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Adapting to climate change on desert rangelands: A multi-site comparison of grazing behavior plasticity of heritage and improved beef cattle[☆]

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ABSTRACT

Climate change is amplifying the spatiotemporal heterogeneity of desert rangeland forages through its impact on precipitation variability. Foraging behavior plasticity (an animal's ability to alter its behavior to cope with environmental variation) could be a key trait for climate adaptation of beef cattle in arid environments. We analyzed GPS-derived movement and activity data of Criollo and commercial beef cattle from eight studies conducted at sites in North and South America to determine whether seasonal and year-to-year behavior plasticity varied significantly between breeds. We calculated dormant/brown season or driest year percent change in foraging behavior relative to growing/green season or wettest year. Compared to commercial beef breeds, Criollo cattle exhibited significantly greater seasonal adjustment in daily distance traveled (20% increase vs. 2% decrease, $P \leq 0.02$) and daily grazing effort (25% vs. 1.5% increase, $P = 0.01$) during the dormant/brown vs. growing/green season. Increase in daily area explored during the dormant/brown season was almost three times greater in Criollo vs. commercial beef cattle ($P = 0.09$). Seasonal adjustment in daily time spent grazing was similar for Criollo and commercial beef breeds. Increase in daily area explored during the dormant/brown season of dry vs. wet years was three times greater for Criollo vs. commercial beef breeds ($P = 0.03$). Criollo cattle tended ($P = 0.09$) to exhibit greater behavior adjustment than commercial beef counterparts in daily distance traveled during the dormant/brown season of dry vs. wet years (22% vs. 4% increase, respectively). No breed differences in adjustment of time spent grazing ($P = 0.36$) or grazing effort ($P = 0.20$) during dormant/brown season of dry vs. wet years were observed. Dry vs. wet year grazing behavior adjustments during the growing/green season were similar for both breeds. Grazing behavior plasticity observed in Criollo cows could be a critical trait for desert beef herds in the face of increasingly variable rainfall patterns occurring as a result of climate change.

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1. Introduction

Coping with annual fluctuations in forage availability is a core challenge of raising livestock on desert rangelands that has defied ancient pastoralist societies and modern farmers and ranchers alike (Huntsinger et al., 2010; Reid et al., 2014). Enormous variability across space and time is an intrinsic feature of dryland ecosystems (Havstad et al., 2009). Forage production often varies an order of magnitude between years (Knapp and Smith, 2001) and substantial seasonal change in the nutritional value of forages is the norm (Pieper, 2005). Climate change is not only amplifying these fluctuations through its impact on precipitation variability in the United States (Briske et al., 2021) and globally (Sloat et al., 2018), but is also thought to be reducing the quality of grasses of the northern Great Plains (Augustine et al., 2018) and the quantity of herbaceous forage biomass produced in the southwestern US (McIntosh et al., 2019). Generations of western US ranchers have excelled at selecting animals that match their ranch environment, but the ability of modern high-producing beef cows to thrive in a world with an increasingly variable forage supply is uncertain (Briske et al., 2021; Estell et al., 2012; Havstad et al., 2016; Holechek et al., 2020).

Beef cows in the US today have higher maintenance requirements compared to cows of the 1970s (Evans et al., 2002) and consequently need greater feed inputs to realize their genetic potential. Fertility of these larger-framed animals decreases significantly when forage is limiting (Terry et al., 2021), a situation that is the rule rather than the exception in arid rangelands. Western US ranchers typically strive to offset forage deficits by feeding hay or protein supplements (Shrum et al., 2018). This common practice, which can account for up to half of a cow-calf operation's costs (Holechek and Hawkes, 1993), can jeopardize the financial sustainability of typical family ranches that in most years struggle to make a profit (Briske et al., 2021; Havstad et al., 2016; Holechek et al., 2011). Thus, the same industry-wide genetic change that accomplished remarkable progress in beef production efficiency over the past five decades (Terry et al., 2021; USDA-ERS, 2019) may have yielded phenotypes that are less well suited for environments with an unpredictable forage supply.

Concern about the sustainability of ranching in arid environments is stimulating novel adaptation strategies including the use of heritage cattle breeds thought to be better adapted to the hotter, drier, and increasingly variable environment of the US desert Southwest (Anderson et al., 2015; Elias et al., 2020; Spiegel et al., 2020). In the Chihuahuan Desert, higher net returns may be realized raising Raramuri Criollo cattle, a Mexican biotype of this heritage breed (Armstrong et al., 2022; McIntosh et al., 2020), because they require fewer inputs (including supplement feed) and thus have lower operating and overhead costs relative to British beef cows (Torell et al., this issue). Compared to improved beef breeds, Raramuri Criollo cattle appear to exhibit a superior ability to adjust their movement and activity patterns to match seasonal forage dynamics (Duni et al., this issue; Nyamuryekung'e et al., 2022; Peinetti et al., 2011; Roacho Estrada et al., this issue; Spiegel et al., 2019). Lighter body weights (McIntosh et al., 2020), reduced preference for palatable grasses (Estell et al., this issue), a mothering style that results in fewer movement constraints (Nyamuryekung'e et al., 2021a; Nyamuryekung'e et al., 2020) and greater tolerance of hot summer temperatures (Nyamuryekung'e et al., 2021b) are thought to partially explain this phenomenon.

Foraging plasticity could be a key behavioral trait for climate adaptation of beef cattle in desert rangelands. Here we use the term 'behavioral plasticity' to indicate an animal's ability to 'alter its behavioral phenotype to cope adaptively with environmental conditions' following Dingemans et al. (2010, p. 81). To date, most breed comparison studies (cited above) made qualitative inferences about the plasticity of behavior of Criollo vs. British beef cows derived from short term studies at a single site, but formal breed comparison of foraging behavior plasticity is lacking (McIntosh et al., this issue). We therefore analyzed secondary data from eight studies conducted over a 16-year

time span at sites in the Chihuahuan Desert (New Mexico, USA), Colorado Plateau (Utah, USA), California Chaparral (California, USA), Sierra Madre Foothills (Chihuahua, Mexico) and Dry Chaco (La Rioja, Argentina). We sought to determine whether seasonal and year-to-year plasticity of key movement and activity metrics of Criollo and commercial beef cattle raised in extensive rangeland pastures varied significantly between breeds. We hypothesized that Criollo cattle would exhibit significantly greater plasticity relative to commercial beef breed counterparts and that breed differences would be consistent across sites regardless of the ecosystem and Criollo biotype considered.

