



## Foraging behavior and body temperature of heritage vs. commercial beef cows in relation to desert ambient heat<sup>☆</sup>

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### ABSTRACT

We studied foraging patterns of Raramuri Criollo (heritage breed, "RC") and Angus x Hereford (commercial beef breed, "AH") cows in relation to ambient heat and body temperature during summer (2016 and 2017) and winter (2017 and 2018) in the Chihuahuan Desert. Cows of each breed grazed separately in two adjacent pastures (~1100 ha) in a crossover design for four weeks in each season/year. Animals were fitted with temperature loggers attached to blank CIDRs (Controlled Internal Drug Release device) devoid of hormones that recorded body temperature (BodyT), and GPS collars that recorded position and ambient temperature (CollarT). All sensor data were logged at 10 min intervals. A landscape thermal map (LandT) was developed from Landsat satellite imagery for habitat analysis using GPS locations chosen by individual collared cows, and air temperature (AirT) was recorded by a nearby weather station. Data were analyzed within four daytime segments: dawn (sunrise – 9AM); pre-noon (9AM – noon); post-noon (noon – 3PM); and dusk (3PM – sunset). ANOVA was used to determine whether BodyT, CollarT, LandT selection, or animal movement variables within each of the four daily segments differed ( $P < 0.05$ ) for RC vs. AH cows. BodyT and CollarT increased as day progressed in both seasons. During summer, RC had lower BodyT and higher CollarT than AH ( $P < 0.05$ ) during the hottest hours of the day. Increasing AirT throughout the day was associated with selection of cooler LandT in RC but not AH during summer. In winter, both breeds selected warmer landscape locations as the day progressed. Compared to AH, RC cows traveled farther, at higher velocities, and spent more time grazing and traveling and less time resting, with largest breed differences observed during the hottest hours of summer days. These results suggest that Raramuri Criollo cows exhibited higher thermotolerance than did AH. Elevated ambient summer temperatures in the Chihuahuan Desert appear to impose fewer constraints on heritage RC movement patterns compared to mainstream commercial AH cows.

### 1. Introduction

Heat stress is a prominent challenge for beef cattle producers in the southwestern United States because of extended hot weather periods

(spring, summer, fall) that are exacerbated by higher relative humidity during the summer monsoon season (Mader, 2014; West, 2003). Climate change trends in the region will likely intensify existing weather-related challenges and affect the economic viability of the beef industry at large

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(Karl et al., 2009; Reeves et al., 2017; St-Pierre et al., 2010). As regional temperature extremes and heat waves become more frequent (McCollum et al., 2017; Nardone et al., 2010; Polley et al., 2013), the need for thermal buffers (e.g., installation of shades and more frequent watering locations) (West, 2003), suppressed animal performance caused by heat-driven reduction in voluntary feed intake (Cook et al., 2007; Koch et al., 2019; Renaudeau et al., 2012) and increased livestock mortality (Mader, 2014) could cause beef cattle ranching across the region to become economically unsustainable.

Cattle, like other homeotherms, possess the ability to regulate body temperature to maintain physiological homeostasis (Collier et al., 2008; Hansen, 2004; Seif et al., 1979; West, 2003). Mechanisms involved in body temperature regulation include physiological adjustments such as changes in respiratory rate, increase in peripheral blood flow, sweating, and/or behavioral adjustments such as seeking shelter and shade or reducing feed intake (Aharoni et al., 2013; Bernabucci et al., 2010; Koch et al., 2019; Long et al., 2014; West, 2003). Both adjustment mechanisms involve energy expenditure (e.g., sweating or moving to seek shade) that would otherwise be used for growth and/or reproduction and that therefore affect animal performance negatively (Long et al., 2014). In addition, ruminants generate substantial metabolic heat from fermentation (Mader, 2014; Renaudeau et al., 2012; Sprinkle et al., 2000) that must be dissipated to the environment. The inability to adequately dissipate this heat load during summer months results in heat stress or hyperthermia (Gaughan et al., 1999; Mader, 2014; Renaudeau et al., 2012). Crescio et al. (2010) reported an increase in mortality of 4% for each degree increase of temperature humidity index above the thermoneutral zone of dairy cattle.

Heat tolerance varies among cattle breeds and is defined as an animal's ability to regulate its core body temperature when exposed to conditions of thermal stress (Renaudeau et al., 2012). Gaughan et al. (1999) reported that crosses of *Bos indicus* (Hereford X Brahman) or *Bos taurus* cattle of African origin (Hereford X Tuli and Hereford X Boran) had intermediate heat load dissipation abilities compared with Brahman (most efficient) or Hereford (least efficient) animals. Other researchers reported that tropical heritage Romosinuano Criollo cattle, that descend from Iberian and North African *Bos taurus* breeds introduced to the Americas in the 16th Century by Spanish Conquistadors, exhibit heat tolerance traits that are comparable to *Bos indicus* cattle (Hammond et al., 1996; Hernández-Cerón et al., 2004). Thermotolerance of Raramuri Criollo cattle, a *Bos taurus* heritage biotype adapted to harsh conditions of the Copper Canyon of Chihuahua, México (Anderson et al., 2015; De Alba Martínez, 2011; McIntosh et al., 2020), has not been determined to our knowledge.

Animals experiencing heat stress usually adjust their behavior such that exposure or assimilation of the stress-inducing stimuli is minimized (Koch et al., 2019; Polley et al., 2013; Renaudeau et al., 2012; Sprinkle et al., 2000). The heat load threshold at which heat stress-associated activities are initiated depends on an animal's physiological stage and differs among breeds (Renaudeau et al., 2012; Sprinkle et al., 2000). Sprinkle et al. (2000) compared behavior of Angus vs. Brahman X Angus vs. Tuli X Angus crossbred cows and reported that Angus accumulated greatest heat loads, spent significantly more daytime hours under shade, and grazed for shorter periods of time compared to *Bos indicus* and African *Bos taurus* crossbreeds which exhibited comparable heat loads and behaviors. Studies comparing grazing behavior of Angus crossbred and Raramuri Criollo cows in the desert of southern New Mexico showed that when forage is scarce or dormant, Raramuri Criollo cows distribute grazing pressure across the landscape (Nyamuryekung'e et al. *this issue*; Peinetti et al., 2011; Spiegel et al., 2019). This results in fewer hotspots of intensive use when comparing patch (pixel) utilization patterns of Raramuri Criollo vs. Angus crossbred counterparts (Nyamuryekung'e et al. *this issue*; Spiegel et al., 2019). Spiegel et al. (2019) noted that during the growing season breeds utilized different ecological states, hence, speculated that breed-related differences in heat tolerance (Raramuri Criollo > Angus crossbreeds) could partially explain these

findings. However, this hypothesis has not been formally tested.

