Agriculture, Ecosystems and Environment 352 (2023) 108521

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Adaptive, multi-paddock, rotational grazing management alters foraging behavior and spatial grazing distribution of free-ranging cattle

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ARTICLE INFO

Keywords:
Foraging selectivity
Grazing velocity
Herd size recursive grazing
Regenerative grazing
Ungulate herbivory

ABSTRACT

Sustainable management of grazinglands depends upon understanding how management practices influence livestock movements in space and time. We conducted a ranch-scale (2,600-ha) social-ecological experiment to examine how foraging behavior of cattle differs between a single large herd rotated adaptively among paddocks (collaborative, adaptive rangeland management; CARM) versus continuous, season-long grazing of paddocks by small non-rotational herds (traditional rangeland management; TRM). We analyzed how differences in cattle movement patterns may be linked to reductions in cattle growth rates and diet quality in the CARM treatment, relative to TRM. Cattle in the CARM treatment exhibited more linear grazing pathways, moved at lower velocity while grazing, and exhibited longer grazing bouts early in the growing season compared to TRM cattle. Grazing time within any given 10 × 10 m area was distributed more unevenly across TRM vs. CARM paddocks in years with average or above-average precipitation, but not in dry years. In all years, areas of high and low grazing intensity were more spatially clustered in TRM than CARM paddocks. Movement patterns of cattle managed using adaptive, multi-paddock rotations at high stock density (CARM) are consistent with less selective foraging. Such cattle form a "grazing front" that moves across the paddock and distributes grazing pressure in a more spatially homogeneous fashion. In years with substantial forage production, TRM cattle spent more time than CARM cattle in preferred areas of the paddock and foraged in more circular patches. In dry years, however, both treatments resulted in similarly even grazing distribution, likely due to limited intra-paddock variation in forage quality and quantity. At the ranch scale, these different intra-paddock movement patterns led to reductions in animal growth rates and no overall effect of grazing management on forage production.

1. Introduction

The need to understand and predict movement patterns of large herbivores remains a fundamental question in ecology with real-world consequences for ecosystem management. It is well established that large herbivores, including livestock, exhibit nonrandom movements, which can involve tracking phenological waves of high-quality forage (e.g. Frank et al., 1998; Merkle et al., 2016; Middleton et al., 2018) or repeatedly returning to high quality foraging locations (e.g. Owen-Smith et al., 2010; Raynor et al., 2016; Geremia et al., 2019) These movement patterns enable herbivores to improve diet quality by consuming more palatable vegetation, and thereby enhance their growth and/or lactation rates. Predicting the effects of management on animal fitness (i.e. individual performance, Gaillard et al., 2010) and ecological processes using geolocation data can inform adaptive decision-making to optimize human livelihoods and ecosystem health. For instance, livestock grazing practices that regulate animal movement affect approximately 26% of the world's land area (Asner et al., 2004) and can lead to landscapes of enhanced diversity and function or can be a major contributor to soil degradation processes and losses of biodiversity (Steinfeld et al., 2006).

Sustainable management of grazinglands depends upon understanding how management practices influence movements of free-ranging livestock in space and time, which often have consequences for livestock performance, forage production, and other objectives including wildlife conservation (Bailey et al., 1996). Livestock distribution is managed via fencing infrastructure in many grazinglands

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https://doi.org/10.1016/j.agee.2023.108521
Received 19 September 2022; Received in revised form 21 March 2023; Accepted 4 April 2023

worldwide. However, the ways in which fences are used, the degree to which they influence livestock movement patterns, and the degree to which managers understand the distribution of grazing livestock within a given paddock all vary widely. Over the past century, rangeland managers and scientists have sought to improve their understanding of how the timing and rate of livestock rotations among multiple paddocks within and among seasons influences livestock grazing patterns, vegetation responses, and livestock production (Sampson, 1951; Briske et al., 2008; Teague and Barnes, 2017; Hawkins et al. 2017). Adaptively rotating livestock among paddocks in response to spatiotemporal variation in forage growth and species composition holds potential for enhancing the provision of multiple ecosystem services from rangelands (Teague and Barnes, 2017; Derner et al., 2021). Yet surprisingly few studies have quantified how multi-paddock rotations influence the movement patterns of livestock within a given paddock, or how grazing patterns might differ if livestock grazed the same area at lower densities over a longer period.

Animal monitoring and tracking technologies have advanced rapidly in recent years, and global positioning system (GPS) tracking collars combined with activity sensors now allow livestock geolocations to be recorded at sufficiently frequent intervals to examine daily movement pathways, while also distinguishing between grazing versus non-grazing movements (Rivero et al., 2021). Prior studies of season-long versus within-season rotational livestock management were primarily conducted within small paddocks (e.g. hectares to 10′s of hectares; Briske et al., 2008), and relied on measurements of forage utilization or direct observations of animals to assess spatial heterogeneity of livestock grazing (e.g. Hart et al., 1993). GPS tracking collars are now increasingly used to quantify livestock distribution on commercial operations at larger spatial scales (>100 ha; e.g. Ganskopp and Bohnert, 2009; Rinella et al., 2011; Homburger et al., 2015; Tobin et al., 2021) but have only rarely been used to compare movement patterns and distribution while actively grazing under different types of rotational management (Probo et al., 2014; Venter et al., 2019). These studies found rotational management reduced the clustering of grazing locations in patches of high forage value relative to season-long grazing in mountainous pastures of the Swiss Alps (Probo et al., 2014), and in a South African grassland (Venter et al., 2019).

We conducted a ranch-scale (2,600-ha) experiment designed to examine how the movement of cattle among paddocks affects multiple rangeland ecosystem goods and services, including forage production, plant diversity, livestock productivity, and the abundance and diversity of grassland birds (Fernández-Giménez et al., 2019; Davis et al., 2020; Augustine et al., 2020). Specifically, we compared how adaptive rotations of a single cattle herd among paddocks during the growing season contrasts with continuous grazing of individual paddocks by a single herd for the duration of the growing season (May – Oct). The latter grazing strategy is traditionally used in this ecosystem (Traditional Rangeland Management, TRM; Bement, 1969). Decisions regarding annual stocking rate and the sequence and timing of cattle movements among paddocks for the adaptive, multi-paddock grazing treatment were made by an 11-member stakeholder group seeking to achieve a suite of vegetation, livestock, and wildlife objectives (see Wilmer et al., 2018); this experimental treatment is hereafter referred to as Collaborative Adaptive Rangeland Management (CARM). For CARM, the 10, 130-ha paddocks were grazed by a single herd of steers managed using adaptive, rotational grazing which incorporated planned year-long rest in 20% of the paddocks.

During the first 5 years of the study (2014 – 2018), key findings regarding desired outcomes were that (1) livestock weight gains were 11 – 16% lower annually in the CARM versus the TRM treatment (Augustine et al., 2020), with significant negative consequences for net revenue (Windh et al., 2019), (2) CARM enhanced habitat for and abundance of grasshopper sparrows *Ammodramus savannarum*) in rested paddocks and horned larks *Eremophila alpestris* in recently grazed paddocks, but did not enhance abundance of a second shortgrass obligate, the thick-billed longspur *Rhynchophanes mccownii* (Davis et al., 2020), and (3) CARM did not affect the relative abundance or productivity of desirable C_3 midgrasses relative to the TRM treatment (Augustine et al., 2020). The latter finding was consistent with subsequent analyses showing that experimental treatments did not affect the probability that tillers of the C_3 perennial midgrass *Pascopyrum smithii* would experience more than one defoliation event per year (i.e., regrazing; Porensky et al., 2021). Given the economic losses associated with reduced livestock weight gain with CARM, we sought to understand the mechanisms underlying this outcome. We hypothesized that weight gains could be affected by differences in energy expenditure as well as by differences in the quality and quantity of forage consumed by cattle grazing at the 10-fold greater stock density in CARM compared to TRM (McCollum et al., 1999; Venter et al., 2019).

To test these hypothesized mechanisms, we recently examined differences in energy expenditure by comparing step rates measured by pedometers placed on cattle in both treatments during 2016 and 2017. This analysis showed that CARM cattle increased step rates on days when they were rotated to a new paddock, as well as during the first several days following a rotation (Plechaty, 2018). However, estimates of the energetic expenditure associated with this increase in step rate indicated that CARM cattle experienced $< 1\%$ increase in total daily energy expenditure, which could not explain the much larger (11–16%) decline in CARM weight gains (Plechaty, 2018). Furthermore, weekly sampling of fecal samples from both treatments to estimate crude protein (CP) in the steer's diets showed that TRM diets contained significantly higher CP than CARM steers during the first half of the grazing season, and then dietary CP in both treatments converged toward the end of the grazing season (Plechaty, 2018). This finding led to the hypothesis that the quality of forage consumed by cattle in CARM may be reduced due to less selective foraging behavior, which could be associated with changes in movement patterns while grazing.

Here, we used GPS collars placed on a subset of the cattle in each treatment to examine differences in daily grazing behaviors and grazing distribution, which could both cause and result from differences in quality and quantity of forage consumed. First, we examined four daily metrics of foraging behavior by steers in both treatments: (1) grazing time per day, (2) mean velocity while grazing, (3) mean duration of individual grazing bouts each day, and (4) tortuosity of movement pathways while grazing. We examined grazing time per day because it often changes in response to the quality and quantity of forage available to cattle (Benvenutti et al., 2006; Spiegal et al., 2019; Nyamuryekung'e et al., 2021; Augustine et al., 2022). We examined daily velocity while grazing and grazing bout duration because these metrics can potentially serve as indicators of changes in individual cattle weight gain as forage conditions change (Sawalhah et al., 2016; McIntosh et al., 2022). We examined the tortuosity of grazing pathways of cattle in both treatments as a potential indicator of how herd size affects the selectivity of grazing by cattle (Sawalhah et al., 2016). Following these analyses of individual steer behavior, we examined how differences in foraging behavior in the two treatments manifested as differences in the spatiotemporal distribution of grazing over the course of a given CARM herd rotation (varying from ~12–40 days depending on forage conditions) and over the course of an entire summer grazing season (~135 days, mid-May to late September). We hypothesized that lower stocking density in TRM (one tenth that of the CARM treatment) would result in more selective foraging behavior, and that movement metrics consistent with this higher selectivity would include higher velocity while grazing, lower grazing bout duration, more tortuous grazing pathways, and more aggregated and uneven grazing distributions.

2. Methods

2.1. Study area and experimental design

Research was conducted at the Central Plains Experimental Range

(CPER) approximately 12 km northeast of Nunn, Colorado, USA (40°50′N, 104°43′W), which is a Long-Term Agroecosystem Research (LTAR) site. Long-term mean annual precipitation at the CPER is 340 mm, of which greater than 80% occurs during the growing season of April through September (Lauenroth and Sala, 1992). Topography is flat to gently rolling; soils range from fine sandy loams on upland plains to alkaline salt flats bordering a large drainage running north-south in the eastern portion of the site. Two C_4 shortgrass species – blue grama (*Bouteloua gracilis*) and buffalograss (*B. dactyloides)* – comprise over 70% of aboveground net primary productivity (Lauenroth and Sala, 1992). C_3 perennial grasses (*Pascopyrum smithii*, *Hesperostipa comata*, and *Elymus elymoides*), C_4 bunchgrasses (*Aristida longiseta*, *Sporobolus cryptandrus*), plains pricklypear cactus (*Opuntia polyacantha*), subshrubs (*Gutierrezia sarothrae*, *Eriogonum effusum*, *Artemisia frigida*), and saltbush (*Atriplex canescens*) are less abundant but generate taller structure on the landscape (Augustine and Derner, 2015).

Twenty 130-ha paddocks were paired into ten blocks where each block contained two paddocks that were similar in terms of soil and plant characteristics, topographic patterns as measured by a topographical wetness index (Beven and Kirkby, 1979), and prior management history of season-long grazing at moderate stocking rates. One paddock in each block pair was randomly assigned to the TRM treatment, and the other was assigned to the CARM treatment (Fig. 1). Previous studies showed that 130 ha paddocks are sufficiently large to allow cattle to exhibit uneven foraging distribution in response to topography, distance to water, and spatial variation in plant composition in this ecosystem (Senft et al., 1985; Gersie et al., 2019).