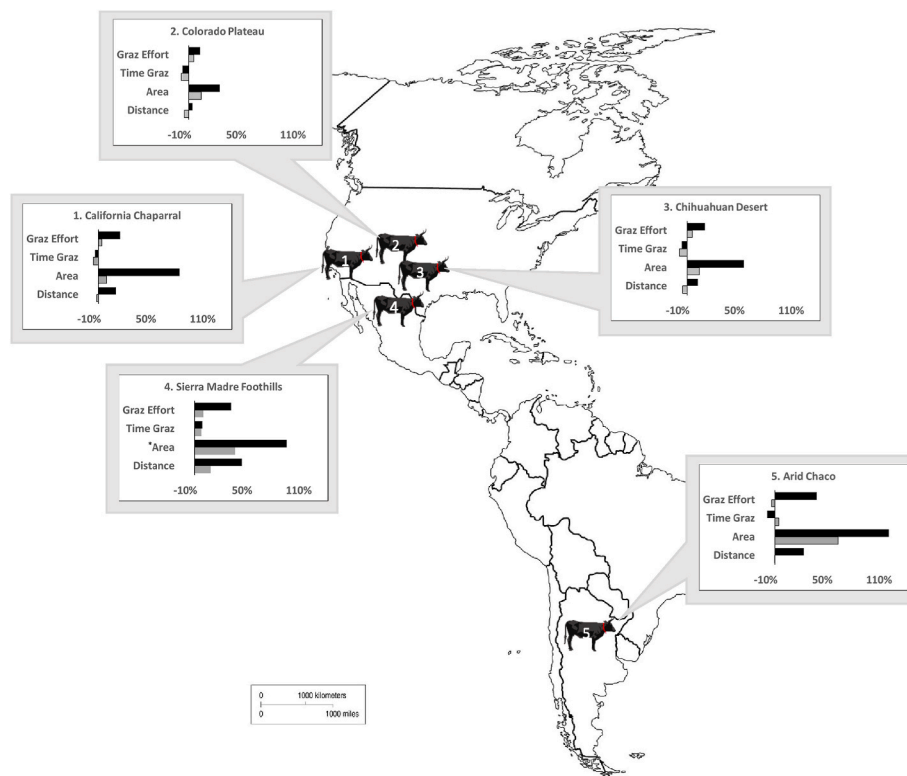
2. Material and methods

We used data from published research conducted by members of our collaboration network at five ranches (Fig. 1) spanning three countries (Argentina, Mexico, and USA) and two continents (North and South America). Studies were conducted at both research (New Mexico, Chihuahua, La Rioja) and commercial ranches (California, Utah) between 2005 and 2021, each ranging from one to three years in duration. Mean annual precipitation at research sites ranged from 600 mm at the California site to 207 mm at the Dugout Ranch in SE Utah. A brief description of each study site is provided below.

2.1. Overview of study sites

The four Chihuahuan Desert studies (McIntosh et al., 2021; Nyamuryekung'e et al., 2022; Roacho Estrada et al., this issue; Spiegel et al., 2019) were conducted at the USDA ARS Jornada Experimental Range (JER) in southern New Mexico, USA (32° 37' N, 106° 40' W). The JER, encompasses 78 266 ha of relatively flat terrain (1300 m–1600 m). Mean annual precipitation is 247 mm, more than 50 percent of which occurs as monsoonal rains between July and September. Mean ambient temperature is highest in June and lowest in January, averaging 36 °C and 13.3 °C, respectively. Vegetation at JER is dominated by honey mesquite (*Prosopis glandulosa*) intermixed with perennial grasses dominated by black grama (*Bouteloua eriopoda*), dropseeds (*Sporobolus* spp.), and threeawns (*Aristida* spp.). Soap-tree yucca (*Yucca elata*) and broom snakeweed (*Gutierrezia sarothrae*) are common subdominants. Lowland grasslands are dominated by tobosa (*Pleuraphis mutica*) and burrograss (*Schleropogon brevifolius*) and occur on soils with high clay content. The grazing pastures where studies were conducted ranged in area from 1165 to 3200 ha with one to five permanent watering points and were stocked lightly (forage utilization <30%) prior to and during the experiments. Season of use and forage conditions during the periods in which studies were conducted are provided in Table 1.

The Colorado Plateau study (Duni et al., this issue) was conducted at the Dugout Ranch in southeast Utah (38° 4' N, 109° 33' W) that encompasses 137 689 ha of private and public lands with rugged topography characterized by steep sandstone cliffs with cottonwood creek beds and shrub-grass covered buttes. The climate is considered cool desert with a mean annual precipitation of 207 mm. Frontal storms comprise 50% of the precipitation and occur in Oct–May while the other 50% falls in June–Sept as monsoonal thunderstorms. Mean annual temperature is 12 °C with mean monthly coldest and hottest temperatures of –1.7 °C and 26 °C occurring in January and July, respectively. Common grasses at the site include Indian ricegrass (*Achnatherum hymenoides*), James' galleta (*Pleuraphis jamesii*), dropseeds (*Sporobolus* sp.), alkali sacaton (*Sporobolus airoides*) and blue grama (*Bouteloua gracilis*). Common shrubs include sagebrushes (*Artemisia* sp.), fourwing saltbush (*Atriplex canescens*), greasewood (*Sarcobatus nesus*), Mormon tea (*Ephedra* sp.) and blackbrush (*Coleogyne ramosissima*). During the annual study periods beginning in November and ending April, cattle were moved through five large pastures ranging in area from 2500 to 3500 ha with several natural and artificial watering sources. Pastures were stocked following USDI Bureau of Land Management year-to-year grazing permit stipulations. Precipitation and NDVI data for the



*Percent change in daily area explored by cattle at site # 4 was scaled using a factor of 0.20

period of study are provided in Table 1.