The objective of this study was to examine foraging patterns of Raramuri Criollo (heritage breed, "RC") and Angus x Hereford (commercial beef breed, "AH") cows in relation to ambient heat and body temperature during summer and winter in large Chihuahuan Desert pastures. Based on previous research conducted with RC (Peinetti et al., 2011; Spiegel et al., 2019) and other Criollo cattle biotypes (Hammond et al., 1996; Hernández-Cerón et al., 2004), we hypothesized that: 1) RC cows would exhibit higher heat tolerance than their AH counterparts; and 2) that breed differences in heat tolerance would result in contrasting activity and habitat selection patterns.

## 2. Materials and methods

### 2.1. Study site

This study was conducted in two adjacent rangeland pastures (pastures 12A and 12C, at 1190 and 1165 ha, respectively) at the Jornada Experimental Range (JER) and was replicated over two years (2016 and 2017). The JER is located in southern New Mexico, USA (32° 37' N 106° 40' W) and encompasses 78,266 ha of relatively flat terrain with elevations ranging from 1300 to 1600 m within the northern Chihuahuan Desert. The climate at this site is typical of hot desert grasslands with a long term mean annual precipitation of 247 mm, approximately 50% of which occurs between July and September. Mean ambient temperature is highest in June and lowest in January, averaging 36.0 °C and 13.3 °C, respectively. During summer (Table 1) we recorded 101 mm of accumulated precipitation, with an average temperature of 23.5 °C and relative humidity ranging from 11.3 to 96.0%. In winter, we recorded an 35 mm of accumulated precipitation, with 7.1 °C average temperature and relative humidity ranging from 7.6 to 99.1%. Long term weather records for this area were reported recently by McIntosh et al. (2019).

Vegetation is dominated by honey mesquite (*Prosopis glandulosa*) intermixed with perennial grasses dominated by black grama (*Bouteloua eriopoda*), dropseeds (*Sporobolus* spp.), and threeawns (*Aristida* spp.) occurring on sandy soils. 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 higher clay content (Havstad et al., 2000; Peinetti et al., 2011). Due to increasingly variable precipitation and an increase in ambient temperature, vegetation of the Chihuahuan Desert has shown a dramatic decrease in perennial grass production over the past 52-yr (McIntosh et al., 2019). Detailed historical forage production data are reported by McIntosh et al. (2019)

### 2.2. Animals and telemetry

All animal handling protocols were approved by New Mexico State University Institutional Animal Care and Use Committee (protocol: 2015–021). Cows of each breed (AH and RC) were randomly selected in summer (nursing cows) and winter (non-nursing cows) from two herds of mature cows (mean BW ~545 kg and ~350 kg for AH and RC, respectively) maintained separately at the JER (Table 1). The study was conducted during the growing and dormant seasons for two years. During sampling periods, cows grazed each pasture for two weeks. Cows of each breed grazed adjacent pastures separately and were switched to the alternate pasture at the end of the second week. This crossover design ensured that both breeds were exposed to the same environment with no social interaction of breeds. At both sites, grazing intensity was estimated to be light to conservative based on key species utilization (Holechek and Galt, 2000). All selected nursing cows had calves that were less than two weeks of age. Cows were fitted with a Global Positioning System (GPS) collar (Lotek® 3300, Lotek Wireless, New Market, ON, Canada) programmed to record animal locations and ambient temperature at 10-min intervals throughout the deployment period (4 weeks). Cows were also fitted with temperature loggers (iButtonLink

**Table 1**

Number of animals, GPS and temperature loggers deployed and retrieved (deployed – retrieved = malfunctioning sensors) on nursing and non-nursing Raramuri Criollo (RC) and Angus Hereford (AH) cows grazing Chihuahuan Desert during summer and winter. GPS and temperature sensors were configured to log data at 10 min intervals. Deployment length for each device type and the difference in sunrise, sunset, day length, and date for LandSat imagery used for thermal environment analysis are also shown. Sunrise and sunset data were retrieved from <http://www.almanac.com>.

Year	Season	Phys. State	Breed	Cows	Deployed		Retrieved		Deployment Length		Sunrise to Sunset	Day Length	LandSat
					GPS	Temp logger	GPS	Temp logger	GPS	Temp logger			
1	Summer	Nursing	RC	14	7	11	6	6	8/25/16	8/26/16	6:46	12:35	9/19/16
			AH	14	7	11	5	11	9/24/16	9/23/16	19:22		
	Winter	Non-nursing	RC	12	7	11	7	7	1/20/17	2/4/17	6:56	10:47	2/25/17
			AH	12	7	11	6	6	2/25/17	2/18/17	17:44		
2	Summer	Nursing	RC	12	9	11	6	9	8/1/17	8/11/17	6:33	13:12	9/5/17
			AH	11	8	11	6	9	9/9/17	9/1/17	19:46		
	Winter	Non-nursing	RC	11	11	10	8	6	1/25/18	2/3/18	6:53	10:55	2/12/18
			AH	11	10	9	9	9	02/28/18	2/20/18	17:48		

LLC, Whitewater WI, USA) affixed to a blank CIDR (Controlled Internal Drug Release device) devoid of hormones inserted intravaginally, and set to record body temperature at 10 min intervals. Temperature loggers were deployed for the entire four-week period in summer 2016 and for two weeks during subsequent sampling periods (Table 1).

### 2.3. Data processing

GPS collar data including latitude/longitude and ambient temperature (CollarT) were downloaded using GPS3000 Host (V2.062; Lotek wireless Inc., Newmarket, ON) after each deployment. Geographic coordinates were converted to the Universal Transverse Mercator (UTM) coordinate system (Zone 13 N) with the North American Datum of 1983. The position vector files were screened for missing records or duplicates before analysis. Data from days of collar deployment and collar retrieval were excluded (Table 1). Collar temperature sensors were located on the GPS motherboard within plastic encasements that hung below an animal's neck and were presumed to record ambient temperature that may have been affected by the collared animal's body temperature (Jiang et al., 2012) although comparison of temperature readings from the collar sensor and our weather station suggest that this effect was likely very small.

Body temperature data were downloaded from temperature loggers (CIDRs with iButton DSI922 L-F5#Thernochron 8 K Memory) after each deployment. Intravaginal temperature readings are known to be a reliable estimate of core body temperature in cattle (Lees et al., 2018) and were therefore used as a proxy for body temperature in this study. Temperature logger data were processed for the second and third weeks of the deployment period.

Deployment and recovery of data from sensors on RC and AH cows typically occurred on different days (breeds were almost always brought into the pens on consecutive days) and therefore one or two days in each weekly data collection period were different for each breed. To verify that sampling days for both breeds had similar ambient temperatures, we retrieved and analyzed 5 min air temperature data from an automated weather station (Campbell CR206 data logger, HMP50 temperature probe) at JER headquarters (AirT, °C) located approximately 3 km from our research pastures. These data were treated as a separate response variable in our ANOVA models.