Each TRM paddock was grazed throughout the growing season (mid-May to early October) by a single small herd of yearling steers that occupied each paddock separately (i.e., none were rested), whereas the CARM paddocks were grazed by a single 10-fold larger herd of yearling steers managed with an adaptive, rotational grazing system, with 20% of the paddocks planned for year-long rest each year (Fernández-Giménez et al., 2019). The rested paddocks were part of the planned grazing

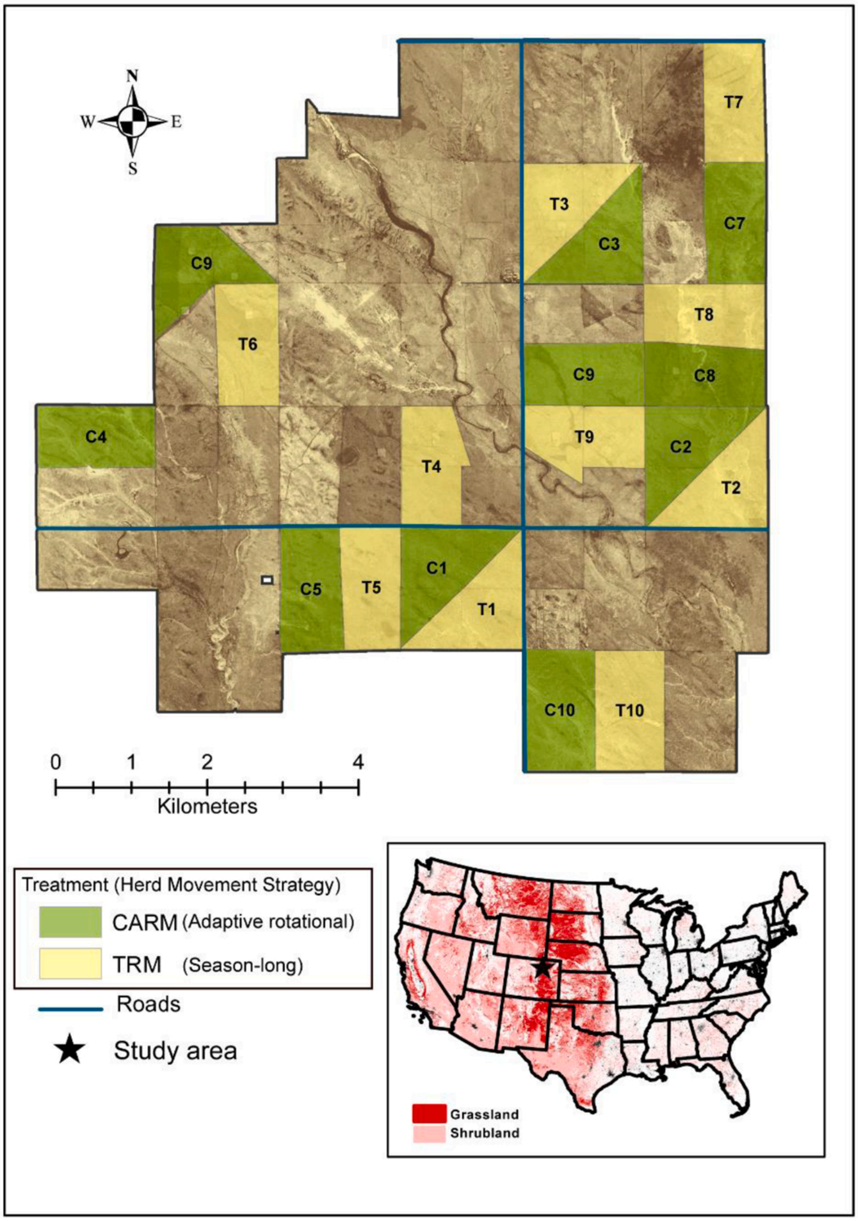


Fig. 1. Map depicting the location of the Central Plains Experimental Range in northeastern Colorado (inset), and the 10 pairs of paddocks (each ~130 ha) used to compare the effects of Collaborative Adaptive Rangeland Management (CARM) versus Traditional Rangeland Management (TRM) on cattle grazing behavior and distribution.

system and were not available for other uses (e.g. leasing or haying). Details of the cattle management strategy applied to the CARM paddocks were decided by the 11-member stakeholder group who used stocking rate adjustments, grazing rotations, and season-long rest as adaptive management tools designed to help achieve specific goals and objectives (Wilmer et al., 2018).

Stakeholders decided on the stocking rate, grazing sequence, and which paddocks to rest each grazing season, and developed a suite of criteria used to rotate cattle in response to real-time conditions of the paddocks during the growing season. The stakeholder decision-making process was intended to produce repeatable, evidence-based decisions that were explicitly tied to management objectives and incorporated local and professional knowledge as well as experimentally-derived monitoring data (Fernández-Giménez et al., 2019).

This analysis reports on data collected during the first five years of the ten year experiment, 2014 – 2018. Each year, the same total number of steers grazed in the CARM and TRM paddocks. The stocking rate was initially set at 214 steers in 2014 based on the recommended moderate stocking rate for the soil and plant communities present in the study area equivalent to 0.61 animal unit months (AUM) ha^{-1}; USDA 2007a,b,c). In subsequent years, the stakeholder group adjusted the stocking rate in April, prior to the May 15th grazing start date, depending on past vegetation conditions and seasonal weather forecasts. Stakeholders increased the stocking rate to 0.64, 0.67, 0.70, and 0.81 AUM ha^{-1} in 2015, 2016, 2017, and 2018 respectively (equivalent to a total of 224, 234, 244, and 280 steers). The TRM stocking rate was also adjusted each study year to match the CARM stocking rate, such that paddocks in the two treatments differed only in the adaptively managed spatiotemporal pattern of cattle movement. Based on annual measurements of forage production in grazing cages combined with the assumption that yearling steers consume 2.6% of their body weight daily at an average weight of 364 kg (800 lbs, which is the approximate weight of steers in this study at the mid-point of the growing season), we estimate that cattle at these stocking rates grazed an average of 23% and 17% of forage produced in the wet years of 2014 and 2015, 27% of forage in the average year of 2017, and 35% and 47% of forage in the drier years of 2016 and 2018, respectively. Pre-treatment vegetation and cattle performance data were collected in 2013, when all 20 paddocks received the TRM treatment.

Which CARM paddocks experienced pulse grazing and which were rested from grazing varied across years and depended on an adaptive grazing management plan developed by the stakeholders as well as on-the-ground, weather-dependent conditions (i.e., forage biomass and cattle behavior) measured weekly during the grazing season (Augustine et al., 2020). Based on weather and vegetation conditions experienced during our study, the CARM herd rotated through 7, 4, 7, 9 and 9 paddocks during 2014 – 2018 respectively (Fig. 2). The timing of rotations among paddocks each year was determined by criteria co-developed by stakeholders and scientists (Wilmer et al., 2018; Augustine et al., 2020). In 2014 and during 2016–2018, cattle were moved when a threshold was met either in vegetation biomass, cattle behavior, or a maximum number of grazing days set for each paddock based on the multiple management objectives. In 2015, the maximum days threshold was removed to allow the rotation to be based primarily on vegetation thresholds. Due to exceptional precipitation and plant growth in 2015 (Fig. 2), long grazing periods (in most cases ~40 days) were required to reduce vegetation to target thresholds, such that the CARM herd only rotated through four paddocks during the grazing season.

In addition to adaptively varying the sequence of grazed paddocks annually, stakeholders chose to implement prescribed burns where they could potentially help achieve objectives for vegetation, livestock production, and wildlife habitat (Wilmer et al., 2018). Stakeholders chose to implement 32-ha patch burns during the autumn (October or November) in blocks one and nine in 2014, block six in 2016, and block 10 in 2017. They hypothesized that removal of a portion of the residual grass in particular paddocks could enhance preferential grazing in patch burned areas with higher forage quality early in the next growing season (Augustine and Derner, 2014), while also creating habitat for certain grassland birds (Augustine and Derner, 2015). Any time that stakeholders decided to implement a patch burn within the CARM treatment, a patch burn of the same size and on the same soil types was implemented in the paired TRM paddock, so that control paddocks only differed in the adaptively managed spatiotemporal pattern of cattle movement.

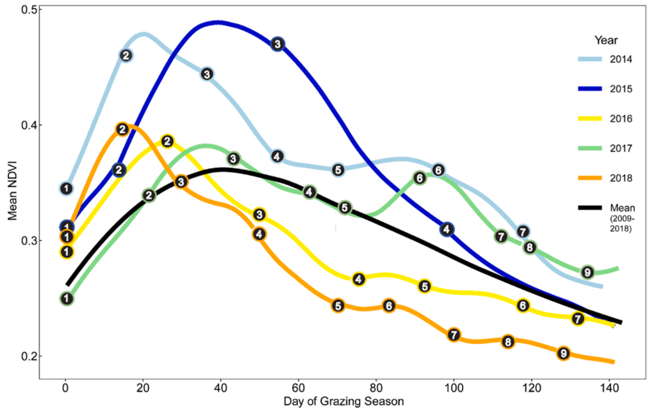


Fig. 2. Seasonal patterns of greenness based on a fusion of NDVI measurements by Landsat and MODIS satellites averaged across the Central Plains Experimental Range in northeastern Colorado, USA, for each of 5 grazing seasons during 2014 – 2018. Yearling steers entered the study paddocks in mid-May each year (represented by Day 0 on the x-axis), and grazed until late September or early October each year (approximately Day 140). Numbers within circles along each curve show dates on which the herd in the Collaborative Adaptive Rangeland Management treatment was rotated into a new paddock during each grazing season. The black curve shows seasonal NDVI averaged over the 10-year period from 2009 to 2018.

2.2. Forage production

We previously showed that productivity of each of the 3 plant functional groups that comprise the primary forage base for cattle (C_3 perennial grasses, C_4 perennial grasses, and forbs) was similar in CARM and TRM in most years and on soil types, although some minor differences occurred for certain soil types and years (Augustine et al., 2020). Here, we additionally analyze whether total forage production (i.e. the sum of C_3 perennial grasses, C_4 perennial grasses, and forbs) differed between the two sets of paddocks, using the same methods. Briefly, we measured peak standing biomass by clipping, drying and weighing each plant functional group in 0.18 m^2 quadrats located inside moveable grazing cages distributed along permanent transects in each. paddock. Each year in early August, we sampled 16 cages in paddocks with the dominant soil types, and 24 cages in paddocks that additionally included salt flats (Augustine et al., 2020). Forage production responses to the CARM versus TRM treatment were analyzed using a linear mixed model in SAS (SAS version 9.4, SAS Institute Inc., Cary, NC), which treated block as a random effect, accounted for repeated measures at each plot over time, and evaluated potential interaction between grazing treatment and year. We also included pretreatment forage production measurements (the average of 2013 and 2014) in each plot as a covariate, and we used the Kenward-Roger method to compute the denominator degrees of freedom.

2.3. GPS collar deployments

Each year (2014 – 2018) we deployed Lotek 3300LR GPS collars on 20 steers in the TRM paddocks (2 steers in each of the 10 paddocks) and 10 steers in the CARM herd. All steers in the experiment were of mixed British beef breeds. Collars were placed on randomly selected steers when they were weighed at the start of the grazing season, and the rechargeable batteries were replaced 2 or 3 times each year to maintain collar operation until steers were weighed at the end of the grazing season. Collars were set to collect GPS fixes at 5-minute intervals, and also had an activity sensor that recorded the percent time with the head down and the rate of neck movement in X and Y directions for each 5-minute interval between fixes. All research followed the Institutional Animal Care and Use Committee protocol (#CPER-4) approved October 2013 and renewed November 2015 by the USDA-Agricultural Research Service in Fort Collins, Colorado, USA.

2.4. *Data screening*

We used the measurements recorded by the activity sensors in the collars to classify each 5-minute interval between GPS fixes as a grazing or non-grazing interval (Augustine and Derner, 2013). We then screened the datasets to remove any 24-hour intervals where the collar did not collect at least 95% of the expected number of 5-minute fixes. Occasionally, when a steer is walking or standing near a fenceline, a GPS fix is recorded near but slightly outside the paddock due to GPS error. In cases where one to three consecutive fixes were outside but within 50 m of the fenceline, we adjusted the GPS fix to be the nearest coordinates located directly on the fenceline. After making these corrections, we also removed any 24-hour intervals where the steer left the paddock for 30 min or longer, including removal of days when the CARM herd was rotated among paddocks. This approach was used because the GPS receiver in the collars did not provide a measure of the accuracy of the fixes, such as the dilution of precision.