The California Chaparral study (Duni et al., this issue) was conducted at Rancho Corta Madera in south-central California (32° 45' N, 116° 34' W) that encompasses 4049 ha of private and public lands of somewhat rugged topography characterized by high-country chaparral and oak savannas, mid-level Jeffrey pine (*Pinus jeffreyi*) stands, and low-lying California Annual grassland. The climate is considered warm-summer Mediterranean with a mean annual precipitation of 601 mm. Most precipitation occurs in December–March. Mean annual temperature is 19.4 °C with mean monthly coldest and hottest temperatures of –15.5 °C and 43.3 °C occurring in January and July, respectively. Common perennial grasses at the site include Thurber needlegrass (*Achnatherum thurberianum*), bromes (*Bromus* sp.), wild oat (*Danthonia californica*), California buckwheat (*Eriogonum fasciculatum*), needlegrass (*Nassella pulchra*), bluegrass (*Poa atropureura*), desert needlegrass (*Stipa speciosa*), and foxtail fescue (*Vulpia myuros* var. *hirsute*) as well as several native annual grasses. Common shrubs and trees include chamise (*Adenostoma fasciculatum*), manzanita (*Arctostaphylos* sp.), big sagebrush (*Artemisia tridentata*), Ceanothus (*Ceanothus* spp.), goldenbush (*Isocoma* sp.), desert almond (*Prunus fasciculata*), bitterbrushes (*Purshia* sp.), and numerous oak species (*Quercus* sp.) as well as Jeffrey Pines, Redshank (*Adenostoma sparsifolium*), and Singleleaf pinyon (*Pinus monophylla*). Cattle had open access to all contiguous vegetation cover types throughout the study periods (~20% annual/perennial grassland, 80% chaparral/woodlands). A large ~20 ha lake serves as the central watering source. Pastures were stocked following USDA NRCS grazing plan recommendations. Season of use and precipitation during the periods in which studies were conducted are provided in Table 1.

The Sierra Madre Foothills study (Roacho Estrada et al., this issue) was conducted at the Rancho Teseachi (28° 48' N, 107° 25' W) belonging to the Universidad Autonoma de Chihuahua. This research ranch encompasses 11 000 ha east of the Sierra Madre Occidental. The climate at this site is characteristic of mountainous regions with cold winters and

hot summers with elevations that vary between 2058 m and 2640 m and topography characterized by progressive ruggedness with increasing elevation. Average annual rainfall is 580 mm, and the average annual relative humidity is 60%. Mean ambient temperature is highest in June and lowest in December, averaging 26 °C and 10 °C, respectively. Vegetation types range from piñon-juniper-grama grass (*Bouteloua* spp.) communities at lower elevations to pine-oak-muhly grasses (*Mulhenbergia* spp.) at higher elevations. Plant community types available at the ranch include disturbed forest, pine forest, oak forest, oak woodland with grassland understory, open grassland, and shrublands. Common woody plant species include *Quercus* spp., *Juniperus* spp., *Pinus* spp., *Rhus trilobata*, *Cercocarpus brevifolius* and *Ceanothus fendleri* among others. Common grasses include *Bouteloua* spp., *Muhlenbergia* spp. and *Aristida* spp. among others. The study was conducted in a 2552 ha pasture using very light stocking rates. The pasture had one permanent watering point and several ephemeral arroyos with running water during the fall sampling season. Forage biomass data for the period of use are shown in Table 1.

The Arid Chaco study (Herrera Conegliano et al., this issue) was conducted at the Campo Anexo Los Cerrillos (29° 59' S, 65° 51' W) belonging to Argentina's Instituto Nacional de Tecnología Agropecuaria (INTA). This research ranch encompasses 8263 ha of typical Arid Chaco rangeland. Climate is semiarid with hot summers and mild winters. January (26 °C) and July (11 °C) are the warmest and coldest months of the year, respectively. Mean annual precipitation is 392 mm with high inter-annual variability ranging from less than 200 to over 600 mm per year. Roughly 80% of annual precipitation occurs as extreme summer monsoon storms between the months of October and March. Topography is fairly flat with slopes of up to 4% and soils are typical Aridisols and Entisols. The dominant vegetation consists of a xerophytic shrubland savanna with dispersed isolated native trees. *Larrea*, *mimozyanthus*, *Senna* spp., and *Capparis* spp. are the dominant shrubs whereas trees of the genus *Aspidosperma* and *Prosopis* are the most

Table 1

Overview of protocols used to calculate foraging behavior variables in each of eight studies included in this analysis, and synthesis of forage biomass, landscape greenness (Normalized Difference Vegetation Index, NDVI), or precipitation data used to classify G (green, growing) and B (brown, dormant) seasons and wet vs. dry years shown in [Table 2](#).