Using UTM GPS coordinates, we calculated distance traveled (km), movement velocity ( $m \cdot \text{min}^{-1}$ ), and activity budget (time spent resting, grazing, or traveling,  $h \cdot \text{day}^{-1}$ ) for each collared cow. GPS fixes were discriminated into activity categories using movement velocity thresholds such that velocities ranging between 0 and  $2.34 m \cdot \text{min}^{-1}$  were classified as resting, those ranging between 2.35 and  $25 m \cdot \text{min}^{-1}$  were classified as grazing, and velocities between 25.01 and  $500 m \cdot \text{min}^{-1}$  were classified as traveling. These threshold values were previously used by Nyamuryekung'et al. (2020) and were adapted from a classification tree model proposed by Augustine and Derner (2013). Time spent engaged in a given activity was calculated by multiplying the number of

GPS fixes classified within that activity by the GPS fix interval (10 min). Although Lotek™ GPS collars used in this study were equipped with 2-axis accelerometers, Continanza (2019) recently showed that including those data in activity classification trees did not improve discrimination compared to algorithms based solely on GPS data (as used in this study).

A landscape thermal map (LandT) was developed for habitat use analyses. This map consisted of a  $30 \times 30$  m pixel raster file derived from thermal infrared band 10 of the Landsat-8 satellite, collected on a 16-day interval at a nominal overpass time of 10:30AM (Anderson et al., 2012). At-sensor thermal radiance was converted to surface radiometric temperature using the MODTRAN atmospheric correction technique (Berk et al., 1998) and a simplified estimation of surface emissivity based on vegetation cover fraction. While this approach might result in an error of absolute land surface temperature, it still offers a platform for comparative spatial and temporal assessment. Land-surface temperature images were then spatially sharpened from native resolution (100 m) to 30 m using a Data Mining Sharpener approach developed by Gao et al. (2012). From all available Landsat images during each sampling period, a single image with the least cloud masking was selected to represent relative landscape thermal conditions for that sampling period (Table 1). LandT values for each GPS coordinate were extracted for corresponding deployment period raster maps using ArcGIS (ESRI, 2018; ArcMap Desktop v. 10.6). Thus, an average value was computed from the extracted value of LandT for each collar animal within distinctive time of the day segments explained below. LandT was assumed to reflect the potential influence of the thermal landscape on spatial distribution of cattle.

### 2.4. Data analysis

Only daytime hours were considered for analysis in order to evaluate spatial selection patterns in search of shade. Sunrise and sunset times were adjusted daily for data analysis (<http://www.almanac.com>). Data were analyzed within four daytime segments (time of day, ToD): dawn (sunrise to midmorning); pre-noon (midmorning to noon); post-noon (noon to midafternoon); and dusk (midafternoon to sunset). Midmorning and midafternoon time was calculated as the mid-point between sunrise and noon (approx. 9:00 a.m.), or noon and sunset (approx. 3:00 p.m.). Sunrise and sunset at the beginning and end of the study occurred between 6:22–6:55 a.m. and 7:06–8:04 p.m. in summer and between 6:39–7:07 a.m. and 5:30–6:01 p.m. in winter (Table 1).

Average daily BodyT dynamics for cows of each breed were initially explored via appropriate graphs (BodyT vs. Time) for each of the summer deployment periods. We reasoned that amplitude of daily BodyT cycles would be inversely related to a breed's ability to dissipate heat. Data from 11 RC to 6 AH cows in summer 2016 and 9 of each in summer 2017 were plotted and visually assessed.

For all subsequent analyses, variables were averaged weekly for each of the four weeks of a sampling period using the MEANS procedure in

SAS 9.3 (SAS Institute, Cary, NC) and a weight statement was added to the computation of their least square means in the following procedure. Data were analyzed assuming a crossover design. Since very few animals (11–14) grazed each ~1100 ha pasture during each four-week period, grazing impact on forage availability or other vegetation attributes was deemed negligible. Data were blocked by Year (1, 2) and pasture (12A, 12C). Breed (RC, AH), ToD (Dawn, Pre-noon, Post-noon, Dusk), and their interaction (Breed-by-ToD) were modeled as fixed effects in an analysis of variance (ANOVA) using the MIXED procedure in SAS 9.3 (SAS Institute, Cary, NC). Year x Pasture, Year x Pasture x Week, and Breed nested within Year x Pasture were modeled as random variables. Data for each season (winter and summer) were analyzed separately using the same model. Temporal resolution for all variables was a day (Table 2).

Response variables included metrics of both physiological and behavioral adaptation to ambient heat. Physiological variables included BodyT (°C) and CollarT (°C), whereas behavioral responses included thermal landscape site selection (LandT, °C), as well as distance traveled (km \* d<sup>-1</sup>), average movement velocity (m \* min<sup>-1</sup>), and activity budget (time spent resting, grazing, or traveling, h \* d<sup>-1</sup>). AirT (°C) data were analyzed to rule out potential data bias derived from our sampling protocol (see above). Lastly, an orthogonal contrast statement was included for each variable analyzed to compare changes in estimates between the coolest (Dawn) and the hottest (Post-noon) time of the day.

ANOVA assumptions were tested for all models to detect deviations from normality and the presence of outliers. Violations of assumptions were detected for distance traveled, movement velocity, and time spent traveling. Various transformations were tested, and a log-transformation was selected. For these variables (distance traveled, average movement velocity, and time spent traveling), medians of back-transformed data were used to interpret results following Ramsey and Schafer (2002). Means were compared via the LSMEANS statement in PROC MIXED using SAS 9.3 (SAS Institute, Cary, NC), and differences were declared statistically detectable at P ≤ 0.05.

### 3. Results

Average BodyT of cows of both breeds showed a clear diurnal cyclic pattern (Fig. 1). However, AH cows showed higher amplitude of diurnal core body temperature compared to RC cows, which were apparently better able to regulate their core temperature and maintain thermo-neutrality (38.5 °C). BodyT of AH cows exceeded 39.5 °C on nine of 14 days in 2016 and four of 14 days in 2017, whereas RC BodyT exceeded 39.5 °C only once in 2016 (Fig. 1).

BodyT and CollarT were both influenced by the interaction of breed x

time of day in summer, and by time of day in winter (Table 2). BodyT increased as a day progressed in both seasons (Fig. 2). In summer, BodyT was lower (P < 0.05) in RC vs. AH cows during post-noon (38.60 vs. 39.01 °C) and dusk (38.77 vs. 39.27 °C) hours (Fig. 2). CollarT also increased as the day progressed and was higher (P < 0.05) for RC vs. AH cows during pre-noon (28.17 vs. 26.66 °C), post-noon (33.05 vs. 31.35 °C) and dusk (33.63 vs. 32.20 °C) hours (Fig. 2). Thus, by the end of the day, body temperature of AH cows was on average half a degree C higher than that of their RC counterparts that were apparently able to tolerate microsites with ambient temperatures 1.7° higher than those of AH cows (Fig. 2). No breed-related differences in BodyT or CollarT were detected in winter; both variables showed an increasing trend as the day progressed (Fig. 2).