2.5. *Grazing behavior analyses*

For each 24-hour period that met all the above criteria, we calculated four daily metrics of foraging behavior. First, we calculated the velocity while grazing (VG, in m/sec) as the mean rate of movement for all 5-min intervals in which the activity sensor classified the animal as grazing during each 24-hour period. Second, for each series of three consecutive GPS fixes where the animal was classified as grazing for the entire 10-minute time period, the smaller angle between the vector connecting the first and second fix, and the vector connecting the second and third fix was calculated. This value was then subtracted from 180. Hereafter, we refer to this as the turn angle while grazing (TAG, deviation from a straight line in degrees). An animal grazing in a straight line would have a turn angle of 0°, while an animal whose first vector is perpendicular to its second vector would have a turn angle of 90°. Third, we calculated the time spent grazing each day (GHrs, in hours) by summing all 5-minute intervals each day that were classified as grazing. Fourth, we calculated the mean grazing bout duration (GBD) each day, where a bout was defined as a continuous string of 5-minute intervals of grazing, separated from other grazing bouts by at least one 5-minute interval of non-grazing activity (Augustine et al., 2022). This method of calculating the grazing bout length corresponds closely to that used by Orr et al. (2001), who defined the end of a grazing bout as when an animal stopped grazing for six minutes or more, and demonstrated that grazing bout duration of sheep varied inversely with forage quality.

To analyze whether these metrics of grazing behavior differed between treatments and/or over time, we fit a linear mixed model for each of the four behavioral metrics (response variables) with treatment modelled as a binary fixed factor and DOS as a continuous fixed variable (varying from 1 to 140 for grazing season that began in mid-May and ended in late September or early October each year). All models included steer identity nested within herd as a random factor, which resulted in a model structure that accounts for repeated measures of individual steers over time assuming a compound symmetry covariance structure. Because the CARM herd rotated between 4 and 9 different paddocks each year, models also included a random intercept for each paddock. For each behavioral metric and year of the study, we fit four different models (linear and quadratic terms for DOS, both with and without treatment), and we selected the one with the lowest Akaike's Information Criterion (AIC). If the final selected model did not include a treatment effect, we graphically display the model results without the treatment effect.

2.6. *Grazing distribution analyses*

To compare the spatial distribution of cattle grazing in CARM versus TRM paddocks, we conducted paired comparisons of grazing distributions of steers in the CARM herd for each grazing rotation relative to steers in the paired TRM paddock. We did this at two different temporal scales. First, for each rotation, we compared the grazing distribution of 2 collared steers in the CARM herd (selected randomly from the pool of available collars with the most days of complete GPS data) to the 2 steers from the paired TRM paddock, for the dates over which the CARM cattle were in the given paddock. For example, if the CARM herd rotated into block 3 on June 1 and rotated out on June 22, then we compared grazing distributions from 2 steers in the CARM paddock of block 3 with 2 steers from the TRM paddock of block 3, for the dates of June 2 – 21. If a collared TRM steer was missing data for any days within that date range, we removed data for the same day for a CARM steer, so that we could compare grazing distributions of CARM vs. TRM steers for the exact same steer-days in each treatment. If one of the TRM collars malfunctioned, then we only used data from one steer in each treatment. If less than 10 days of complete GPS collar and activity sensor data were available for either treatment during a given rotation, then that rotation was not analyzed. To quantify grazing distribution, we created vectors connecting each pair of consecutive grazing fixes, and calculated the number of grazing seconds associated with each meter of the vector based on its length and the time elapsed between fixes (typically 5 min). We then intersected these vectors with all 10 × 10 m grid-cells within the paddock, calculated the cumulative number of grazing seconds intersecting each grid-cell, and removed grid-cells that were within 50 m of a water source or paddock corner. We refer to the resulting 10-m resolution raster layer for each rotation as a 'heat map' of grazing distribution.

The previous analysis has the advantage of comparing grazing distributions for the same number of animals (2) over the same portion of the growing season. However, it does not address the fact that CARM paddocks are grazed for a short time by 10-fold more cattle, while TRM paddocks are grazed at 10-fold lower stocking density for the entire grazing season. To obtain a better understanding of cumulative, season-long grazing distribution of each herd for a given paddock, we conducted a second analysis. For each of the rotations, we calculated the total number of grazing days for which the 10 collars in the CARM herd successfully collected full datasets during the dates of the rotation, and the total number of grazing days for which the 2 collars in the paired TRM paddock collected full datasets over the course of the entire grazing season. For whichever treatment contained more steer-days of data, we randomly removed individual days from that dataset until it included the same number of steer-days as the other treatment. For example, during the first rotation in 2014, the CARM herd spent 13 days in block 10 of the experiment, and the 10 collars on these cattle collected a cumulative total of 124 steer-days of complete data (out of a potential total of 130 if all functioned perfectly). Both collars on steers in the paired TRM paddock collected more than 124 days of data over the full grazing season, so we randomly selected one steer, and then randomly removed days until the dataset contained 124 steer days. We then followed the same procedure described above of creating vectors between grazing fixes, dividing these into 1-m segments that represented grazing seconds spent moving along that vector, intersecting the 1-m segments with a 10 × 10 m grid of the paddock, and calculating total cumulative grazing seconds in each grid cell. This allowed us to generate heatmaps of cumulative grazing seconds for each treatment pair, such that the heatmaps for each treatment are generated from the same number of steer-days, thereby controlling for the influence of sample size on grazing distribution (e.g. TRM represents a small herd grazing over a ~135-day season, and CARM represents a 10-fold larger herd grazing for a shorter period time, varying from 12 to 41 days).

For all heat maps, we first calculated Camargo's Evenness Index to quantify the shape of the histogram of grazing time per pixel, where values close to 1 indicate that all grid-cells were grazed at close to the expected mean grazing intensity and values close to 0 indicate most grid-cells differed substantially from the mean [with some grazed intensively and many remaining ungrazed; Payne et al. (2005)]. However, Camargo's Evenness Index does not explicitly account for the degree of spatial autocorrelation in grazing intensity values across a paddock. To evaluate differences in the degree of spatial clustering of grid-cells with similar grazing intensity, we calculated Moran's *I* for each heat map. Moran's *I* approaches 1 as more grid-cells are adjacent to grid-cells of similar values (e.g. if all grid-cells with high grazing intensity occurred next to one another in half the paddock, and grid-cells with no grazing occurred next to one another in the other half), is equal to zero under perfectly random distribution of grid-cells, and approaches − 1 when grid-cells alternate between low and high values in a checkerboard fashion. We calculated Camargo's Evenness and Moran's *I* for each CARM/TRM rotation at both short and long temporal scales, and then used a linear mixed model to test whether these indices differed between treatments in some or all of the 5 years of the experiment, where sample size within each year was the number of rotations. Fixed predictors included treatment and a burn x treatment interaction, to test whether the patch burns (present in rotation 2 and 3 of 2015, rotation 1 of 2017 and rotation 1 of 2018) affected the magnitude of the difference between CARM and TRM in terms of either Camargo's Evenness or Moran's *I*.

3. Results

3.1. Forage and cattle production

Total forage production was similar across the two sets of treatment paddocks for all years of the study (Treatment x Year interaction: $F_{3,232} = 1.58$, $P = 0.20$; Treatment main effect: $F_{1,97.3} = 0.73$, $P = 0.39$; Fig. 3). In contrast to the forage production results, and as previously reported by Augustine et al. (2020), cattle growth rates (kg/animal/day) were reduced by an average of 14.1% in CARM vs. TRM across the five treatment years, with no significant variation in the magnitude of this reduction among years (Fig. 3).

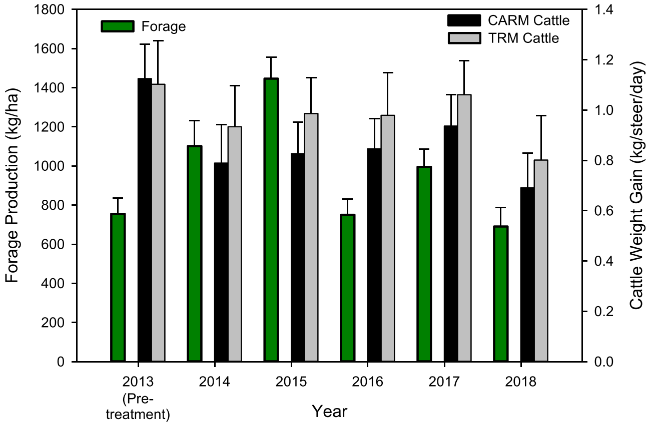


Fig. 3. Annual variation in forage production and cattle weight gains within the Collaborative Adaptive Rangeland Management (CARM) experiment in northeastern Colorado. Forage production was similar in both the Traditional Rangeland Management (TRM) and the CARM treatment in all years (Treatment x Year interaction: $P = 0.54$; Treatment main effect: $P = 0.47$). Cattle weight gains are taken from Augustine et al. (2020). Gains were similar in both sets of paddocks during the pre-treatment year of 2013, when all pastures were managed under TRM. Across all treatment years (2014 – 2018), weight gains in the CARM treatment averaged 14.1% lower than the TRM treatment.

3.2. Foraging behavior metrics

Analyses of generalized linear mixed models for each of the foraging behavior metrics showed that turn angle and grazing bout duration differed between CARM and TRM treatments in all 5 years, and typically varied linearly over the grazing season (Table 1). Mean velocity while grazing showed more complex variation over time that was best fit by a quadratic response to the day of grazing season, and differed between CARM and TRM treatments in 3 of 5 years (Table 1). Grazing time per day was similar between treatments in 4 of 5 years, and varied both linearly (3 of 5 years) and in a quadratic manner (2 of 5 years).

During 2014–2018, annual precipitation, vegetation greenness, and forage production varied widely (Figs. 2, 3). Above-average precipitation received as frequent storms throughout the growing seasons of 2014 and 2015 resulted in substantially above-average forage production (Fig. 3). During these two wet years, foraging pathways of TRM cattle showed substantially greater tortuosity, with mean turn angles while grazing of ~40° during the first two thirds of the growing season, and 35° during the latter third of the growing season. In contrast, CARM cattle grazed in more linear pathways, with turn angles typically in the range of 30 – 35° throughout the grazing season (Fig. 4a,b). Furthermore, in both years, TRM cattle tended to forage at a greater velocity than CARM cattle during the first two-thirds of the grazing season, with velocities converging in the last third of the season (Fig. 4c,d). This difference was especially large in 2015, whereas differences were smaller and more variable in 2014, such that a simple linear model was most parsimonious (Fig. 4c). Mean grazing bout duration was significantly greater in CARM vs. TRM during the first third of the grazing season in both 2014 and 2015 (Fig. 4 e,f). Differences between treatments in grazing time per day were minimal in 2014 and varied by rotation in 2015 (Fig. 4 g,h).

During the latter three years of the study, more xeric conditions prevailed, with total forage production being below-average in 2016, near-average in 2017, and below-average again in 2018 (Fig. 2). In all three of these years, CARM cattle again grazed in substantially more linear pathways for the first four or five rotations of the grazing season (encompassing the first 90 days of the grazing season; Fig. 5a-c), although the magnitude of the difference between CARM and TRM was reduced compared to the wet years. Additionally, CARM cattle grazed at a lower velocity during the first half of the grazing season, with the differences being largest in 2016 and 2018 (Fig. 5d-f). Even in 2017 when the data were best fit by a quadratic model without a treatment effect, grazing velocity during the first third of the season was in the range of 6 – 8 m min^{-1} on most days for CARM cattle, and in the range of 9 – 11 m min^{-1} for TRM cattle. Furthermore, grazing bout duration was elevated in CARM relative to TRM cattle during the first 20 days of the grazing season in all 3 years, corresponding to the first rotation in 2016 and 2017, and the first two rotations in 2018 (Fig. 5). Differences between treatments in grazing time per day for 2016 – 2018 were minimal (Fig. 5j-l).

3.3. Grazing distribution

GPS collars successfully collected sufficient data to analyze Camargo's Evenness Index and Moran's *I* for 6 of 7 rotations in 2014, 4 of 4 rotations in 2015, 7 of 7 rotations in 2016, 6 of 9 rotations in 2017, and 7 of 9 rotations in 2018 (see Appendix 1 for all values by year and rotation). Using these data, we examined differences in the grazing distribution of CARM versus.