Experiment ^a	Protocols used to derive foraging behavior variables from GPS data	Seasonal ^b or annual forage biomass, rainfall (PPT), or NDVI
Roacho Estrada. et al. (this issue) – Jornada Experimental Range, USA	For both these experiments, daily distance traveled was calculated adding consecutive distances between 5 min interval location coordinates. Daily time spent grazing was calculated using movement velocity and 2 axis motion sensor index thresholds. Daily area explored was estimated using 95% probability Kernel Density analysis.	Forage biomass was 609.4 kg/ha in spring and 558.5 kg/ha in fall of 2005. Annuals which presumably responded to heavy winter rain contributed significantly to spring forage biomass. Forage biomass was 446.0 kg/ha in spring and 501.9 kg/ha in fall of 2005.
Roacho Estrada. et al. (this issue) – Rancho Teseachi, Mexico		
Spiegel et al. (2019) – Jornada Experimental Range, USA	Daily distance traveled was calculated adding consecutive distances between 5 min interval location coordinates. Daily time spent grazing was calculated using movement velocity thresholds. Daily area explored was estimated using Time Local Convex Hull analysis.	Pre-green NDVI ^c = 0.167 ± 0.019 on Jun 15, 2008 Peak-green NDVI = 0.267 ± 0.044 on Aug 18, 2008
Nyamuryekung'e et al. (2022) – Jornada Experimental Range, USA	Daily distance traveled was calculated adding consecutive distances between 10 min interval location coordinates. Daily time spent grazing was calculated using movement velocity thresholds (2.35–25 m/min). Average dispersion radius from each animal's location centroid and Minimum Convex Polygon analyses were used to estimate daily area explored.	2015/16: PPT 237.1 mm ^d ; NDVI ^e : 0.207 (s), 0.128 (w) 2016/17: PPT 247.2 mm; NDVI: 0.186 (s), 0.123 (w) 2017/18: PPT 307.4 mm; NDVI: 0.281 (s), 0.138 (w)
McIntosh et al., (2021) – Jornada Experimental Range, USA	Daily distance traveled was calculated adding consecutive distances between 5 min interval location coordinates. Daily time spent grazing was calculated using movement velocity thresholds (2.35–25 m/min). Daily area explored was estimated using Minimum Convex Polygon analysis.	2015/16: PPT 199.9 mm ^f ; NDVI ^e : 0.245 (s), 0.090 (w) 2016/17: PPT 243.1 mm; NDVI: 0.195 (s), 0.105 (w)
Herrera C. et al. (this issue), Campo Anexo Los Cerrillos, Argentina	Daily distance traveled was calculated adding consecutive distances between 10 min interval location coordinates. Daily time spent grazing was calculated using movement velocity thresholds (1–20 m/min). Daily area explored was estimated using Minimum Convex Polygon analysis.	2015/16: PPT 415 mm; Forage 432.5 kg/ha (s); 242.1 kg/ha (w) 2016/17: PPT 394 mm; Forage 127.7 kg/ha (s); 88.0 kg/ha (w)
Duni et al. (this issue), Dugout Ranch, USA	For both these experiments, daily distance traveled was calculated adding consecutive distances between 10 min interval location coordinates. Daily time spent grazing was calculated using movement velocity thresholds (2.35–25 m/min). Daily area explored was estimated using Minimum Convex Polygon analysis.	2020: PPT 10.2 mm (w); 142.0 mm (es); NDVI ^e 0.177 (w); 0.187 (es) 2021: PPT 22.3 mm (w); 81.3 mm (es); NDVI 0.183 (w); 0.180 (es)
Duni et al. (this issue), Corta Madera Ranch, USA		Fall 2018: PPT 128.78 mm ^g ; NDVI ^e 0.518 Winter 2019: PPT 344.16 mm; NDVI 0.520

^a A description of research sites, cattle, and monitoring equipment used in each experiment are provided in the methods section.

^b summer (s), winter (w), or early spring (es).

^c MODIS Images were used to calculate NDVI.

^d Precipitation recorded at USDA ARS JER HQ.

^e Landsat 8 Images were used to calculate NDVI.

^f Precipitation recorded at USDA ARS JER Red Lake.

^g Precipitation recorded in Alpine, CA <https://raws.dri.edu/cgi-bin/rawMAIN.pl?caCALP>.

common. The herbaceous understory is dominated by C₄ perennial grasses, including *Trichloris* spp., *Chloris* spp., *Pappophorum* spp., *Aristida* spp, and *Setaria* spp. Seven major vegetation units were identified in the 1183 ha pasture used for this study and are described in detail by [Herrera Conegliano et al. \(this issue\)](#). The study pasture was stocked moderately and had one permanent drinking water source. Forage biomass and precipitation data for the study period are shown in [Table 1](#).

2.2. Overview of animals, sensors, and primary data

Raramuri Criollo was the heritage breed used at the four North American ranches, and Argentine Criollo was used at the South American site. Phenotypic characteristics, origin, and ancestry of each of these biotypes are discussed in detail by [Armstrong et al. \(2022\)](#) and [McIntosh et al. \(2020\)](#). It is important to note that the geographic origin of Raramui Criollo cattle used in the USA and Mexico differed slightly. The USDA ARS Jornada herd (New Mexico, USA), which supplied animals to the California and Utah ranches, was initially comprised of cattle

Table 2

Mean grazing behavior metrics for commercial and Criollo cattle reported in eight published studies included in this analysis. Data for each season and year in which experiments were conducted are shown. Seasons with higher (G, green) and lower (B, brown) availability of green forages as inferred from field measurements, weather records, or satellite greenness indices are shown. For studies that were replicated over multiple years, the rainiest year in series (W) is indicated. Seasonal or annual precipitation or greenness (NDVI) details are shown in [Table 1](#).