Ambient temperature (AirT) was not different for each breed's deployment days, ruling out the potential temperature bias due to sampling protocol (Fig. 3). AirT increased as the day progressed and reached maximum temperature during post-noon in summer (29.84 °C) and between post-noon and dusk (17.02 vs. 17.41 °C; P = 0.18) in winter (Fig. 3). AirT was lowest during dawn hours in both seasons (22.63, 6.08 °C; summer and winter respectively; Fig. 3).

Habitat selection in relation to landscape surface temperature (LandT) was influenced by time of day in both seasons (Table 2), and there was no breed difference in land surface temperature selected by each breed within any of the time of day segments (Fig. 3; but see results of orthogonal contrast analysis below). Spatial distribution maps of each breed are shown in a companion paper reporting results from an in-depth analysis of landscape use (Nyamuryekung'e et al., this issue). In summer, cattle selected sites with progressively cooler land surface temperatures (LandT) as the day progressed (dawn 45.66 °C, pre-noon 45.41 °C, post-noon 45.24 °C, and dusk 45.11 °C) whereas, in winter habitat selection followed the opposite trend (dawn 23.70 °C, pre-noon 24.02 °C, post-noon 24.03 °C, and dusk 23.96 °C; Fig. 3). However, it is worth noting that a single image derived from the Landsat-8 satellite, collected at a nominal overpass time of 10:30AM was used for this analysis, and that LandT indicates a relative temperature value.

All activity variables (distance traveled, movement velocity, time spent resting, grazing, and traveling, shown in Fig. 4) were influenced by the interaction of breed x time of day in both seasons except time spent traveling in summer (Table 2). In summer, RC cows traveled farther than AH during pre-noon (0.61 vs. 0.38 km, P = 0.01), post-noon (1.31 vs. 0.62 km, P < 0.01) and dusk (1.36 vs. 0.63 km, P < 0.01), and moved at higher velocities than AH during dawn (7.02 vs. 5.32 m \* min<sup>-1</sup>, P = 0.04), pre-noon (4.01 vs. 2.49 m \* min<sup>-1</sup>, P < 0.01), post-noon (5.69 vs. 2.74 m \* min<sup>-1</sup>, P < 0.01) and dusk (6.11 vs. 2.80 m \* min<sup>-1</sup>, P < 0.01). In winter, RC cows traveled farther than AH during dawn (0.53 vs. 0.41

**Table 2**

Effects of year (2016 or 2017) and pasture (12A or 12C) blocking factors, and of breed (RC or AH), time of day (ToD; dawn, pre-noon, post-noon, dusk) and their interactions on body temperature and behavior of Angus Hereford and Raramuri Criollo cows grazing Chihuahuan Desert pastures in summer (nursing cows) and winter (non-nursing cows) of two consecutive years (2016–2018).

Dependent Variables	Summer					Winter				
	Block Effects		Main Effects		Interaction Effects	Block Effects		Main Effects		Interaction Effects
	Year	Pasture	Breed	ToD	Breed*ToD	Year	Pasture	Breed	ToD	Breed*ToD
BodyT (°C) <sup>a</sup>	0.01	0.57	0.16	<0.01	<0.01	0.04	0.80	0.51	<0.01	0.25
CollarT (°C) <sup>b</sup>	0.16	0.53	0.08	<0.01	0.02	0.59	0.91	0.73	<0.01	0.16
AirT (°C) <sup>d</sup>	0.03	0.74	0.51	<0.01	<0.01	0.75	0.99	0.89	<0.01	0.94
LandT (°C) <sup>c</sup>	0.19	0.88	0.88	<0.01	0.09	<0.01	0.22	0.85	<0.01	0.09
Distance Traveled (km*d <sup>-1</sup> )	0.78	0.58	0.01	<0.01	<0.01	0.12	0.25	<0.01	<0.01	<0.01
Movement Velocity (m*min <sup>-1</sup> )	0.88	0.53	0.01	<0.01	<0.01	<0.01	0.15	<0.01	<0.01	<0.01
Time Resting (h*d <sup>-1</sup> )	0.18	0.63	0.01	<0.01	<0.01	<0.01	0.12	0.01	<0.01	<0.01
Time Grazing (h*d <sup>-1</sup> )	0.86	0.64	0.03	<0.01	<0.01	0.03	0.34	0.15	<0.01	<0.01
Time Traveling (h*d <sup>-1</sup> )	0.63	0.96	0.01	<0.01	0.09	0.06	0.57	0.02	<0.01	<0.01

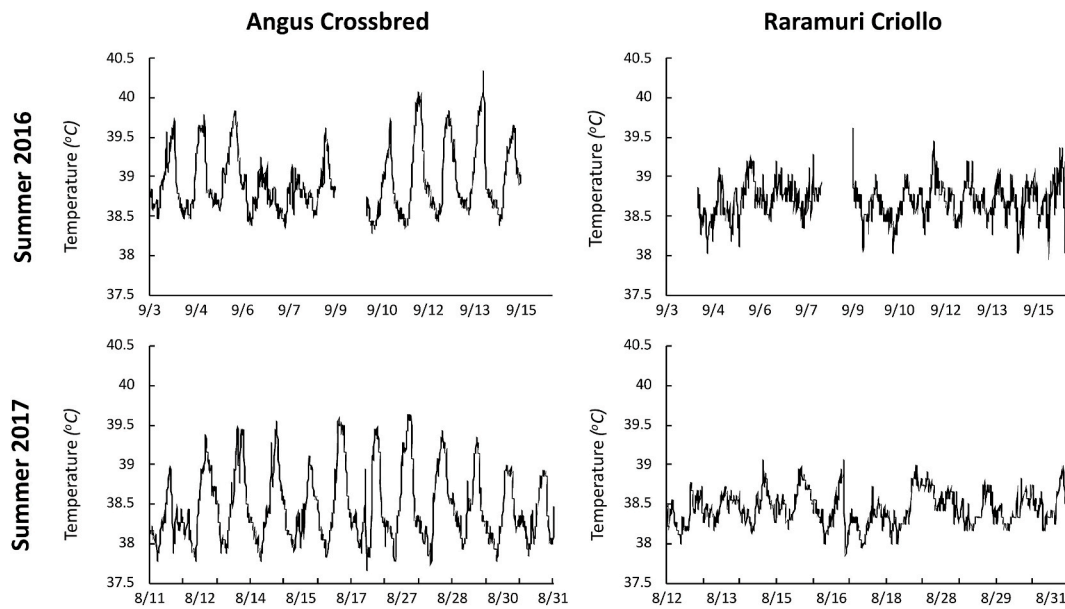
<sup>a</sup> Intravaginal temperature.

<sup>b</sup> GPS collar temperature sensor.