TRM steers at two different temporal scales. First, over the course of a single CARM rotation, we compared the distribution of 1 or 2 steers in the CARM herd with the same number of steers in the paired TRM herd over the same number of days. Camargo's Evenness Index was significantly greater in CARM vs. TRM for these short-term comparisons in

Table 1

Comparison of generalized linear mixed models predicting 4 mean daily turning angle while grazing (TA), mean daily velocity while grazing (Vel), mean daily grazing bout duration (GBD), and total grazing time per day (GT) as a function of grazing management treatment (CARM vs. TRM) and day of the grazing season for each of 5 years at the Central Plains Experimental Range in northeast Colorado, USA. We considered models with both a linear and quadratic response for day of grazing season and present the fit of the model that minimized Akaike's Information Criterion (AIC) and maximized the Akaike weight (w_i) in Figs. 4 and 5.

		With treatment effect		No treatment effect		With treatment effect		No treatment effect	
Response	Year	Linear AIC	Quadratic AIC	Linear AIC	Quadratic AIC	Linear w_i	Quadratic w_i	Linear w_i	Quadratic w_i
TA	2014	19,085.6	19,083.9	19,101.6	19,099.5	0.30	**0.70**	0.00	0.00
TA	2015	19,923.4	19,935.4	19,930.9	19,943.2	**0.97**	0.00	0.02	0.00
TA	2016	21,294.8	21,302.7	21,308.9	21,315.4	**0.98**	0.02	0.00	0.00
TA	2017	15,950.2	15,966.5	15,954.5	15,970.7	**0.90**	0.00	0.10	0.00
TA	2018	18,455.1	18,471.6	18,459.2	18,475.7	**0.89**	0.00	0.11	0.00
Vel	2014	10,128.7	10,132.7	10,120.5	10,125.5	0.02	0.00	**0.91**	0.07
Vel	2015	11,153.9	11,048.4	11,281.8	11,155.5	0.00	**1.00**	0.00	0.00
Vel	2016	10,962.2	10,934.1	11,072.3	11,033.9	0.00	**1.00**	0.00	0.00
Vel	2017	8630.3	8591.9	8624.5	8586	0.00	0.05	0.00	**0.95**
Vel	2018	9473.9	9431.4	9501	9458	0.00	**1.00**	0.00	0.00
GBD	2014	27,717.1	27,705.6	27,718.5	27,707.3	0.00	**0.70**	0.00	0.30
GBD	2015	28,356.5	28,366.8	28,385	28,393.1	**0.99**	0.01	0.00	0.00
GBD	2016	31,379.6	31,381	31,390.2	31,390.4	**0.66**	0.33	0.00	0.00
GBD	2017	22,714.5	22,723.9	22,729.5	22,738.2	**0.99**	0.01	0.00	0.00
GBD	2018	27,238	27,242	27,248	27,253	**0.88**	0.12	0.01	0.00
GT	2014	9972.6	9812.3	9963.5	9806.1	0.00	0.04	0.00	**0.96**
GT	2015	9054.9	9070.6	9051.9	9066.8	0.18	0.00	**0.82**	0.00
GT	2016	9847.5	9864.8	9842.3	9859.7	0.07	0.00	**0.93**	0.00
GT	2017	7236.7	7256.4	7290.5	7309.8	**1.00**	0.00	0.00	0.00
GT	2018	7935.3	7747.7	7926.7	7740	0.00	0.02	0.00	**0.98**

years of average to above-average productivity (Fig. 6a; Year x Treatment interaction: $F_{4,24} = 5.58$; $P = 0.003$; treatment contrasts for 2014, 2015 and 2017: $P \leq 0.033$), but not in the two dry years (treatment contrasts for 2016 and 2018: $P = 0.060$ and 0.55). Analysis of spatial clustering using Moran's *I* showed that at the short time-scale, grazing was significantly more clustered in TRM compared to CARM paddocks in all 5 years (Fig. 6b). The magnitude of the difference between CARM and TRM varied across years (Fig. 6b; Year x Treatment interaction: $F_{4,24} = 8.61$, $P < 0.0002$), but was always significantly less than zero (Fig. 6b; $P < 0.01$ for all yearly contrasts).

For example, during the first rotation of 2014 (wet year), heat maps of the grazing distribution of two TRM steers revealed tortuous grazing pathways, in contrast to more evenly distributed and linear grazing pathways for two CARM steers monitored over the same time period (Fig. 7, upper panels; Carmargo's Evenness Index of 0.33 in CARM vs. 0.21 in TRM).

Grid-cells of high grazing intensity were also more spatially clustered in TRM compared to CARM (Fig. 7, upper panels; Moran's *I* of 0.50 vs 0.38). By contrast, during the third rotation of 2018 (a dry year and a time when vegetation greenness was declining), grazing distribution heat maps showed minimal differences between treatments in grazing pathway tortuosity (Fig. 8, upper panels), although TRM cattle still moved at a higher velocity while grazing than CARM cattle (Fig. 5c). In contrast to 2014, the histograms of cattle grazing distribution were similarly clustered around the mean for both CARM and TRM (Fig. 8; Camargo Evenness Indices of 0.18 vs, 0.19), but grazing intensity was still more spatially clustered in TRM (Fig. 8; Moran's *I* of 0.31 vs. 0.39).

To understand grazing distributions across the entire season for a given paddock, we examined a larger number of steers in the CARM paddock compared to a longer number of days grazed by a single steer in the TRM paddock. Results were very similar to the short-term analysis, with greater Carmago Evenness in CARM vs. TRM in the average and wet years (Fig. 6a; Year x Treatment interaction: $F_{4,24} = 7.49$; $P < 0.0064$; treatment contrasts for 2014, 2015 and 2017: $P \leq 0.001$), but not in the dry years (treatment contrasts for 2016 and 2018: $P = 0.14$ and 0.93). For season-long comparisons, grazing distribution again was more spatially aggregated in TRM compared to CARM in all 5 years (Fig. 6b; Year x Treatment interaction, $F_{4,24} = 0.67$ $P = 0.62$; Treatment main effect, $F_{1,24} = 23.97$, $P < 0.0001$), consistent with our previous finding that TRM cattle typically grazed in more tortuous pathways.

When we visualized 125 steer-days of GPS tracking in the wet year of 2014, treatment differences in grazing distribution became even more apparent than they were using a shorter timeframe (Fig. 7, lower panels). CARM grazing was again distributed more evenly compared to TRM (Camargo's Evenness Index of 0.59 vs. 0.35), and grid-cells of high grazing intensity were notably more spatially clustered in TRM compared to CARM (Moran's *I* of 0.50 vs 0.38). In the drier year of 2018, metrics were again more similar between treatments (Fig. 8, lower panels; Camargo Evenness Indices of 0.55 and 0.53 for CARM vs. TRM), but grazing intensity was still more spatially clustered in TRM (Moran's *I* of 0.42 vs. 0.49). In other words, when vegetation was productive, TRM paddocks contained more grid-cells experiencing either high intensity grazing (e.g. >200% of the expected mean grazing intensity) or no grazing at all, while CARM grazing distribution included more grid-cells with grazing intensity closer to the mean.

The presence of a patch burn within a given block of paddocks increased the magnitude of the difference between CARM and TRM treatments for the short-term analysis of Camargo's Evenness (Treatment x Burn interaction: $F_{1,24} = 4.91$, $P = 0.03$), because TRM cattle exhibited stronger selection for patch burns and hence grazed more unevenly compared to paired CARM paddocks with patch burns. However, over the course of the entire growing season, patch burns did not affect the difference in evenness between CARM and TRM (Treatment x Burn interaction: $F_{1,24} = 1.12$, $P = 0.30$). Similarly, the presence of patch burns slightly increased the magnitude of the difference in short-term Moran's *I* between CARM and TRM (because cattle were more spatially aggregated on patch burns in TRM compared to CARM; Burn x Treatment interaction; $F_{1,24} = 4.34$, $P = 0.048$), but did not affect the difference between treatments over the full growing season (Burn x Treatment interaction: $F_{1,24} = 0.16$, $P = 0.70$).

4. Discussion

Using a ranch-scale experiment, we found strong and repeatable differences in steer movement patterns and grazing distributions between the continuously grazed TRM treatment and the adaptive, multi-paddock, rotationally grazed CARM treatment. These differences were

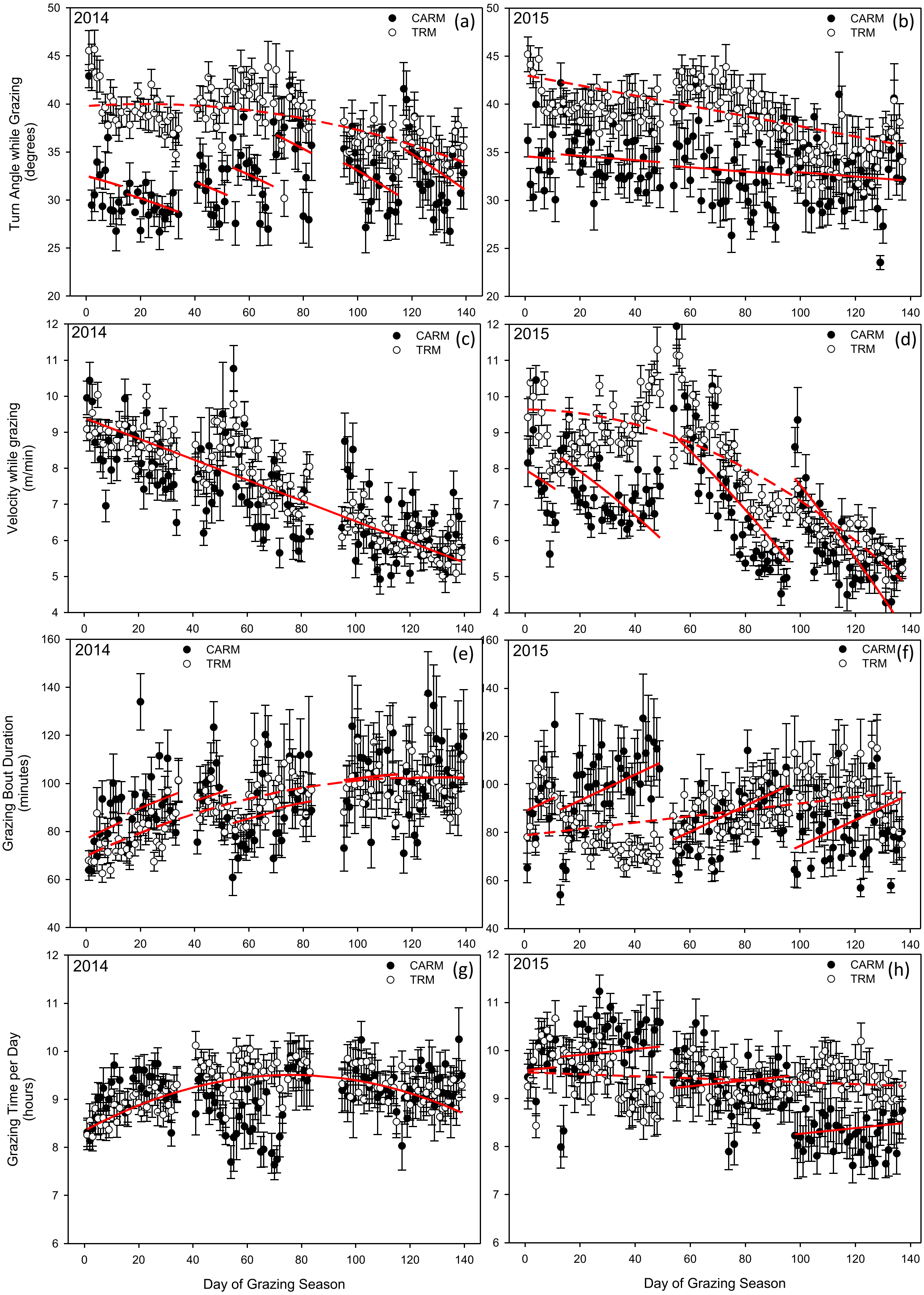


Fig. 4. Daily foraging behavior metrics from steers in a Collaborative Adaptive Rangeland Management (CARM) versus a Traditional Rangeland Management (TRM) treatment at the Central Plains Experimental Range in northeast Colorado during two years with above-average precipitation and forage production. Symbols show daily means for steers in each treatment, and bars show 1 standard error. Red curves show the fit of the most parsimonious linear mixed model. The timing of rotations in a given year can be seen as changes in the random intercept of the red curve for the CARM treatment within the grazing season (see also Fig. 2). The red curve for the TRM treatment is based on the average of intercepts from all 10 TRM paddocks.