Ecosystem	Citation	Year	Season	Commercial				Criollo			
				Distance Traveled (km*d ⁻¹)	Area Explored ^a (ha*d ⁻¹)	Time Spent Grazing ^a (h*d ⁻¹)	Grazing Effort ^b	Distance Traveled (km*d ⁻¹)	Area Explored (km*d ⁻¹)	Time Spent Grazing (h*d ⁻¹)	Grazing Effort ^b
Chihuahuan Desert	Roacho Estrada et al. (this issue)	2005	Spring (G)	9.56	381.1	9.88	0.97	10.32	456.7	9.29	1.11
			Fall (B)	7.92	330.60	10.27	0.77	10.79	795.40	9.46	1.14
	Spiegel et al. (2019)	2008	Pre-green (B)	6.23	18.26	9.28	0.67	8.20	49.69	9.63	0.85
			Peak green (G)	6.18	37.69	11.28	0.55	7.06	40.25	10.23	0.69
			Summer (G)	6.43	69.06	8.46	0.76	7.96	147.11	9.00	0.89
	Nyamuryekung'e et al. (2022)	2015–16	Winter (B)	4.36	62.70	6.50	0.67	9.16	338.10	8.57	1.07
			Summer (G)	5.21	70.22	7.96	0.65	7.30	139.86	9.61	0.76
		2016–17	Winter (B)	6.52	182.40	7.71	0.85	9.47	322.56	8.98	1.05
			Summer (G)	4.37	40.81	7.56	0.58	7.57	161.87	9.75	0.78
		2017–18 (W)	Winter (B)	4.96	105.82	6.95	0.71	6.96	181.93	6.61	1.05
			Summer (G)	8.63	325.23	8.42	1.02				
	McIntosh et al. (2021)^c	2015–16	Winter (B)	9.77	271.78	8.96	1.09				
Summer (G)			10.12	248.58	8.47	1.19					
2016–17 (W)		Winter (B)	11.23	545.17	7.45	1.51					
		Summer (G)									
Sierra Madre Foothills	Roacho Estrada et al. (this issue)	2005	Fall (G)	4.61	39.50	10.91	0.42	4.46	38.70	10.06	0.44
			Spring (B)	5.38	123.50	11.68	0.46	6.67	226.80	10.86	0.61
Dry Chaco	Herrera C. et al. (this issue)	2015–16 (W)	Summer (G)	5.70	95.00	9.48	0.60	4.90	43.30	9.53	0.51
			Winter (B)	5.50	126.40	9.29	0.59	6.40	116.00	9.46	0.68
	2016–17	Summer (G)	5.90	97.70	9.70	0.61	6.20	119.50	11.57	0.84	
		Winter (B)	6.10	195.20	10.66	0.57	8.10	208.80	9.65	0.54	
Colorado Plateau	Duni et al. (this issue)	2020 (W)	Spring (G)	6.22	96.12	8.87	0.70	6.84	103.80	9.74	0.70
			Winter (B)	5.48	85.12	8.31	0.66	6.61	118.03	8.89	0.74
	2021	Spring (G)	6.13	84.88	8.86	0.69	5.85	102.10	9.44	0.62	
		Winter (B)	4.67	88.77	6.91	0.68	6.49	154.60	8.91	0.73	
California Chaparral	Duni et al. (this issue)	2018–19	Fall (B)	5.56	51.39	9.42	0.59	6.53	81.43	9.57	0.68
			Winter (G)	5.67	47.35	9.94	0.57	5.53	43.90	9.92	0.56

^a Estimates of these behavior variables were likely influenced by the method used to derive each metric; however, method-related biases were consistent within studies. Methods used to derive foraging behavior variables are summarized in [Table 1](#).

^b Grazing effort was defined as distance traveled (km) per hour spent grazing.

^c This was the only study conducted with yearling steers, all the other studies used in this analysis included mature cows, either dry or nursing.

from the lower and hotter areas of the Copper Canyon in Chihuahua, Mexico (Estell, 2021). The Rancho Teseachi herd in Chihuahua (Mexico) was made up of animals from higher altitude (colder) areas of the Canyon (Felipe Rodriguez A., pers. comm.). Commercial beef breeds included Black Angus (California, Chihuahua, and La Rioja), Red Angus (Utah), Hereford (Chihuahua) and Black Angus x Hereford crossbred cattle (Chihuahua and New Mexico). Black Angus cows used in La Rioja are described as belonging to the 'La Rioja Ecotype' of the breed since these animals were a product of a cross absorption program conducted over multiple generations that involved breeding local cows (some of which may have had Criollo genetics) to purebred Black Angus bulls.

Criollo and commercial cows co-grazed study pastures at all sites, except for two of four New Mexico experiments (Nyamuryekung'e et al., 2022; Spiegel et al., 2019). All cattle had grazed study pastures previously. The first year of the Utah study was the exception, however; Criollo cattle were introduced to the ranch a few weeks prior to the initiation of data collection. Therefore, only data gathered during the second and third year of this study were included in this analysis. In all cases, study protocols were approved by the corresponding Animal Care and Use Committees. Mature cows (4 y or older) were used in all studies except in the McIntosh et al. (2021) experiment which monitored yearling steers and did not include a commercial beef breed control. Cows in the Roacho Estrada et al. (this issue), Spiegel et al. (2019) and California (Duni et al., this issue) experiments were not nursing a calf during the study period. In all other studies, cows were nursing young calves either in summer (Herrera Conegliano et al., this issue; Nyamuryekung'e et al., 2022) or spring (Duni et al., this issue). No feed supplements were used during periods when animals were being monitored. Raramuri Criollo cows used at the North American sites were on average 179 kg lighter than their commercial breed counterparts (388 vs. 564 kg for R. Criollo vs. beef breeds), whereas Argentine Criollo cows weighed roughly the same as their Angus counterparts (400 vs. 420 kg, for A. Criollo vs. beef breed).

Cows at the US and Mexico sites were monitored with Lotek GPS collars for cattle (Lotek Wireless, New Market ON, Canada). Earlier studies used the Lotek 2200 model which included a GPS receiver, two axis accelerometer and temperature sensor. More recent studies used newer models (Lotek 3300 and Lotek Litetrack) which also included a GPS receiver, a two- or three-axis accelerometer and a temperature sensor. The La Rioja study used a GPS collar manufactured by INTA's agricultural engineering department. All tracking devices, regardless of model, were store-on-board such that logged data were stored on the device's memory and downloaded to a portable computer for post processing and analysis once the monitoring period had concluded. All collars were powered by rechargeable batteries that were typically able to power the device for periods of two weeks (collars used in La Rioja) to six months (collars used in Utah). Five to eleven cows of each breed were fitted with GPS collars at each site. In some cases collars were rotated among different cows on a weekly or bi-weekly basis, whereas in other studies the same cows were monitored throughout each season. The rate of collar failure varied across sites and years and usually involved two or three devices per breed and site. However, in all cases data were retrieved from at least three sensors (cows) per breed, and most studies were able to use data from five or more cows of each breed. In earlier studies GPS data were differentially corrected after retrieval. This procedure, commonly used in earlier GPS tracking studies, was designed to offset accuracy distortions generated by the US Department of Defense Selective Availability program. This program was discontinued in May 2000.

