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Original Research

Movement Dynamics and Energy Expenditure of Yearling Steers Under Contrasting Grazing Management in Shortgrass Steppe ☆

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ABSTRACT

A potential mechanism for lower livestock weight gains with rotational grazing is the additional movement and associated energy expenditures incurred with rotation of animals among paddocks. We evaluated these metrics in 2016 and 2017 using pedometers affixed to free-ranging naïve yearling steers grazing semiarid, shortgrass steppe under contrasting grazing management treatments with the same stocking rate: traditional season-long (mid-May to October) grazing management and collaborative adaptive rangeland management (CARM) at a ranch scale (2-600 ha: ten 130-ha paddocks for each treatment). Mean daily number of steps by steers in paddocks during the grazing season, excluding those associated with moves between paddocks, were 3.0% lower (2016) and 7.8% greater (2017) for CARM, but energy expenditures did not differ significantly between treatments in either year. Daily step counts decreased in traditional rangeland management (TRM) as the grazing season progressed. Step counts decreased from day 1 to day 8 in CARM paddocks following rotation of steers. Steers in the TRM treatment took more steps daily than CARM steers in the first third of the grazing season, but this reversed in the last third of the grazing season. These findings suggest that observed 12%–16% reductions in livestock weight gains with CARM were not influenced by differences in total grazing season steps as energy expenditures of steers did not differ. Two additive influences of within-season steer movement dynamics suggest that forage quality was the primary driver for the decrease in weight gains in CARM. First, fewer steps in the early growing season, when forage quality is highest, indicate reduced selectivity for nutrient-rich patches. Second, more steps by yearlings in the late growing season suggest that these heavier animals expending more energy for maintenance were searching to satisfy gut fill as forage quantity and quality on offer per steer was limiting with the 10-fold higher stocking density.

Introduction

Quantifying movements and resulting energy expenditures of free-ranging livestock in extensive rangeland systems has been persistently difficult (Walker et al. 1985; Ungar et al. 2005, 2018). Di-

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rect visual observations of grazing animals (e.g., Hart et al. 1993; Odadi et al. 2009) or video recording have the limitations of being labor intensive, can only be conducted during daylight hours, and are of insufficient temporal resolution (e.g., few measurements across grazing seasons; Kokin et al. 2014; Nyamuryekung'e et al. 2016; Ungar et al. 2018). More recent animal movement estimates are available from Global Positioning System (GPS) collars linked with other sensors such as heart rate monitors (Brosh et al. 2006; Aharoni et al. 2009, 2013). This technology has limitations with temporal resolution, however, as GPS collars typically record information every 5−15 minutes. Also, the linear distance between two consecutive GPS readings fails to account for nonlinear movements of livestock during the time period. Thus, both direct visual observation and GPS collar methodologies likely underestimate patterns and dynamics of livestock movements and their associated energy expenditures.

Early use of pedometers assessed cow movements on rangelands (Walker et al. 1985; Anderson and Urquhart 1986; Dunn et al. 1988; Funston et al. 1991). Recent technological advancements in pedometers have resulted in capacity to assess animal behavior on rangelands. In addition to pedometers measuring the number of steps taken, three-dimensional accelerometers allow for more efficient assessments of animal energy allocation compared with field or video observations (Robert et al. 2009; Nielsen et al. 2010; Kokin et al. 2014). Most of the applications of pedometers, however, have focused on dairy cows confined in barns or small paddocks, primarily for estrous detection (Roelofs et al. 2005; Holman et al. 2011) or early detection of lameness (O'Callaghan et al. 2003; Mazrier et al. 2006).

Prescriptive and adaptive rotational grazing systems have been associated with reduced animal weight gains, compared with season-long continuous grazing at the same ranch-scale stocking rate (Briske et al. 2008, 2011; Hawkins 2017; Augustine et al. 2020; Derner et al. 2021). This finding has been speculated to be attributable to additional movement of rotated animals among paddocks and the novelty of entry into new paddocks, especially if the animals are naïve (Walker et al. 1985; Launchbaugh and Howery 2005; Derner et al. 2008). Manager decisions influence animal stocking density and distribution patterns within paddocks and, thus, influence animal distance traveled and behavior (Anderson and Kothmann 1980; Gammon and Roberts 1980; Bailey et al. 1996; Wilmer et al. 2018), as well as having consequences for energy allocation (Thanner et al. 2014).

We evaluated animal movements and associated energy expenditures by affixing pedometers to free-ranging yearling steers in a semiarid rangeland under contrasting grazing management treatments: TRM using season-long continuous grazing and collaborative adaptive rangeland management (CARM), which explicitly incorporates decision making from an 11-member stakeholder group (Wilmer et al. 2018; Fernandez-Gimenez et al. 2019; Augustine et al. 2020). These grazing treatments were applied at a ranch scale (2 600 ha) with a diverse assemblage of soils and plant communities in a total of twenty 130-ha paddocks. Livestock weight gains measured over 5 yr of treatments have consistently been 11−16% lower for steers in CARM (Augustine et al. 2020). We hypothesized that 1) naïve free-ranging steers would exhibit greater movements during the early versus later days in the grazing duration *within* a paddock in CARM and 2) steers in the CARM treatment would exhibit different animal movement dynamics (such as step counts, lying or standing time) across the grazing season due to both *within*-paddock activities associated with exploring multiple new paddocks during the grazing season and *between*-paddock movements (i.e., rotations).