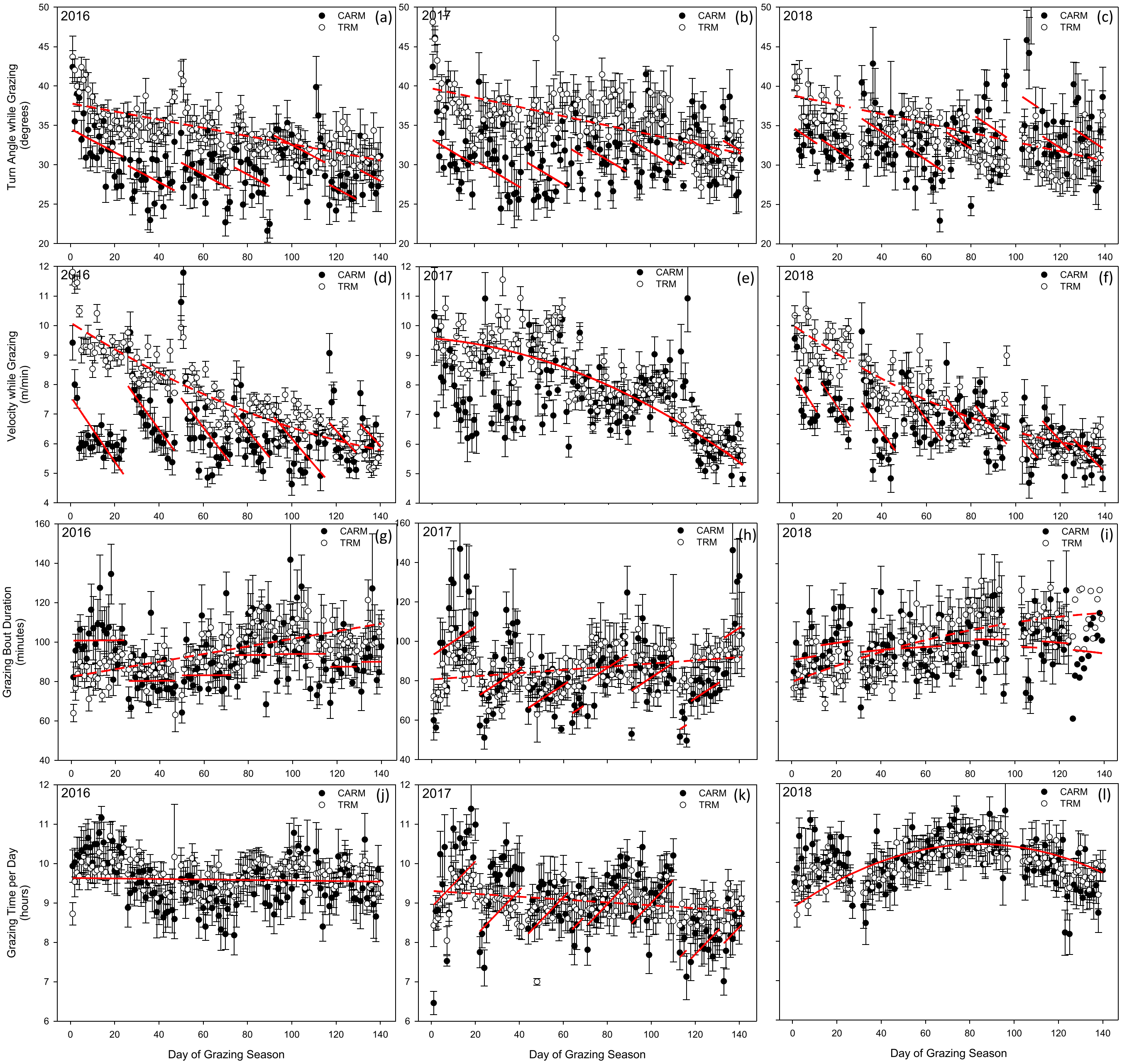


Fig. 5. Daily foraging behavior metrics from steers in a Collaborative Adaptive Rangeland Management (CARM) versus a Traditional Rangeland Management (TRM) treatment at the Central Plains Experimental Range in northeast Colorado during years with below-average (2016 and 2018) to average (2017) precipitation and forage production. Symbols and curves follow Fig. 4.

uniformly consistent with our overall hypothesis that in the CARM treatment with higher stocking densities, cattle foraging behavior would be less selective. Moreover, results show that differences in grazing selectivity between treatments were strongest when forage quality was highest (early in the growing season and in years with above-average precipitation). When forage quality was lower, TRM grazing behavior was more similar to the low-selectivity patterns observed in the CARM treatment.

Considerations of spatial and temporal scales of analyses are critical to understanding how foraging ecology and management of free-ranging livestock affect rangeland ecosystems. Prior analyses of rotational versus season-long grazing management implemented with relatively small (~24–26 ha) and spatially homogenous paddocks found neutral or negative effects on cattle weight gains (McCollum et al., 1999; Hart et al., 1993), minimal effects on cattle grazing distribution (Hart et al., 1993), and negative effects of the quality of forage consumed by cattle (McCollum III and Gillen, 1998). However, an important factor in the interpretation of these findings was that cattle grazing in small, homogenous paddocks have little opportunity for selective grazing patterns that could lead to notably uneven use of the landscape over the course of a growing season. One study demonstrated that increasing the spatial scale of continuously grazed paddocks (by an order of magnitude, to 207 ha) led to substantially uneven grazing distribution, but did not implement a comparable rotational grazing treatment at this larger spatial scale (Hart et al., 1993). Here, when we paired season-long continuous (TRM) and adaptive multi-paddock rotational (CARM) grazing treatments within sufficiently large paddocks to allow for selective grazing patterns (Senft et al., 1985; Gersie et al., 2019), CARM consistently reduced cattle weight gains (Augustine et al., 2020) and diet quality (Plechaty, 2018) across a wide range of precipitation

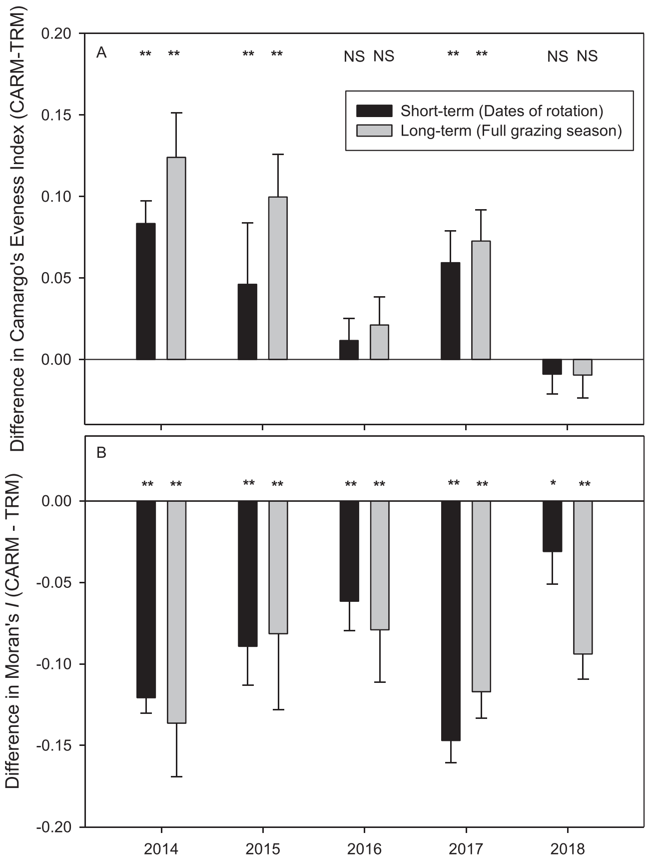


Fig. 6. Differences between management treatments in terms of cattle grazing distribution as measured by Camargo's Eveness Index (A) and Moran's I (B). The former is a measure of the spread of grazing seconds per pixel around the mean, where a map with all pixels equal to the mean would have a value of 1 (perfectly even grazing distribution). The latter is a measure of spatial clustering of pixels with a similar number of grazing seconds adjacent to one another. Both indices were calculated from the type of 10 × 10 m pixel maps shown in Figs. 7 and 8 for each rotation in each year. * * indicates $P < 0.05$, * indicates $P < 0.10$, and NS indicates $P > 0.1$ for tests of whether a given bar is different from zero. Grazing was more evenly distributed around the mean in CARM compared to TRM paddocks in 2014, 2015 and 2017 (A). Grazing distribution was more spatially clustered in TRM compared to CARM in all years (B).

conditions. At the same time, we found no effect of grazing treatment on total forage production (Fig. 3). Previous analyses of production by specific functional groups stratified by soil type also found no effect of grazing treatment on production for the two dominant ecological sites within the experiment, but perennial grass production was reduced in the CARM treatment in a third ecological site (salt flats) that occurred in a portion of 3 of the 10 experimental blocks of paddocks (Augustine et al., 2020).

Our analysis of foraging behavior metrics found that CARM cattle consistently foraged in more linear pathways, with the largest differences documented in years with average or above-average precipitation (2014, 2015 and 2017; Figs. 4,5). In contrast, TRM cattle foraged in significantly more tortuous pathways, and often moved at higher velocity while grazing (Figs. 4,5). Previous analyses showed that declines in mean grazing velocity below 7 m min^{-1}, which is associated with the animal exploring less area within each grazing bout, were associated with reduced weight gain of yearling steers (Augustine et al., 2022). Furthermore, CARM cattle often grazed at a lower velocity during the first third of the growing season, typically moving at rates of 5 – 8 m min^{-1}. In contrast, grazing velocity of TRM cattle never fell below 7 m min^{-1} during the first third of the growing season in any year of the study. Additionally, we note that differences in the grazing velocity metric were not as strong as grazing path tortuosity because CARM cattle typically increased grazing velocity notably during the first 1–2 days after a rotation to a new paddock, and then gradually returned to a lower grazing velocity as length of time in the paddock progressed (Figs. 4, 5).

These metrics are consistent with more selective grazing by TRM cattle, as they moved within a small herd, weaved through the vegetation, and covered a greater distance within each 5-minute grazing interval. In contrast, CARM cattle grazed within a 10-fold larger herd in more linear pathways and covered a shorter distance per 5-minute interval, resulting in consumption of vegetation directly along their linear paths (Video 1). Early in the growing season, the slow, linear CARM foraging pattern is likely to include greater intake of standing dead vegetation intermixed within the new growth, as well as fewer bites of forb individuals that are sparsely scattered through the grass-dominated swards. We suggest that this effect of herd size on foraging behavior is the primary driver of reduced individual cattle performance (i.e., weight gain) in CARM. We also note that cattle in this shortgrass ecosystem gain weight most rapidly during the first third of the growing season (typically > 1.5 kg head^{-1} day^{-1}, and up to 2 kg head^{-1} day^{-1}), when vegetation is growing rapidly (Fig. 2), and gains decline to < 1 kg head^{-1} day^{-1} in the second half of the growing season (Kearney et al., 2022). Differences in grazing pathway tortuosity and velocity between the treatments were greatest in the first third of the growing season, during this most important period for animal weight gain.

The mean daily grazing bout duration (GBD) can also be an indicator of changes in forage quality and quantity that affect cattle weight gain (Augustine et al., 2022). Indeed, we found that GBD of TRM cattle increased consistently after peak greenness each year, as vegetation was beginning to senesce and resource recovery (i.e., sought-after regrowth) halted. This increase was largest in the dry years of 2016 (from 82 to 110 min) and 2018 (from 80 to 120 min) and minimal in 2017 when a second pulse of precipitation and re-greening occurred late in the growing season (see Fig. 2). Increases in GBD were coincident with declines in grazing velocity during the last third of the growing season in all 5 years, consistent with our previous conclusion that these two metrics in combination serve as a useful indicator of declining individual performance (i.e., cattle weight gain; Augustine et al., 2022). In fact, due mostly to low forage quality (Kearney et al., 2022), cattle weight gains often become so low under both CARM and TRM during the last 30 days of the grazing season that a recent economic analysis suggests selling the steers at day 105 increases profitability (Baldwin et al., 2022).