Quality control of cattle GPS data retrieved from the collars was typically conducted by inspecting GPS dilution of precision (DOP) values for each GPS fix and excluding points with very large DOP numbers (>20), normally a very small proportion of all fixes. Location data were then converted to geographic coordinates using a GIS software, typically an ESRI product (www.esri.com), to map cattle location in study pastures and identify points that occurred outside of the study

pastures which were typically excluded from analysis. Movement and activity metrics derived from location coordinates were calculated using either MS Excel spreadsheets or GRAZETOOLS, a software package designed to automate this process (Gong et al., 2020). Details regarding the protocols used to calculate the four foraging behavior metrics used in this analysis are provided in Table 1, and resulting primary foraging behavior data used in this analysis are provided in Table 2. We recognize the limitations of combining multiple studies with different experimental designs for analysis, however the utility of cross-site analyses of data collected at multiple locations and scales is increasingly being recognized as a valuable tool for examining patterns in large complex datasets (e.g. Raynor et al., 2021).

2.3. Analysis of secondary data

Average distance traveled ($\text{km}\cdot\text{d}^{-1}$), area explored ($\text{ha}\cdot\text{d}^{-1}$), and time spent grazing ($\text{h}\cdot\text{d}^{-1}$) by Criollo vs. commercial beef cattle during growing/green vs dormant/brown seasons or in dry vs. rainy years were extracted from the papers included in this analysis (Table 2). A secondary metric was developed by calculating the ratio of distance traveled to time spent grazing (km traveled per h spent grazing) which was used as a measure of foraging effort (Table 2). We computed seasonal and year-to-year behavior differences between dormant/brown season or driest year and growing/green season or rainiest year. Differences were expressed as a percentage of growing/green season or rainiest year behavior metric values and were calculated as follows:

$$\left(\frac{B - G}{G}\right) * 100$$

where B is the value of a behavior metric during the dormant/brown season or driest/drier year, and G is the value of the same metric during the growing/green season or the rainiest year. Positive percentages indicate greater distances traveled, area explored, hours spent grazing or grazing effort during the dormant/brown or driest year vs. growing/green season or rainiest year. Negative percentage values indicate the opposite.

Four of the studies included in this analysis were conducted over multiple years; one study was replicated in three consecutive years (Nyamuryekung'e et al., 2022), while the other three studies were repeated twice (Duni et al., this issue; Herrera Conegliano et al., this issue; McIntosh et al., 2021). In all cases, behavior metrics for each breed and season were averaged across years to compute seasonal differences.

Our seasonal analysis involved two approaches. First, we compared mean percent change of each behavior metric in Criollo and commercial beef animals including data from the eight individual experiments. However, because half the experiments were conducted at the Chihuahuan Desert site, we were concerned that patterns observed in this ecosystem would bias our overall results. Therefore, we conducted a second comparison involving ecosystems ($n = 5$) where results from all four Chihuahuan Desert studies were averaged.

Year-to-year difference analysis included the subset of four studies conducted over multiple years. Here we computed behavior difference between the wettest and driest year of the study. For the Nyamuryekung'e et al. (2022) study, which included three years' worth of data, we compared behavior during the rainiest year with each of the two drier years. Separate inter-annual difference comparisons were conducted for growing/green and dormant/brown seasons.

Our data did not meet ANOVA assumptions; therefore we used the non-parametric Wilcoxon two sample test to compare seasonal or annual changes in foraging behavior of commercial vs. Criollo cattle. Independent tests were conducted for each of the four behavior metrics considered. We used PROC NPAR1WAY in SAS 9.4 (SAS Institute, Cary, NC) to conduct all analyses. Breed differences were declared statistically detectable at $P \leq 0.05$. Because the number of studies available was

Table 3

Percent seasonal or annual change of four grazing behavior metrics derived from data logged by GPS collars deployed on commercial and Criollo beef cattle grazing extensive rangeland pastures (see Table 1 for details). Mean values shown are dormant/brown season (a, b) or driest year (c) percent change in foraging behavior relative to growing/green season (a, b) or wettest year (c). Wilcoxon Two Sample Test was used to compare percent change of foraging behaviors of commercial vs. Criollo cattle.

Behavior variable ^a	Commercial (Mean % change ± SEM)	Criollo (Mean % change ± SEM)	Wilcoxon Two Sample Test Statistic	P ^b
<i>a. Seasonal behavior change – experiments (n = 8)^c</i>				
Distance traveled	-2.47 ± 4.52	18.40 ± 5.36	33	<0.01
Area explored	46.10 ± 33.93	120.68 ± 53.42	44	0.09
Hours spent grazing	-4.81 ± 3.76	-4.12 ± 2.41	55	0.48
Grazing Effort	2.94 ± 5.28	23.89 ± 4.90	36	0.01
<i>b. Seasonal behavior change – ecosystems (n = 5)^d</i>				
Distance traveled	-1.56 ± 5.53	22.67 ± 8.04	17	0.02
Area explored	59.41 ± 40.15	157.10 ± 83.53	21	0.11
Hours spent grazing	-3.36 ± 3.92	-3.37 ± 2.96	27	0.50
Grazing Effort	1.99 ± 2.58	27.09 ± 6.13	15	0.01
<i>c. Year-to-year behavior change (n = 5)^e</i>				
<i>Growing/green season</i>				
Distance traveled	20.90 ± 11.12	20.40 ± 5.16	19	0.45
Area explored	39.42 ± 18.25	44.45 ± 37.22	22	0.36
Hours spent grazing	6.29 ± 2.98	10.67 ± 7.90	19	0.45
Grazing Effort	13.16 ± 7.37	9.66 ± 3.18	22	0.37
<i>Dormant/brown season</i>				
Distance traveled	3.83 ± 10.85	21.48 ± 6.8	14	0.09
Area explored	22.58 ± 25.56	74.92 ± 11.71	12	0.03
Hours spent grazing	0.56 ± 7.42	10.20 ± 9.84	18	0.36
Grazing Effort	2.90 ± 4.52	12.38 ± 8.02	16	0.20

^a Units associated with original data were km*d⁻¹, ha*d⁻¹, h*d⁻¹, and km traveled per hour grazed, for distance traveled, area explored, hours spent grazing and grazing effort, respectively. Original data shown in Table 2.