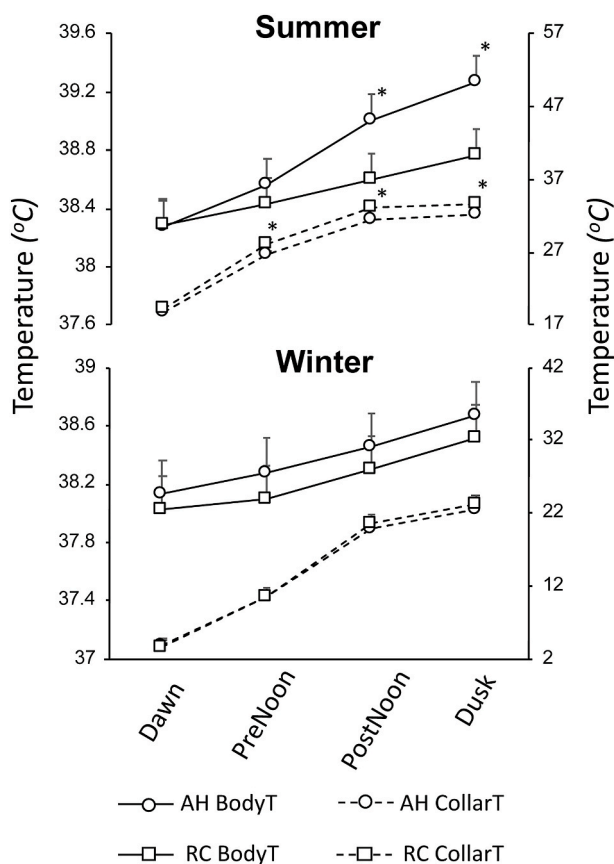
<sup>c</sup> Temperature derived from Landsat 8 image thermal NIR band.

<sup>d</sup> Weather station temperature.





**Fig. 1.** Core body temperature (BodyT) monitored with intravaginal temperature loggers (iButton sensors) set to record data every 10 min for two weeks. Data were retrieved from a group of Angus Hereford crossbreds (AH; 11 in 2016 and 9 in 2017) and Raramuri Criollo (RC; 6 in 2016 and 9 in 2017) nursing cows grazing Chihuahuan Desert rangelands during summer in 2016 and 2017. The subsequent days of the experiment are omitted from analysis.



**Fig. 2.** Core body temperature (BodyT °C, solid lines; Primary Y-axis) and ambient temperature in the proximity of cows (CollarT °C, dashed lines; Secondary Y-axis) of Raramuri Criollo (RC) and Angus x Hereford (AH) beef cows on desert rangeland during summer (2016–17) and winter (2017–18) of two consecutive years. Temperature is plotted against four time of day segments: dawn (sunrise to midmorning); pre-noon (midmorning to noon); post-noon (noon to midafternoon); and dusk (midafternoon to sunset). Asterisks signify breed difference within time of day segment.

km,  $P < 0.01$ ), pre-noon (1.27 vs. 0.86 km,  $P < 0.01$ ), post-noon (1.07 vs. 0.55 km,  $P < 0.01$ ) and dusk (1.09 vs. 0.63 km,  $P < 0.01$ ), and moved at faster velocities than AH during dawn (3.26 vs. 2.68  $m \cdot min^{-1}$ ,  $P = 0.03$ ), pre-noon (8.00 vs. 5.81  $m \cdot min^{-1}$ ,  $P < 0.01$ ), post-noon (5.76 vs. 3.10  $m \cdot min^{-1}$ ,  $P < 0.01$ ) and dusk (6.00 vs. 3.64  $m \cdot min^{-1}$ ,  $P < 0.01$ ). Raramuri Criollo cows spent more time grazing than AH during post-noon (1.62 vs. 1.01 h,  $P < 0.01$ ) and dusk (1.58 vs. 1.02 h,  $P < 0.01$ ) and more time traveling than AH during dawn (0.12 vs. 0.05 h,  $P < 0.01$ ), pre-noon (0.08 vs. 0.02 h,  $P < 0.01$ ), post-noon (0.20 vs. 0.06 h,  $P < 0.01$ ) and dusk (0.20 vs. 0.05 h,  $P < 0.01$ ), but spent less time resting than AH cows during post-noon (1.97 vs. 2.73 h,  $P < 0.01$ ) and dusk periods (1.90 vs. 2.69 h,  $P < 0.01$ , Fig. 4). In winter, RC cows spent more time grazing during dusk (1.12 vs. 0.78 h,  $P < 0.01$ ) and traveling during pre-noon (0.12 vs. 0.10 h,  $P = 0.02$ ) post-noon (0.17 vs. 0.04 h,  $P < 0.01$ ) and dusk (0.16 vs. 0.08 h,  $P = 0.03$ ), but reduced time spent resting during pre-noon (0.96 vs. 1.13 h,  $P = 0.01$ ), post-noon (1.77 vs. 2.02 h,  $P < 0.01$ ) and dusk (1.60 vs. 2.01 h,  $P < 0.01$ ) when compared to their AH counterparts (Fig. 4). However, it is worth mentioning that these values only represent a portion of the time (daytime hours) when cattle would have been active. For more complete estimates of 24 h activity patterns of Raramuri Criollo vs. AH cattle we refer the readers to Nyamuryekung'e et al. (2021).

The orthogonal contrast statement comparing the coolest (dawn) and hottest (post-noon) time of day showed increasing BodyT and CollarT for both breeds as daily temperatures (AirT) became hotter, irrespective of season (Table 3). In summer, habitat use (LandT) showed no daily trend for AH but RC cows tended to select pixels with cooler LandT in the afternoon (Table 3). In winter, a trend to select warmer pixels in the afternoon was detected irrespective of breed (Table 3). In summer, as day temperatures increased, distance traveled increased for RC; however, as day temperatures increased distance traveled decreased for AH cows (Table 3). Both breeds tended to travel farther as ambient temperatures increased in winter, although the magnitude of change was larger for RC (Table 3). In summer, both breeds moved at slower velocities as ambient temperatures increased, whereas the opposite was observed in winter when, again, a larger increase in velocity was observed in RC (Table 3). Both breeds tended to spend more time resting as temperatures increased on summer days; in winter, a similar trend was detected for AH cows whereas RC cows spent similar time resting