Although we found that declining forage quality and quantity as the season progressed were associated with increased GBD and declining grazing velocity, GBD was only consistently elevated in CARM compared to TRM during the first 1 or 2 rotations of each year. After that, GBD of CARM cattle declined and did not differ from TRM cattle. We suggest increased GBD during the first rotation may reflect a period of learning to forage within a large herd while vegetation is still at low biomass, but subsequent rotations into paddocks with fresh forage of greater biomass resulted in lower GBD as they explored the new forage conditions and adjusted to higher per capita forage availability.

Finally, we found that both CARM and TRM cattle typically grazed for 9 – 10 h per day. Daily grazing time did not differ between treatments or show consistent temporal trends across years. Although grazing time per day can decline significantly between growing versus dormant seasons in semi-arid grazinglands (e.g., Brosh et al., 2006), we did not find a consistent change in grazing time per day as vegetation began to senesce. For detection of more subtle, within-season changes in forage conditions that affect movement decisions and concomitant cattle weight gain, our results suggest grazing velocity, pathway tortuosity, and bout duration are more sensitive indicators than daily grazing time.

The differences in grazing behaviors of CARM versus TRM cattle not only have implications for animal performance, but also manifest as notable differences in grazing distribution, which has potential

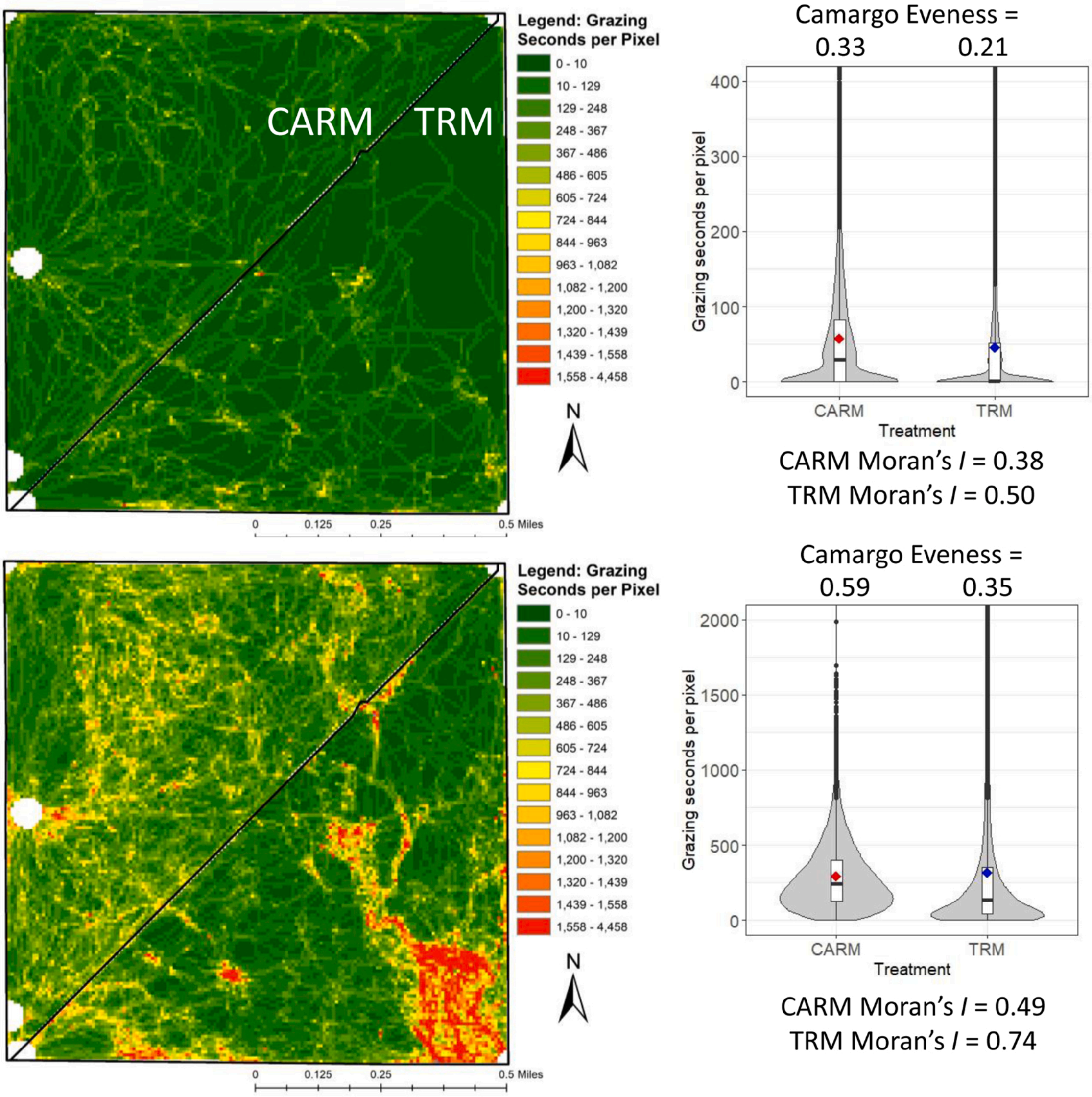


Fig. 7. Example of grazing distribution heat maps from one pair of paddocks in the Collaborative Adaptive Rangeland Management experiment in northeastern Colorado, USA. The upper heat map shows grazing distribution of 2 steers in each paddock during May 17 – 29, 2014. The lower heat map shows the distribution of 1 steer in TRM during May 17 – September 25 for a total 125 tracking days versus 10 steers in CARM during May 17–29th for a total of 125 tracking days. Violin plots on the right illustrate the distribution of grazing intensity across pixels in each heat map and treatment, where the mean expected value per pixel under perfectly even grazing distribution is shown as a red and blue diamond. Above each violin plot, we show the associated Camargo's Eveness index, which provides an index of the shape. This eveness index approaches 0 as more of the pixels contain values much greater than and less than the mean (e.g. TRM violins), and 1 as more pixels are equal to the expected mean (e.g. CARM violins). For each heat map, we also calculated Moran's I at a 10-m neighborhood, which approaches 1 when pixels with similar values are spatially clustered next to one another.

implications for vegetation responses and ecosystem management. The more linear and slower grazing pattern of CARM cattle resulted in a substantially more even distribution of grazing intensity in years of average to above-average precipitation. In other words, a greater area of the CARM paddock experienced grazing intensities closer to the expected mean value under perfectly even grazing distribution. In contrast, TRM paddocks contained more areas with no grazing and more areas with grazing intensity substantially above the mean. This supports the idea that adaptive rotational grazing could potentially reduce repeated grazing of the same locations and plants within a paddock. However, in TRM, high amounts of repeated grazing experienced by certain parts of a given paddock are offset by lower amounts of repeated grazing across other portions of the same paddock. Indeed, a concurrent study of how frequently tillers of *Pascopyrum smithii* (a productive and palatable forage grass) were defoliated found that at the ranch-scale, an average of 40% of tillers were grazed $\geq$ 1 time, and 10% of tillers were grazed $\geq$ 2 times per season in both CARM and TRM paddocks (Porensky et al., 2021), with no significant differences between treatments in the probability of regrazing randomly-selected tillers. In addition, the treatments did not differ in abundance or productivity of C_3 perennial grasses (Augustine et al., 2020) or all forage species combined (Fig. 3). Thus, patch grazing by cattle in TRM paddocks in the wet years does not seem to translate into undesirable effects on key forage grasses.

Furthermore, in the two dry years (2016 and 2018), grazing intensity was similarly distributed around the expected mean of perfectly even grazing in CARM and TRM. Stocking rates in our study and in the western Great Plains generally are set at levels that avoid severe shortages of forage in droughts, but still will result in more intense grazing in dry years and low grazing intensity in wet years. The similarly even grazing distribution in CARM and TRM in dry years when forage is more limiting, combined with the fact that even the palatable grasses have considerable adaptations to tolerate herbivory (Milchunas et al., 2008;

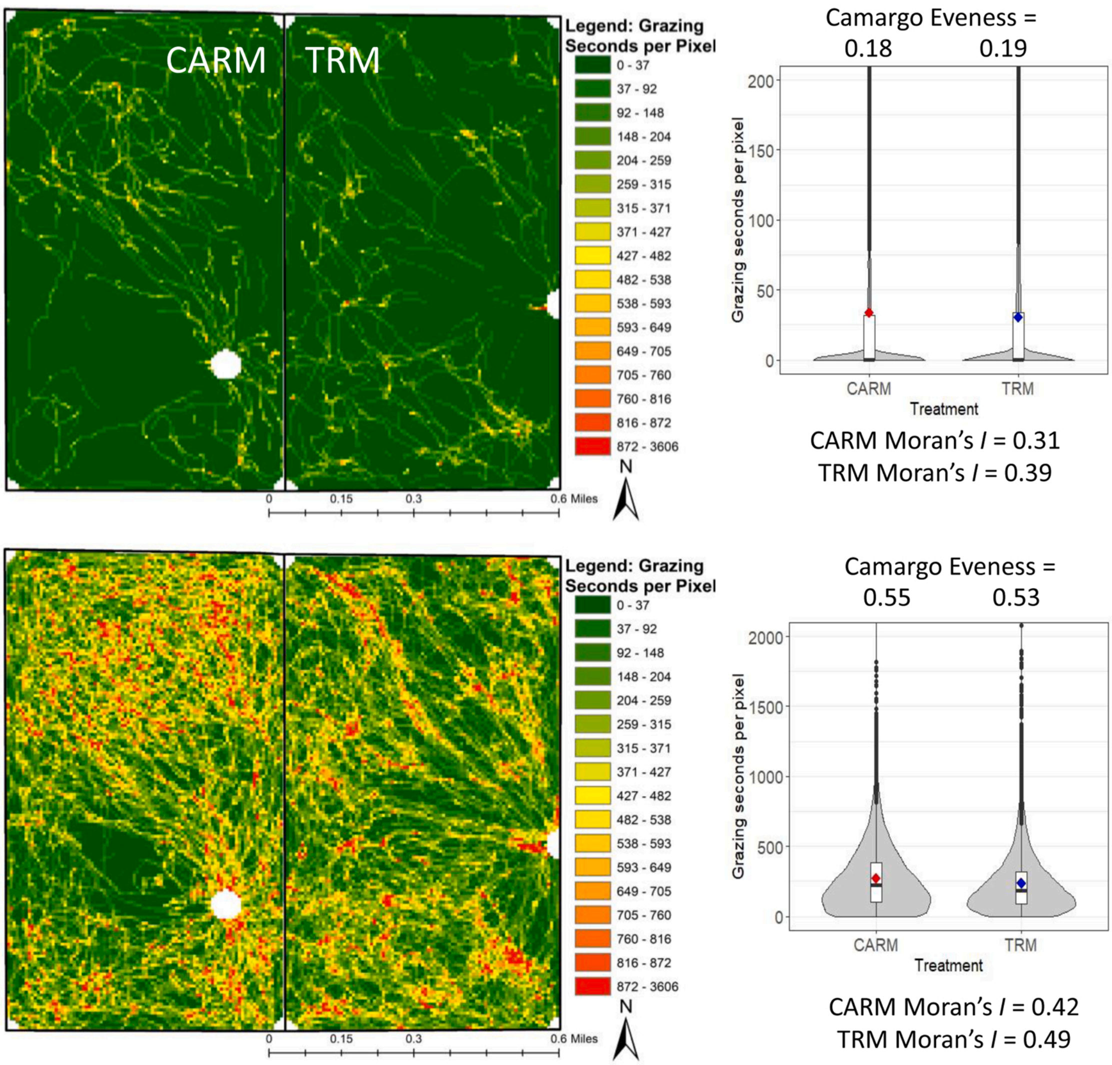
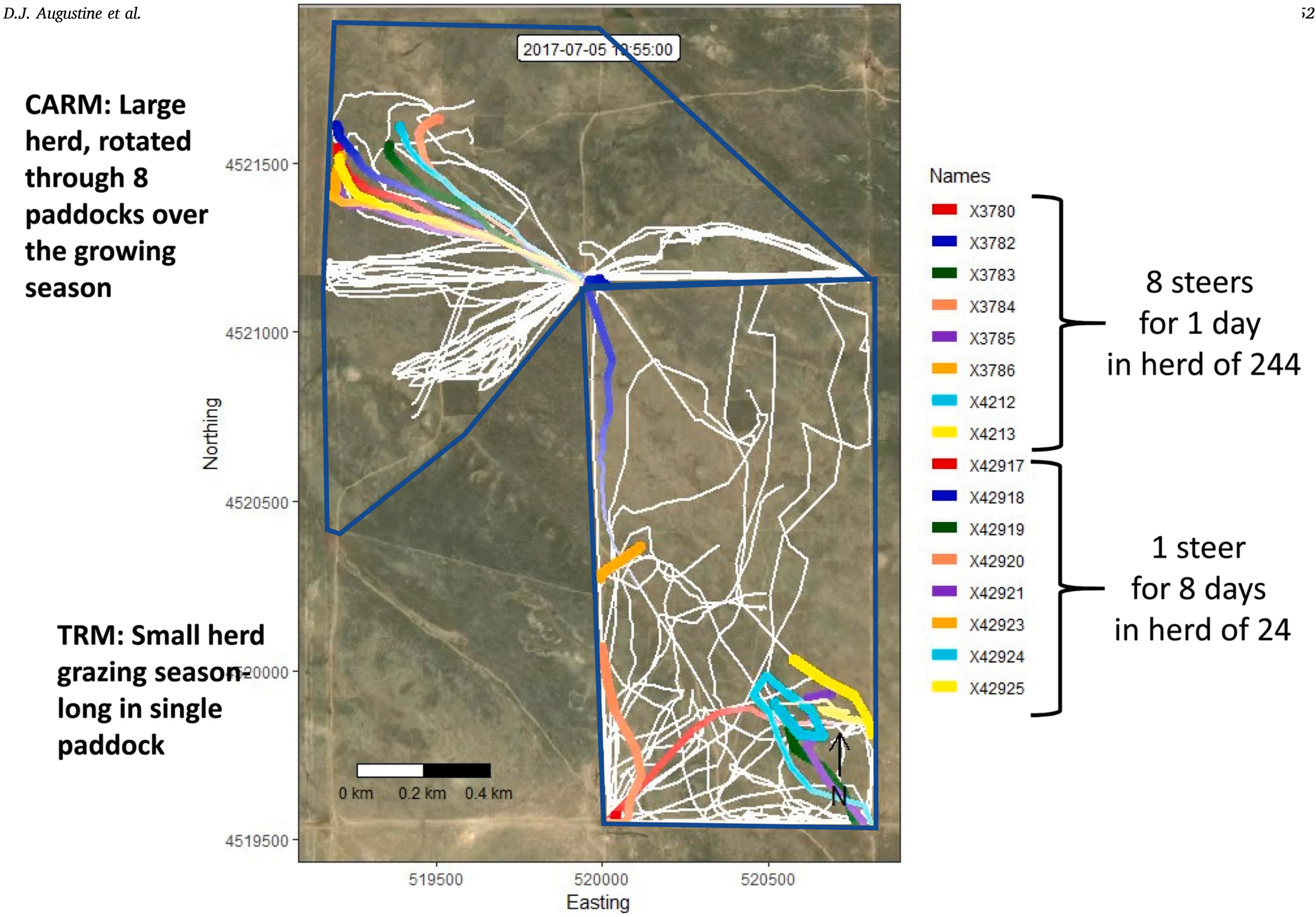


