VU located closest to the drinker, and was the VU that ranked first in bare soil cover (55%), perhaps as a result of historical overgrazing in areas close to the water drinker, a worldwide phenomenon that has been well studied (Mysterud and Ostbye, 1999; Martín and Lagomarsino, 2000; Holechek et al., 2011; Butti, 2015). This VU may also be particularly prone to soil erosion which raises concerns about the relative conservation value of raising Argentine Criollo in this ecosystem. A follow up replicated long term grazing study where Argentine Criollo and Angus cows graze separate pastures and which began in 2018 will measure the environmental footprint of raising Criollo vs. British cattle on Arid Chaco rangelands. This study is also investigating fertility of CA and AA herds, previously shown to be similar (Anderson et al., 2015), to make inferences about the financial sustainability of the system.

Patterns of selection of the dense shrubland (DS) and the ephemeral stream ecotone (ESE), two of the VUs that were farthest from water, showed marked seasonal contrast that was especially pronounced in AA cows in 2016. Cows avoided DS in summer, CA more so than AA, despite the fact that it offered greater grass biomass than the adjacent and equally distant Ephemeral Stream Ecotone (ESE) which tended to receive use more frequently. In winter, cows showed indifference (CA) or preference (AA) for DS and strong avoidance of ESE. Historical infrequent use in summer followed by heavier winter use (a pattern observed especially in AA cows) could have favored shrub encroachment in DS, the VU with greatest shrub cover, by protecting woody plants from herbivory during the growing season. Conversely, greater summer use of VUs, including those closer to the drinker (a pattern observed especially in AC cows) may have favored higher levels of browsing during the growing season, which likely suppressed shrub growth and recruitment. Notably, the fragmented shrubland and ESE were the VUs that exhibited the least shrub cover (22% and 23%, respectively). Thus, seasonal patterns of VU preference could pose two different rangeland conservation challenges; on the one hand, the potential for accelerated shrub encroachment with grazing regimes similar to those observed in AA cows, and on the other, the risk of soil erosion close to the drinker with grazing that resembles the patterns observed in AC cows (see above). Soil erosion and woody plant encroachment in drylands, which sometimes occur in tandem, are serious global ecosystem degradation concerns (Puttock et al., 2014; Archer et al., 2017), therefore rangeland conservation tradeoffs associated with raising heritage vs. commercial beef cattle on Arid Chaco rangeland need to be addressed in further detail.

A degree of complementarity in the use of VUs was observed in this study. Subsequent analyses of the monitoring data reported here (results not shown) found that there was a degree of complementarity in pasture use between breeds (Herrera Conegliano et al., 2019). Feeding site overlap of AC and AA collared cows occurred on 27% or 48% of the total area grazed by both breeds in summer and winter of 2016, respectively. These results, while preliminary (given that only 20% of all animals were monitored), suggest that a more homogeneous use of rangeland pastures could be achieved with mixed grazing of AA and AC cows, especially in summer. However, impacts of this grazing strategy on herd-wide adaptation to climate variability (AC showed greater plasticity than AA) and rangeland conservation would require rigorous investigation.

5. Conclusions

Argentine Criollo cows at our site exhibited greater behavioral plasticity, suggesting better ability to rapidly cope with changing forage and climate conditions compared to Aberdeen Angus. The rangeland conservation implications of raising AC vs. AA require further investigation.

CRediT authorship contribution statement

Oscar A. Herrera Conegliano: Conceptualization, Methodology, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Lisandro J. Blanco:** Conceptualization, Methodology, Funding acquisition, Supervision, Writing – review & editing. **Santiago A. Utsumi:** Writing – review & editing. **Andres F. Cibils:** Conceptualization, Methodology, Writing – review & editing. **Maria G. Cendoya:** Conceptualization, Formal analysis, Writing – review & editing. **Florencia Jaimes:** Conceptualization, Supervision, Writing – review & editing. **Andres F. Moltoni:** Resources, Software. **Patricia Ricci:** Conceptualization, Supervision, 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.2022.104827.

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