^b P values shown correspond to one-sided P > Z derived from Wilcoxon's Normal Approximation.

^c Results from all published experiments were included in this analysis; four in New Mexico (USA), and one in each of the Utah (USA), California (USA), Chihuahua (Mexico), and La Rioja (Argentina) sites. Multiple year data were averaged for New Mexico, Utah, and La Rioja experiments. See Table 1 for details.

^d Results from the four New Mexico experiments were averaged for this analysis. Data included correspond to averages for each of five ecosystems shown in Fig. 1.

^e Multiple year data from two experiments in New Mexico (USA), one experiment in Utah (USA) and another in La Rioja (Argentina) were used in this analysis. One of the New Mexico experiments had three years' worth of data thus yielded two data points; i.e. the two driest years of the series were compared to the wettest of the three years.

relatively small (n = 5 to 8), tests that yielded P values between 0.05 and 0.1 were considered to be marginally significant.

3. Results

3.1. Seasonal grazing behavior plasticity

Compared to commercial beef cows, Criollo cattle exhibited significantly greater seasonal adjustment in daily distance traveled (P ≤ 0.02) and daily grazing effort (P = 0.01) in both experiment- and ecosystem-level analyses (Table 3 a, b). This difference was consistent across all sites, regardless of ecosystem, Criollo biotype, or commercial breed considered (Fig. 1). Compared to the growing/green season, Criollo cows traveled on average 20% farther each day and exhibited a 25% increase in daily grazing effort during the time of year when forages were dormant/brown (Table 3a, b). Commercial cows tended to travel slightly shorter daily distances on average (-2%) and exhibited a very modest average increase in daily grazing effort (2.5%) during the dormant vs. growing season (Table 3a, b). A degree of variation in

commercial breed response was observed across sites (Fig. 1). During the dormant/brown season, increase in daily area explored, relative to the growing/green season, was almost three times greater in Criollo vs. commercial beef cows (1.4 vs. 0.5-fold difference, respectively) but breed differences were only marginally significant (Table 3a, b). Still, remarkable consistency across experiment sites was observed (Fig. 1).

Seasonal adjustment in daily time spent grazing was similar for Criollo and improved breeds in both experiment- (P = 0.48) and ecosystem-level (P = 0.50) analyses (Table 3a, b). Both breeds spent roughly 4.5% less time grazing on average during the dormant/brown vs. growing/green seasons. Seasonal variation in this foraging behavior metric tended to vary somewhat across sites (Fig. 1).

3.2. Year-to-year grazing behavior plasticity

Comparison of dry vs. wet year grazing behavior during the growing/green season yielded no statistically detectable differences between Criollo and improved beef cattle for any of the four metrics analyzed (Table 3c). However, Criollo cattle showed detectably greater

behavior adjustment than commercial beef cows in daily area explored during dormant/brown seasons of dry vs. wet years ($P = 0.03$, Table 3c). Increase in estimated hectares explored per day in dry vs. wet years was three times greater for Criollo than commercial beef cows (0.75 vs. 0.22-fold difference, respectively, Table 3c). The magnitude of this difference between breeds was almost identical to that observed in the seasonal analyses above (Table 3a, b). Criollo cattle also tended to exhibit greater behavior adjustment than commercial beef counterparts in daily distance traveled during the dormant season of dry vs. wet years (22% vs. 4% increase, respectively) but such differences were only marginally significant ($P = 0.09$, Table 3c). No statistical breed differences in adjustment of time spent grazing ($P = 0.36$) or grazing effort ($P = 0.20$) were observed when comparing dry vs. wet year dormant season grazing behavior (Table 3c).

4. Discussion

Cross-site analyses of secondary data from studies conducted in Argentina (Herrera Conegliano et al., this issue), Mexico (Roacho Estrada et al., this issue) and the United States (Duni et al., this issue; Nyamuryekung'e et al., 2021a; Nyamuryekung'e et al., 2022; Roacho Estrada et al., this issue; Spiegel et al., 2019) provided general support for our hypothesis that Criollo cattle would exhibit greater foraging behavior plasticity compared to improved beef cows. Seasonal or year-to-year plasticity in daily distance traveled, daily area explored and grazing effort (three metrics associated with forage search patterns) was three to ten times greater for Criollo cattle vs. commercial beef breeds. Behavior plasticity differences were observed regardless of site characteristics (vegetation, topography), Criollo cattle biotype, or commercial breed considered. Interestingly, no difference between Criollo and commercial beef cows was observed in seasonal or year-to-year plasticity in daily hours spent grazing. This metric likely tracked daily forage intake (Aharoni et al., 2009), a behavior more tightly controlled by animal physiology than environment-related factors. Greater nutritional demands of lactation during summer or spring vs. early to mid-pregnancy in late fall and winter (which were similar in relative terms for all cows) likely influenced seasonal behavior changes in both breeds. Year-to-year plasticity in this metric, particularly during the dormant/brown season, was highly variable among sites. Differences in management including spring calving dates and, therefore, specific gestation stage of cows at each of the four sites included in this analysis were possibly responsible for this result.

Behavioral plasticity in livestock has been studied in the context of animal personalities (Dingemans and Reale, 2005), also referred to as stress coping styles (Koolhaas et al., 1999), temperaments (Réale et al., 2007) or behavioral syndromes (Sih et al., 2004). Wesley et al. (2012) and Goodman et al. (2016) studied personalities (behavioral syndromes) of a herd of New Mexico crossbred range beef cows and classified animals into behavioral types using a suite of foraging behaviors including GPS-derived metrics used in this analysis. They reported that cows that exhibited a less rigid behavioral type (i.e. higher behavioral plasticity) not only explored larger areas of rangeland pastures but also exhibited higher fertility levels relative to counterparts with a more rigid personality. In our analysis, we observed some variation in seasonal behavior plasticity of improved breeds across sites (perhaps associated with variation in behavioral types), yet Criollo cattle consistently showed greater seasonal or year-to-year behavior adjustment. Although the behavior-fertility relationship reported by Wesley et al. (2012) and Goodman et al. (2016) was not addressed in any of the studies analyzed, McIntosh et al. (2022) reported that day-to-day variation (plasticity) in two of the metrics included in our analysis (distance traveled and area explored) was positively associated with weight gains in Criollo and Criollo crossbred steers during the dormant/brown season. During the growing/green season, McIntosh et al. (2022) reported that day-to-day adjustments in forage search paths explained most of the variation in steer weight gains. Greater ability to adjust forage search patterns in

response to temporal variability of forage resources in desert environments should conceivably confer greater fitness (Smith and Blumstein, 2008) but research addressing this hypothesis in heritage vs. modern high-producing beef cattle is currently lacking.