Fig. 8. Example of grazing distribution heat maps from one pair of paddocks in the Collaborative Adaptive Rangeland Management experiment in northeastern Colorado, USA. The upper heat map shows grazing distribution of 2 steers in each paddock during June 12–27, 2018. The lower heat map shows the distribution of 1 steer in TRM during May 11 – September 28, 2018, for a total of 125 tracking days versus 10 steers in CARM during June 12 – 27, 2018, for a total of 125 tracking days. Violin plots on the right illustrate the distribution of grazing intensity across the pixels in each heat map and treatment, where the mean expected value per pixel under perfectly even grazing distribution is shown as a red and blue diamond. See Fig. 6 for interpretation of the Camargo Eveness and Moran's I index values.

Blumenthal et al., 2020) may explain the lack of treatment effects on vegetation composition and productivity, at least during the first 5 years of this experiment. In addition, even if a TRM herd returned to the same 10 × 10 m pixel several times over the course of the growing season, they may not defoliate the same individual plants. In shortgrass rangeland, C_3 and C_4 perennial grasses are often co-mingled at a fine spatial scale, such that C_3 grasses may be defoliated during a patch visit in May or June, while C_4 grasses may be preferentially grazed during a revisit later in the summer. All of these factors may contribute to a lack of negative effects of season-long cattle grazing on the C_3 perennial grasses. Additionally, we note that while the treatments have not altered productivity of the vegetation, they do alter the vertical structure (Davis et al., 2020), and this aspect of vegetation heterogeneity deserves further analysis.

One consistent difference between CARM and TRM, both in wet and dry years, was in the spatial clustering of areas grazed at a given intensity (Figs. 6, 7, 8b). Grazing distribution maps are based on 2 collared steers in most TRM paddocks (20 total collared steers in the TRM paddocks), representing 7–10% of the animals in TRM herds. Prior analyses of TRM cattle showed the two collared animals often grazed near one another and preferentially returned to lowlands and flat plains (Gersie et al., 2019). Smaller herd size and the more tortuous grazing pathways are consistent with stronger patch selection by TRM cattle, leading to greater spatial aggregation of grid-cells experiencing repeatedly high grazing intensity. Revisits to grazing sites may lead to cyclic movements among known sites within home ranges or, in this case, locations within a paddock and may improve the rate and/or quality of food intake by individual herbivores in a herd structure (Fryxell, 1995; Edwards et al., 1996). Circular routes ("looping movement") are considered to be an optimal mode of search (Turchin, 1998) especially in areas of high nutritional value, in which individuals might spend more time (Dai et al., 2007).

In contrast, CARM maps are based on 10 collars representing 3 – 5% of the animals in the herd. As a result, the collared CARM steers are more likely to be separated by other uncollared animals, simply due to a lower proportion wearing collars. This is a limitation of our season-long analyses, but not the short-term (individual rotation) analyses. The short-term analyses (comparing 1 vs. 1 or 2 vs. 2 steers in each treatment) show that TRM steers are more likely to return to preferred areas of the paddock and forage in more circular trajectories, while CARM individuals forage in longer and more linear paths across the entire paddock. Thus, CARM herds appear to form a "grazing front" that moves



Video 1. Movement patterns of steers in a CARM versus a TRM paddock during July of 2017. Blue lines show the boundaries of a pair of 130-ha paddocks in the experiment, where the upper paddock received the CARM treatment and lower paddock received the TRM treatment. The video shows movement patterns of 8 steers on 1 day (July 5, 2017) in the CARM paddock, in comparison to 1 steer for 8 days (July 1–5 and July 7–9, 2017) in the TRM paddock.A video clip is available online. Supplementary material related to this article can be found online at doi:10.1016/j.agee.2023.108521.

across the paddock and distributes grazing pressure in a spatially more regular fashion (Video 1). However, one of our key findings from the season-long analyses was that distributions of the grazing time per pixel were similar between treatments in the dry years, when grazing is more intense. Under these dry conditions, CARM neither reduced the amount of the paddock that was undergrazed, nor reduced the amount of the paddock that was intensively grazed.

Finally, we note that in years and paddocks where patch burns were implemented (in both treatments), grazing distribution was more strongly influenced in the TRM paddock, because cattle showed stronger selection for the burns when grazing at low stock density. Thus, patch burning appears to be a more effective means to manipulate grazing distribution within a paddock under TRM. Under CARM, patch burning had less influence on within-paddock grazing distribution because cattle still grazed off the burns to meet intake requirements, but further analyses are still needed to assess whether patch burns enhanced quality of the overall diet consumed by CARM cattle while grazing paddocks with patch burns.

5. Conclusions

Our movement analysis supports the hypothesis that adaptive, multi-paddock rotation of cattle at high stock density constrains selective foraging, as these cattle move more slowly and in more linear pathways while foraging. As a result, the adaptively rotated cattle form a “grazing front” that moves across the paddock and distributes grazing pressure in a spatially more even fashion. This grazing behavior results in lower diet quality, presumably because the rotational cattle are constrained to selecting bites from available forage directly in their line of travel and not employing foraging tactics involving more preferential use of high-quality bites and forage patches. Such a grazing pattern ultimately leads to reduced weight gain for CARM compared to TRM cattle. Cattle grazing paddocks for the entire growing season were more likely to return to preferred areas and forage in more circular movements, at least in years with substantial forage production. In dry years, however, both treatments resulted in similarly even grazing distribution, which may explain the lack of an effect of grazing management on forage production. Thus, our assessment of GPS telemetry data within a multi-year socioecological experiment illustrates how grazing management practices can influence the growth rate of free-ranging livestock by altering their movement patterns.

CRediT authorship contribution statement

Justin D. Derner, David J. Augustine, and Lauren M. Porensky designed and implemented the study. All authors facilitated stakeholder meetings and contributed to discussions of data analyses. Sean P. Kearney and David J. Augustine wrote scripts to calculate daily behavioral metrics, and Sean P. Kearney wrote the script to generate grazing distribution heat maps from tracking data. David J. Augustine conducted statistical analyses and wrote the main manuscript text, Edward J. Raynor and David J. Augustine prepared the figures, and all authors reviewed and edited the manuscript.

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.

Acknowledgements

We thank David Smith for management of the GPS collars in the field and lab throughout this study, and Nicole Kaplan for extensive efforts in organizing, managing and manipulating datasets derived from the collars. We thank the CPER livestock crew including Melissa Johnston, Jake Thomas, Jeff Thomas, Tamarah Jorns, Averi Reynolds, Nick Dufek, Matt Mortenson, Pam Freeman, Anna Shadbolt and numerous summer student workers for their management of the CARM and TRM herds, and the Crow Valley Livestock Cooperative, Inc. for providing the cattle. Finally, we gratefully acknowledge the CARM Stakeholder Group, consisting of Kim Obele and Stephanie Magnuson (USDA-Forest Service), Matt Pollart (Colorado State Land Board), Terri Schulz (The Nature Conservancy), Ted Toombs (Environmental Defense Fund), Seth Gallagher and Angela Dwyer (Bird Conservancy of the Rockies), Casey Matney and Annie Overlin (Colorado State University Extension), Rachel Murph (Natural Resource Conservation Service), and the Crow Valley Livestock Cooperative, Inc. (Steve Anderson, Leonard Ball, Dana Bowman, Andy Lawrence, and Jeff Wahlert). This research is a contribution from the Long-Term Agroecosystem Research (LTAR) network. LTAR is supported by the United States Department of Agriculture.

Research data

The datasets used and/or analyzed during the current study are available from the corresponding author on request, and will be made publicly available via USDA (https://data.nal.usda.gov) if the paper is accepted for publication.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108521.

References

Asner, G., Elmore, A., Olander, L., Martin, R., Harris, A., 2004. Grazing systems, ecosystem responses, and global change. Annu. Rev. Environ. Resour. 29, 261–299.

Augustine, D.J., Derner, J.D., 2013. Assessing herbivore foraging behavior with GPS collars in a semiarid grassland. Sens. (Basel) 13, 3711–3723.

Augustine, D.J., Derner, J.D., 2014. Controls over the strength and timing of fire–grazer interactions in a semi-arid rangeland. J. Appl. Ecol. 51, 242–250.

Augustine, D.J., Derner, J.D., 2015. Patch-burn grazing management, vegetation heterogeneity, and avian responses in a semi-arid grassland. J. Wildl. Manag. 79, 927–936.

Augustine, D.J., Derner, J.D., Fernández-Giménez, M.E., Porensky, L.M., Wilmer, H., Briske, D.D., 2020. Adaptive, multipaddock rotational grazing management: A ranch-scale assessment of effects on vegetation and livestock performance in semiarid rangeland. Rangel. Ecol. Manag. 73, 796–810.

Augustine, D.J., Raynor, E.J., Kearney, S.P., Derner, J.D., 2022. Can measurements of foraging behaviour predict variation in weight gains of free-ranging cattle? Anim. Prod. Sci. 62, 926–936.

Bailey, D., Gross, J., Laca, E., Rittenhouse, L., Coughenour, M., Swift, D., Sims, P., 1996. Mechanisms that result in large herbivore grazing distribution patterns. J. Range Manag. 49, 386–400.