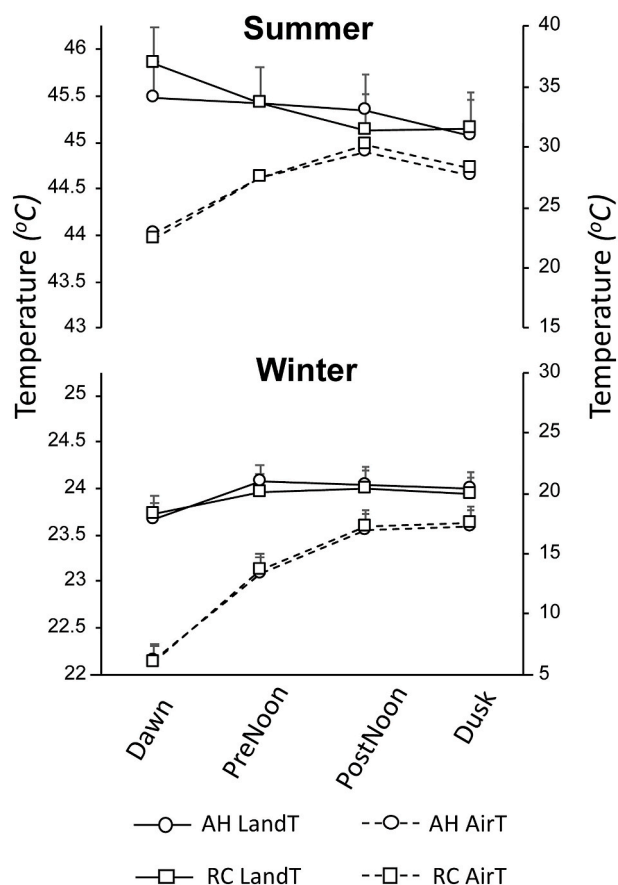


Fig. 3. Surface temperature derived from the Landsat-8 satellite, collected at a nominal overpass time of 10:30AM representing pixels selected (LandT °C, solid line; Primary Y-axis) by Raramuri Criollo (RC) and Angus Hereford (AH) cows grazing Chihuahuan Desert rangeland, and air temperature recorded at a nearby weather station (AirT °C, dashed line; Secondary Y-axis) for days in which each breed was monitored. Data for four time of day segments are shown: dawn (sunrise to midmorning); pre-noon (midmorning to noon); post-noon (noon to midafternoon); and dusk (midafternoon to sunset). Data were collected during summer (2016, 2017) and winter (2017, 2018) of two consecutive years.

regardless of increase in daily temperature (Table 3). Angus x Hereford cows reduced grazing time as the day became hotter in summer, a trend that was not observed in RC, for which grazing time was apparently not affected by the higher afternoon temperatures. In winter, both breeds spent more time grazing during the warmer afternoons (Table 3). Time spent traveling in summer by AH cows was apparently not affected by hotter afternoon temperatures, whereas RC cows increased travel time as day temperature became hotter. During winter, both breeds tended to walk farther in the (warmer) afternoons (Table 3).

#### 4. Discussion

The objective of this study was to examine interactions between foraging patterns and body temperature of Raramuri Criollo (heritage breed) vs. Angus x Hereford (commercial breed) beef cattle in relation to ambient heat. These results support our first hypothesis that predicted that RC cows would exhibit higher heat tolerance than their AH counterparts. Raramuri Criollo cows maintained lower body temperature (BodyT) during the hottest hours of summer afternoons despite being exposed to apparent higher local ambient temperatures (CollarT) than their AH counterparts. Raramuri Criollo cows appeared to accumulate less body heat during the day perhaps due to a superior ability to dissipate heat load as suggested by reduced diel variation in their core

body temperature. No breed differences in core body temperature or collar temperature were observed in winter when heat stress conditions were absent.

An animal's ability to dissipate heat load is mainly dependent on the thermal gradient between its body surface and its immediate environment (Bernabucci et al., 2010; Gaughan et al., 2010; Nardone et al., 2010; Renaudeau et al., 2012). An increase in ambient temperature in the proximity of an animal (CollarT) would likely flatten the temperature gradient and slow heat dissipation resulting in an increase in core body temperature. Severity of thermal stress would therefore depend on the magnitude and possibility of excess heat dissipation during the cooler nighttime hours when the animal-environment temperature gradient is likely steepest (Renaudeau et al., 2012). Accordingly, an apparent BodyT nadir occurred at dawn for both breeds and increased along with AirT and CollarT throughout the day. Daytime increase in AirT and CollarT caused a progressively shallower animal-environment thermal gradient, particularly in summer, likely increasing heat stress conditions. Behavioral responses measured in this study suggest that RC cattle were better able to cope with such conditions compared to AH. Raramuri Criollo cows increased movement rates during hot afternoon vs. cool morning hours and were therefore apparently able to select cooler landscape pixels (afternoon vs. morning pixels) which would have helped them dissipate heat more effectively. The opposite pattern was observed for AH cattle, who reduced afternoon vs. morning travel and did not adjust their selection of surface temperatures in the afternoon. Because cows in this study were likely close to peak lactation during summer experiment dates, high energy requirements and increased metabolic heat (Brosh et al., 2004; Kadzere et al., 2002; NRC, 2016) may have exacerbated heat load conditions in both breeds.

Heat dissipation rates are also affected by cow size, a trait that determines surface area to volume ratio, as well as adipose tissue deposition patterns, and coat and skin traits. Angus x Hereford and Raramuri Criollo cows used in this study weighed approximately 545 kg vs. 350 kg, respectively. A calculation of each breed's surface area to volume ratio using published heart girth (AH: 182 cm; RC: 170 cm) and body length (AH: 146 cm vs. RC: 90 cm) measurements of AH (Jeffery and Berg, 1972) and RC (McIntosh et al., 2020) cows with similar body weights to those of our study cows (AH: 528 kg; RH: 367 kg) resulted in a 16% higher surface area-volume ratio in RC vs. AH cows (RC:  $0.096 \text{ cm}^2 \cdot \text{cm}^{-3}$  vs. AH:  $0.083 \text{ cm}^2 \cdot \text{cm}^{-3}$ ). This difference may have allowed RC cows in our study to dissipate heat at higher rates compared to AH counterparts.

Meat quality analyses of Criollo steers from our research site and elsewhere have all reported leaner animals with high meat tenderness and moderate marbling scores (Anderson et al., 2015; Garriz 1984; McIntosh et al., 2021) with Criollo animals consistently accumulating less subcutaneous back fat compared to European breeds. Higher deposition of subcutaneous fat in European breeds provides a degree of insulation during the winter months but can slow heat dissipation in hot desert environments where Criollo biotypes would have a significant advantage. Other physiological differences between Criollo and European beef breeds could have contributed to breed-related differences in heat dissipation rates. For example, a study investigating coat and skin histology of Criollo Limonero cattle (Venezuela), found an increased frequency of slick hair gene with lighter coat color in their herd alongside increased sweat gland size and high rate of blood capillaries irrigating the dermis layer, all of which are traits that are linked with favorable heat dissipation ability (Landaeta-Hernández 2011).