Weaker expression of behavior plasticity in improved beef cows observed in this study could be the result of an unavoidable genetic tradeoff of decades of selecting high-producing dams able to wean calves suited for feedlot environments. Compared to the 1970s, more beef is produced in the US today with a smaller herd of brood cows that wean heavier and faster-growing calves which yield more meat at slaughter (Terry et al., 2021; USDA-ERS, 2019). This industry-wide shift, that is said to have lowered the overall environmental footprint of US beef in terms of water and land use, as well as greenhouse gases emitted per kilogram of meat produced (Terry et al., 2021 and references therein), appears to have occurred at the expense of diminished foraging abilities essential for thriving in increasingly heterogeneous rangeland environments. Terry et al. (2021) recognized that 'the biological optimum for the foraging cow-calf sector and the grain-fed feedlot sectors is often antagonistic' (p.6). Selecting a climate-adapted herd of brood cows for arid environments may require redefining the desired suite of traits needed for efficient beef production in hotter and more variable extensive cow-calf systems. Rethinking arid land beef cow biotype standards may, in some instances, require a reassessment of beef supply chains (feedlot vs. grass fed) best suited for rangeland calf crops (Spiegel et al., 2020). Our analyses provide strong support for the view that heritage cattle possess foraging traits that could be vital for climate adaptation of desert ranching.

Contrasting patterns of foraging behavior of Criollo vs. commercial beef cattle are usually attributed to lighter body weight or smaller body size/frame and lower daily dry matter intake of heritage cattle (Nyamuryekung'e et al., 2022; Peinetti et al., 2011). Body size is a known driver of foraging behavior patterns of herbivores (Illius and Gordon, 1996) yet grazing plasticity differences analyzed here did not appear to be greater at North American sites, where Criollo cows were considerably smaller/lighter than their beef breed counterparts, vs. the Argentina study, where cows of both breeds had roughly the same body weight (Herrera Conegliano et al., this issue). Interestingly, grazing behavior of Argentine Criollo and Angus cows deviated from the general pattern of growing/green season convergence and dormant/brown season divergence observed at all four North American sites. During the growing season (summer) when cows were nursing a calf, Argentine Criollo dams explored significantly smaller areas of the pasture compared to Angus counterparts. During winter, when cows were dry, both breeds explored similarly large areas of the research pasture each day (Herrera Conegliano et al., this issue). Nonetheless, Argentine Criollo cows showed levels of seasonal or year-to-year behavior plasticity that were comparable to those of their North American relatives. It is likely that initial North African and Iberian genotypes and centuries of close-to-natural selection in low input production systems (Armstrong et al., 2022) may have resulted in hard-wired behavior patterns observed across sites. Teasing apart animal-, environment-, and grazing management-related drivers of foraging behavior differences was beyond the scope of the experiments we analyzed. Controlled mechanistic studies are needed to identify underlying physiological and metabolic processes responsible for the breed-related behavior plasticity differences observed.

In addition to conferring climate adaptation advantages, grazing behavior plasticity of Criollo cattle has the potential to yield significant adaptation co-benefits (as defined by Chastin et al., 2021). Spiegel et al. (2019) reported that during the weeks immediately preceding forage green up, a time of the year when herbaceous forages in the Chihuahuan Desert reach their annual biomass nadir, spatiotemporal patterns of grazing of Criollo cows resulted in fewer hotspots of intense use (defined as vegetation patches grazed multiple times for > 2h), relative to commercial beef breed counterparts. Two separate studies included in our analysis (Nyamuryekung'e et al., 2022; Spiegel et al., 2019) reported

that compared to commercial beef cattle, Criollo cows spent less time grazing desert vegetation patches dominated by black grama (*Bouteloua eriopoda*), a palatable perennial grass of high conservation value that has declined significantly over that past century. Estell et al. (this issue) found less black grama in diets of Criollo vs. commercial beef cows, providing independent corroboration of feeding site selection patterns described by Spiegel et al. (2019) and Nyamuryekung'e et al. (2022). At the Corta Madera Ranch, the California Chaparral site included in this analysis, the rancher has observed more frequent grazing in shrub dominated upland areas, previously avoided by his commercial beef herd, as well as recovery of riparian lowlands since introducing Criollo cattle eight years ago (Rob Paulin, personal communication). By spreading herbivory pressure across a broader variety of vegetation patches and plant species, the flexible foraging strategy observed in Criollo cows across all sites could create opportunities for climate adapted beef production systems that impose a smaller footprint on most desert environments. Ongoing long-term grazing studies conducted at the Chihuahuan Desert (USA), Sierra Madre Foothills (Mexico), and Arid Chaco (Argentina) research sites described above, will seek to test this hypothesis and determine the conservation tradeoffs associated with more dispersed grazing impacts (Spiegel et al., 2020).

5. Conclusions

Compared to commercial beef cows, Criollo cattle exhibited significantly greater ability to adjust forage search patterns in response to seasonal or year-to-year fluctuations in forage availability and greenness. We argue that grazing behavior plasticity observed in Criollo cows could be a critical trait for desert beef herds in the face of increasingly variable rainfall patterns occurring as a result of climate change. Significant co-benefits of using Criollo genetics as a tool for climate adaptation could include lowering the environmental footprint of beef production in arid environments.

Disclaimer

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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.

Data availability

Data will be made available on request.

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