Baldwin, T., Ritten, J.P., Derner, J.D., Augustine, D.J., Wilmer, H., Wahlert, J., Anderson, S., Irisarri, G., Peck, D.E., 2022. Stocking rate and marketing dates for yearling steers grazing rangelands: Can producers do things differently to increase economic net benefits? Rangelands 44, 251–257.

Bement, R.E., 1969. A stocking-rate guide for beef production on blue-grama range. J. Range Manag. 22, 83–86.

Benvenutti, M.A., Gordon, I.J., Poppi, D.P., 2006. The effect of the density and physical properties of grass stems on the foraging behaviour and instantaneous intake rate by cattle grazing an artificial reproductive tropical sward. Grass Forage Sci. 61, 272–281.

Beven, K.J., Kirkby, M.J., 1979. A physically based, variable contributing area model of basin hydrology. Hydrol. Sci. J. 24, 43–69.

Blumenthal, D.M., Mueller, K.E., Kray, J.A., Ocheltree, T.W., Augustine, D.J., Wilcox, K. R., 2020. Traits link drought resistance with herbivore defence and plant economics in semi-arid grasslands: The central roles of phenology and leaf dry matter content. J. Ecol. 108, 2336–2351.

Briske, D.D., Derner, J.D., Brown, J.R., Fuhlendorf, S.D., Teague, W.R., Havstad, K.M., Gillen, R.L., Ash, A.J., Willms, W.D., 2008. Rotational grazing on rangelands: Reconciliation of perception and experimental evidence. Rangel. Ecol. Manag. 61, 3–17.

Brosh, A., Henkin, Z., Ungar, E., Dolev, A., Orlov, A., Yehuda, Y., Aharoni, Y., 2006. Energy cost of cows' grazing activity: Use of the heart rate method and the Global Positioning System for direct field estimation. J. Anim. Sci. 84, 1951–1967.

Dai, X.H., Shannon, G., Slotow, R., Page, B., Duffy, K.J., 2007. Short-duration daytime movements of a cow herd of African elephants. J. Mammal. 88, 151–157.

Davis, K.P., Augustine, D.J., Monroe, A.P., Derner, J.D., Aldridge, C.L., 2020. Adaptive rangeland management benefits grassland birds utilizing opposing vegetation structure in the shortgrass steppe. Ecol. Appl. 30, e02020.

Derner, J.D., Augustine, D.J., Briske, D.D., Wilmer, H., Porensky, L.M., Fernández-Giménez, M.E., Peck, D.E., Ritten, J.P., 2021. Can Collaborative Adaptive Management Improve Cattle Production in Multipaddock Grazing Systems? Rangel. Ecol. Manag. 75, 1–8.

Edwards, G.R., Newman, J.A., Parsons, A.J., Krebs, J.R., 1996. The use of spatial memory by grazing animals to locate food patches in spatially heterogeneous environments: an example with sheep. Appl. Anim. Behav. Sci. 50, 147–160.

Fernández-Giménez, M.E., Augustine, D.J., Porensky, L.M., Wilmer, H., Derner, J.D., Briske, D.D., Stewart, M.O., 2019. Complexity fosters learning in collaborative adaptive management. Ecol. Soc. 24.

Frank, D.A., McNaughton, S.J., Tracy, B.F., 1998. The ecology of the earth's grazing ecosystems: Comparing the Serengeti and Yellowstone. BioScience 48, 513–521.

Fryxell, J., 1995. Aggregation and migration by grazing ungulates in relation to resources and predators. ⋅. In: Sinclair, A.R.E., Arcese, P. (Eds.), Serengeti II: Dynamics, Management, and Conservation of an Ecosystem. Univ. Chicago Press, pp. 257–273.

Gaillard, J.M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M., Van Moorter, B., 2010. Habitat-performance relationships: Finding the right metric at a given spatial scale. Philos. Trans. R. Soc. B: Biol. Sci. 365, 2255–2265.

Ganskopp, D.C., Bohnert, D.W., 2009. Landscape nutritional patterns and cattle distribution in rangeland pastures. Appl. Anim. Behav. Sci. 116, 110–119.

Geremia, C., Merkle, J.A., Eacker, D.R., Wallen, R.L., White, P.J., Hebblewhite, M., Kauffman, M.J., 2019. Migrating bison engineer the green wave. Proc. Natl. Acad. Sci. USA 116, 25707–25713.

Gersie, S.P., Augustine, D.J., Derner, J.D., 2019. Cattle Grazing Distribution in Shortgrass Steppe: Influences of Topography and Saline Soils. Rangel. Ecol. Manag. 72, 602–614.

Hart, R.H., Bissio, J., Samuel, M.J., Waggoner Jr, J.W., 1993. Grazing systems, pasture size, and cattle grazing behavior, distribution and gains. J. Range Manag. 46, 81–87.

Hawkins, H.-J., Short, A., Kirkman, K.P., 2017. Does Holistic Planned Grazing™ work on native rangelands? Afr. J. Range Forage Sci. 34, 59–63.

Homburger, H., Lüscher, A., Scherer-Lorenzen, M., Schneider, M.K., 2015. Patterns of livestock activity on heterogeneous subalpine pastures reveal distinct responses to spatial autocorrelation, environment and management. Mov. Ecol. 3.

Kearney, S.P., Porensky, L.M., Augustine, D.J., Derner, J.D., Gao, F., 2022. Predicting spatial-temporal patterns of diet quality and large herbivore performance using satellite time series. Ecol. Appl. 32, e2503.

Lauenroth, W., Sala, O.E., 1992. Long-term forage production of North American shortgrass steppe. Ecol. Appl. 2, 397–403.

McCollum III, F.T., Gillen, R.L., 1998. Grazing management affects nutrient intake by steers grazing tallgrass prairie. J. Range Manag. 51, 69–72.

McCollum III, F.T., Gillen, R.L., Karges, B.R., Hodges, M.E., 1999. Stocker cattle response to grazing management in tallgrass prairie. J. Range Manag. 52, 120–126.

McIntosh, M.M., Cibils, A.F., Estell, R.E., Gong, Q., Cao, H., Gonzalez, A.L., Nyamuryekung'e, S., Spiegal, S.A., 2022. Can cattle geolocation data yield behavior-based criteria to inform precision grazing systems on rangeland? Livest. Sci. 255, 104801.

Merkle, J.A., Monteith, K.L., Aikens, E.O., Hayes, M.M., Hersey, K.R., Middleton, A.D., Oates, B.A., Sawyer, H., Scurlock, B.M., Kauffman, M.J., 2016. Large herbivores surf waves of green-up during spring. Proc. R. Soc. Soc. B 283, 1833.

Middleton, A.D., Merkle, J.A., McWhirter, D.E., Cook, J.G., Cook, R.C., White, P.J., Kauffman, M.J., 2018. Green-wave surfing increases fat gain in a migratory ungulate. Oikos 127, 1060–1068.

Milchunas, D.G., Lauenroth, W.K., Burke, I.C., Detling, J.K., 2008. Effects of grazing on vegetation. Ecology of the Shortgrass Steppe: A Long-term Perspective. Oxford University Press,, New York, New York, USA, pp. 389–446.

Nyamuryekung'e, S., Cibils, A.F., Estell, R.E., McIntosh, M., VanLeeuwen, D., Steele, C., González, A.L., Spiegal, S., Continanza, F.G., 2021. Foraging Behavior of Heritage versus Desert-Adapted Commercial Rangeland Beef Cows in Relation to Dam-Offspring Contact Patterns. Rangel. Ecol. Manag. 74, 43–49.

Orr, R.J., Penning, P.D., Rutter, S.M., Champion, R.A., Harvey, A., Rook, A.J., 2001. Intake rate during meals and meal duration for sheep in different hunger states, grazing grass or white clover swards. Appl. Anim. Behav. Sci. 75, 33–45.

Owen-Smith, N., Fryxell, J.M., Merrill, E.H., 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. Philos. Trans. R. Soc. B: Biol. Sci. 365, 2267–2278.

Payne, L., Schindler, X., Parrish, D.E., Temple, J.K., S.A, 2005. Quantifying spatial pattern with evenness indices. Ecol. Appl. 15, 507–520.

Plechaty, T.R., 2018, Yearling cattle diet quality, diet composition, and behavior under multiple stocking rate in the northern mixed-grass prairie and continuous versus collaborative adaptive rangeland management in the shortgrass steppe. MS Thesis, University of Wyoming, Laramie, WY.

Porensky, L.M., Augustine, D.J., Derner, J.D., Wilmer, H., Lipke, M.N., Fernandez-Gimenez, M.E., Briske, D.D., Grp, C.S., 2021. Collaborative adaptive rangeland management, multipaddock rotational grazing, and the story of the regrazed grass plant. Rangel. Ecol. Manag. 78, 127–141.

Probo, M., Lonati, M., Pittarello, M., Bailey, D.W., Garbarino, M., Gorlier, A., Lombardi, G., 2014. Implementation of a rotational grazing system with large paddocks changes the distribution of grazing cattle in the south-western Italian Alps. Rangel. J. 36, 445–458.

Raynor, E.J., Joern, A., Nippert, J.B., Briggs, J.M., 2016. Foraging decisions underlying restricted space use: effects of fire and forage maturation on large herbivore nutrient uptake. Ecol. Evol. 6, 5843–5853.

Rinella, M.J., Vavra, M., Naylor, B.J., Boyd, J.M., 2011. Estimating influence of stocking regimes on livestock grazing distributions. Ecol. Model. 222, 619–625.

Rivero, M.J., Grau-Campanario, P., Mullan, S., Held, S.D., Stokes, J.E., Lee, M.R., Cardenas, L.M., 2021. Factors affecting site use preference of grazing cattle studied from 2000 to 2020 through GPS tracking: A review. Sensors 21, 2696.

Sampson, A.W., 1951. A symposium on rotation grazing in North America. J. Range Manag. 4, 19–24.

Sawalhah, M.N., Cibils, A.F., Maladi, A., Cao, H., Vanleeuwen, D.M., Holechek, J.L., Black Rubio, C.M., Wesley, R.L., Endecott, R.L., Mulliniks, T.J., Petersen, M.K., 2016. Forage and weather influence day versus nighttime cow behavior and calf weaning weights on rangeland. Rangel. Ecol. Manag. 69, 134–143.

Senft, R., Rittenhouse, L., Woodmansee, R., 1985. Factors influencing patterns of cattle grazing behavior on shortgrass steppe. J. Range Manag. 38, 82–87.

Spiegal, S., Estell, R.E., Cibils, A.F., James, D.K., Peinetti, H.R., Browning, D.M., Romig, K.B., Gonzalez, A.L., Lyons, A.J., Bestelmeyer, B.T., 2019. Seasonal divergence of landscape use by heritage and conventional cattle on desert rangeland. Rangel. Ecol. Manag. 72, 590–601.

Steinfeld, H., Gerber, P., Wassenaar, T.D., Castel, V., Rosales, M., Rosales, M., de Haan, C., 2006, Livestock's long shadow: environmental issues and options. United Nations Food & Agriculture Organization, Rome, Italy.

Teague, R., Barnes, M., 2017. Grazing management that regenerates ecosystem function and grazingland livelihoods. Afr. J. Range Forage Sci. 34, 77–86.

Tobin, C.T., Bailey, D.W., Stephenson, M.B., Trotter, M.G., 2021. Temporal changes in association patterns of cattle grazing at two stocking densities in a central arizona rangeland. Animals 11.

Turchin, P., 1998. Quantitative Analysis of Movement: Measuring And Modeling Population Redistribution in Animals and Plants. Sinauer Associates,, Sunderland, Massachusetts.

Venter, Z.S., Hawkins, H.J., Cramer, M.D., 2019. Cattle don't care: Animal behaviour is similar regardless of grazing management in grasslands. Agric., Ecosyst. Environ. 272, 175–187.

Wilmer, H., Derner, J.D., Fernández-Giménez, M.E., Briske, D.D., Augustine, D.J., Porensky, L.M., 2018. Collaborative adaptive rangeland management fosters management-science partnerships. Rangel. Ecol. Manag. 71, 646–657.

Windh, J., Ritten, J., Derner, J., Paisley, S., Lee, B., 2019. Economic cost analysis of continuous-seaso-long versus rotational grazing systems. Western Econ. Forum 17, 62–72.