The broad range of coat colors of RC cattle compared to the fairly uniform black color of commercial cattle used in this study (AH) could have potentially influenced our results. A phenotypic characterization of Raramuri Criollo cows used in this study showed that relatively few individuals of this biotype (~15%) exhibit black-colored coats (McIntosh et al., 2020). We conducted exploratory analyses to assess potential impacts of RC coat color (including black coats) and found no relationship between this variable and body temperature (Nyamuryekung'e,

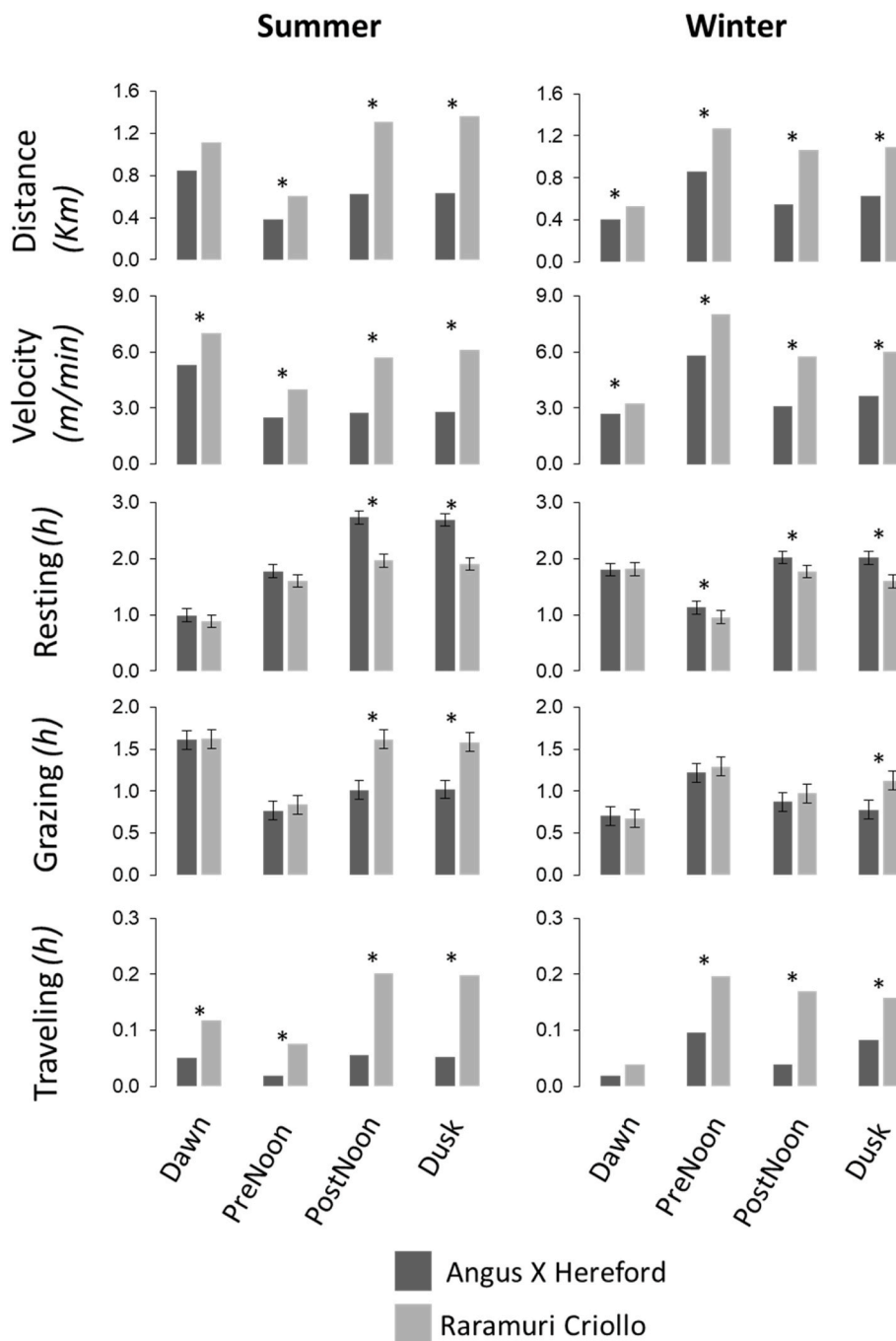


Fig. 4. Least square means  $\pm$  SE and medians of back-transformed log means (distance, velocity, and time spent traveling) for movement and activity variables of Raramuri Criollo (RC) and Angus Hereford (AH) cows within four time of day segments: dawn (sunrise to midmorning); pre-noon (midmorning to noon); post-noon (noon to midafternoon); and dusk (midafternoon to sunset). Both breeds grazed Chihuahuan Desert rangelands during summer (2016, 2017) and winter (2017, 2018) of two consecutive years. Asterisks signify breed difference within time of day segment and variables with no standard error bars are back-transformed means of a log-transformation.

unpublished data). The reduced number of individuals in each coat color group precluded formal statistical comparisons but our analysis, while preliminary, suggests that at our site coat color was likely not a major driver of breed-related body temperature differences. Breed differences in coat hair length, metabolic rates, and milk production (Carabaño et al., 2019), all of which affect heat production and/or dissipation, could also explain body temperature results. Further research to determine how coat characteristics and animal physiology affect body temperature of RC and AH cows is needed.

Our results support the prediction that breed differences in heat tolerance would result in contrasting activity patterns. Not only did we document overall breed differences in distance traveled, movement velocity, time spent grazing and traveling (RC > AH) and time spent resting (RC < AH), but were able to show that such differences were largest during the hottest hours of summer days. These results suggest

that Raramuri Criollo cows exhibit superior thermotolerance and agree with findings from earlier studies with other Criollo cattle biotypes (Hammond et al., 1996; Hernández-Cerón et al., 2004) and African *Bos taurus* cattle (Sprinkle et al., 2000). Reduction in time spent grazing (and associated increase in time spent resting) during hottest hours of summer days was observed in AH but not in RC cows. Heat stressed animals commonly seek to decrease metabolic heat load production by reducing dry matter intake (Aharoni et al., 2013; Koch et al., 2019; Seif et al., 1979; Sprinkle et al., 2000). The temperature threshold that triggers this behavior differs among cattle breeds (Carabaño et al., 2019). For example, dry matter (DM) intake of dairy cows begins to decline when ambient temperatures exceed 25 °C (Kadzere et al., 2002), whereas for most beef breeds, DM intake begins to drop at approximately 30 °C (Bernabucci et al., 2010). Our results suggest that the temperature threshold at which DM intake declines may be higher for RC vs. AH

**Table 3**

A comparison of physiological and behavioral variables during the coolest (Dawn) and hottest (Post-noon) hours of the day for Raramuri Criollo (RC) and Angus Hereford (AH) cows.

Variables	Summer		Winter		Trend		p Value	
	Dawn	Post-noon	Dawn	Post-noon	Summer	Winter	Summer	Winter
<b>BodyT (C)</b>								
Angus X Hereford (AH)	38.27	39.01	38.13	38.46	+	+	<0.01	<0.01
Raramuri Criollo (RC)	38.29	38.60	38.03	38.30	+	+	<0.01	<0.01
<b>CollarT (C)</b>								
Angus X Hereford (AH)	18.85	31.35	3.79	19.85	+	+	<0.01	<0.01
Raramuri Criollo (RC)	19.16	33.05	3.49	20.69	+	+	<0.01	<0.01
<b>AirT (C)</b>								
Angus X Hereford (AH)	22.84	29.56	6.09	16.86	+	+	<0.01	<0.01
Raramuri Criollo (RC)	22.44	30.13	6.06	17.17	+	+	<0.01	<0.01
<b>LandT (C)</b>								
Angus X Hereford (AH)	45.47	45.35	23.67	24.05	=	+	0.49	<0.01
Raramuri Criollo (RC)	45.85	45.13	23.73	24.01	-	+	<0.01	<0.01
<b>Distance Traveled (Km)</b>								
Angus X Hereford (AH)	0.85	0.66	0.41	0.55	-	+	<0.01	<0.01
Raramuri Criollo (RC)	1.12	1.31	0.53	1.07	+	+	0.02	<0.01
<b>Velocity (m/min)</b>								
Angus X Hereford (AH)	5.32	2.74	2.68	3.09	-	+	<0.01	<0.01
Raramuri Criollo (RC)	7.02	5.69	3.26	5.76	-	+	<0.01	<0.01
<b>Time Resting (h./day)</b>								
Angus X Hereford (AH)	0.99	2.73	1.80	2.02	+	+	<0.01	<0.01
Raramuri Criollo (RC)	0.88	1.97	1.82	1.77	+	=	<0.01	0.34
<b>Time Grazing (h./day)</b>								
Angus X Hereford (AH)	1.61	1.01	0.70	0.87	-	+	<0.01	<0.01
Raramuri Criollo (RC)	1.62	1.62	0.67	0.97	=	+	0.98	<0.01
<b>Time Traveling (h./day)</b>								
Angus X Hereford (AH)	0.05	0.06	0.02	0.04	=	+	0.65	<0.01
Raramuri Criollo (RC)	0.12	0.20	0.04	0.17	+	+	<0.01	<0.01

Both breeds grazed Chihuahuan Desert rangeland pastures during summer and winter. Trends, increasing (+), decreasing (-), and the same (=), and statistical significance for each variable within season and breed were evaluated using a contrast statement (Dawn vs. Post-noon).

cattle. In winter, we also observed breed-related differences in activity patterns but the magnitude of such differences during afternoon hours (warmest) was noticeably smaller than in summer. Divergent winter activity patterns of RC and AH cows in this study may have been more closely associated with contrasting foraging strategies to cope with forage scarcity previously observed in these breeds (Peinetti et al., 2011; Spiegall et al., 2019).

Our ANOVA models showed no breed-specific thermal landscape selection patterns (LandT) in either summer or winter; however, dawn vs. post-noon contrast analyses within breeds suggested that only RC cattle selected cooler afternoon vs. morning pixels. Increasing AirT throughout the day during summer was associated with overall selection of cooler landscape pixels (LandT). Conversely, in winter, increasing AirT during the course of a day was associated with selection of warmer landscape pixels (LandT) regardless of breed. Landscape heterogeneity in vegetation and terrain drives ecological processes that dictate movement and resource use patterns of herbivores that graze extensive rangeland (Bailey et al., 1996; Hobbs, 1996, 1999; Kaufmann et al., 2013; Launchbaugh and Howery, 2005; Smith, 1988). Thermal heterogeneity affects landscape use patterns of organisms as they seek to meet thermoregulation needs (Hovick et al., 2014; Sears et al., 2011) and is strongly influenced by the interaction between temperature (AirT) and vegetation (Carroll et al., 2016; Hovick et al., 2014). Vertical vegetation structure shapes the fine-scale thermal environment, offering refuges of biological significance to fauna during peak diurnal heat hours (Carroll et al., 2016; Hovick et al., 2014). Surface temperatures measured at desert sites not far from our research pastures often exceed 65 °C during hottest hours of a summer day (Sears et al., 2011). Heat extremes such as these would force animals to seek refuge, given that temperatures >50 °C can inhibit biological processes and result in protein denaturation (Carroll et al., 2016; Hansen, 2004). Our results highlight the importance of the thermal landscape in influencing spatial distribution patterns of livestock on desert rangeland. Interestingly, this non-forage factor has received limited attention in existing conceptual models of

spatial distribution of livestock (Bailey et al., 1996; Launchbaugh and Howery, 2005) despite its importance (Black Rubio et al., 2008 and references therein). Further research is needed to determine the relative weight of the thermal environment (in relation to biotic drivers) on spatial distribution of cattle breeds that exhibit contrasting heat tolerance.

Paleo-climatologists have classified the 2000 to 2018 drought of the southwestern United States as the second driest 18-year period since 800 CE (Stahle, 2020). The severity of conditions is projected to worsen by the mid-21st century, with vapor-pressure deficits likely to cause the most severe drought episodes of the past millennium (Williams et al., 2020). These predicted changes are projected to cause cascading effects that will disrupt current levels of provisioning ecosystem services (Karl et al., 2009; Polley et al., 2013; Walther, 2010). The heatwave experienced in the summer of 1995 in the mid-central United States caused a \$28 million loss to the cattle industry due to animal mortality and reduced performance (Hahn, 1999). Mitigating the heat stress challenges projected to affect beef cattle in the southwestern US might depend on the use of adapted cattle genetics (Carabaño et al., 2019; Gaughan et al., 2010, 2019). Our results suggest that heritage breeds such as the Raramuri Criollo could be a valuable resource for ranchers seeking to adapt to challenges associated with a hotter and drier Chihuahuan Desert ecosystem.

## 5. Conclusions

Active adaptive management is the process of preparing for uncertainties using sound scientific knowledge to develop mitigation actions before severe or irreversible damage occurs (Briske et al., 2015; Marshall and Smajgl, 2013; McCollum et al., 2017). Genetic selection for higher-producing animals has probably caused heat stress susceptibility due to the close relationship between metabolic heat generation and protein production levels (Bernabucci et al., 2010; Kadzere et al., 2002; Nardone et al., 2010; Renaudeau et al., 2012). Heritage breeds can offer



mitigation opportunities due to their adaptation to harsh environments through natural selection (Rook et al., 2004). Our study highlights Raramuri Criollo cattle as an option for mitigating heat stress losses in southwestern US ranching systems and offers a simple tool for monitoring thermal tolerance in breeds.

### CRedit authorship contribution statement

**Shelemia Nyamuryekung'e:** Investigation, Formal analysis, Writing – original draft, writing of first draft. **Andres F. Cibils:** Conceptualization, Supervision, Writing – review & editing. **Richard E. Estell:** Conceptualization, Writing – review & editing, Resources. **Matthew McIntosh:** Investigation, Writing – review & editing. **Dawn VanLeeuwen:** statistical analysis, Writing – review & editing. **Caitriana Steele:** Software, Writing – review & editing. **Alfredo L. González:** Investigation, Resources. **Sheri Spiegel:** Conceptualization, Writing – review & editing. **Leonel Avendaño Reyes:** methods, Writing – review & editing. **Felipe A. Rodríguez Almeida:** methods, Writing – review & editing. **Martha Anderson:** Software, Writing – review & editing.

### Declaration of competing interest

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

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