Methods

Site description

This experiment was conducted at the US Department of Agriculture–Agricultural Research Service (USDA-ARS) Central Plains Experimental Range (40°50′N, 104°43′W), located 12 km northeast of Nunn, Colorado. This site was part of the USDA Long-Term Agroecosystem Research network (https://ltar.ars.usda.gov). Long-term mean annual precipitation was 340 mm with approximately four-fifths of this occurring during the primary growing season of April through September (Irisarri et al. 2016). In 2016, annual precipitation was 256 mm with 193 mm falling between April and September. Total annual precipitation in 2017 was 382 mm with 308 mm falling during the primary growing season. Elevation was 1 600−1 691 m, and mean temperature was 8.3°C. Topography was mainly composed of gently rolling hills, and vegetation was dominated by the C_4 perennial grasses blue grama (*Bouteloua gracilis* [Wild ex. Kunth] Lag. ex. Griffiths) and buffalograss (*B. dactyloides* [J. T. Columbus]) with co-occurring C_3 perennial grasses western wheatgrass (*Pascopyrum smithii* [Rydb.] A. Löve) and needle-and-thread (*Hesperostipa comata* [Trin & Rupr.] Barkworth) (Augustine et al. 2020). The most common forb was scarlet globemallow (*Sphaeralcea coccinea* [Nutt.] Rydb.), and the most common subshrub was prairie sagewort (*Artemisia frigida* Willd).

Experimental design

British and British-cross, mostly Angus and Angus-cross, yearling steers *(Bos taurus)* weighing 271 ± 1 kg in 2016 and 270 ± 1 kg in 2017 were used in two different grazing treatments: 1) CARM, with rotational grazing decision making conducted by a participatory stakeholder group consisting of 11 members including ranchers, nongovernmental conservation organizations, and state and federal land managers (Wilmer et al. 2018; Fernandez-Gimenez et al. 2019; Augustine et al. 2020) and 2) TRM of season-long continuous grazing (Bement 1969). We applied grazing treatments in a ranch-scale (2 600 ha) experiment with each treatment randomly applied to a 130-ha paddock in each of 10 blocks. Paddock pairing was based on soils, ecological sites, plant communities and production, and topographical wetness index (Wilmer et al. 2018; Augustine et al. 2020). Because ecological sites have implications for livestock diet quality and weight gain (Reynolds et al. 2019), paddocks were assigned to an ecological site (Loamy Plains or Sandy Plains) based on the dominant ecological site found within the paddock boundaries (USDA NRCS 2007a; 2007b; Augustine et al. 2020). The Loamy Plains ecological site primarily consisted of C_4 shortgrasses, had low productivity, and was assigned to three paddocks in each treatment (USDA NRCS 2007a; Augustine et al. 2020). The Sandy Plains ecological site had higher productivity, was codominated by shrubs and C_3 perennial grasses, and was assigned to three paddocks in each treatment (USDA NRCS 2007b). If paddocks were not dominated by a single ecological site, they were classified as mixed (four paddocks in each treatment).

The Stakeholder Group collaborated with an interdisciplinary research team to use near real-time monitoring information, experiential knowledge, and seasonal weather forecasts to make grazing management decisions for beef production, vegetation, wildlife habitat, and social objectives. Triggers were determined for movement of cattle among paddocks, paddock sequence of use, and resting of paddocks for proactive drought management (Wilmer et al. 2018; Augustine et al. 2020). This resulted in a complex and nonlinear learning process among stakeholders with numerous feedback loops (Fernandez-Gimenez et al. 2019). The TRM treatment is used on both private and public grasslands in the region and has been demonstrated to be sustainable for livestock production over several decades (Bement 1969; Derner et al. 2020; Raynor et al. 2020).

Both grazing treatments were stocked with the same annual stocking rate (234 yearling steers in 2016 and 244 yearling steers in 2017), and paddocks were grazed between mid-May and early October. Stocking rates were considered moderate across all ecological sites in the study area (Augustine et al. 2020; Raynor et al. 2020). Stocking density differed between treatments, with a 10-fold higher value in the CARM (1.8−1.9 animals/ha) compared with the TRM (0.18−0.19 animals/ha) treatment because the Stakeholder Group used one herd for the CARM treatment (rotated among the 10 paddocks), whereas 10 individual, smaller herds grazed each of the TRM paddocks for the entire grazing season. In the CARM treatment, stakeholders planned to rest two pastures per year and used additional triggers to rotate animals, so not all rotations were of equal length (see Wilmer et al. 2018 for details).

Pedometers for measuring animal movement and behavior

To quantify steer movement (i.e., step count numbers) and behavior (percent time standing and lying), we affixed IceTag pedometers (IceRobotics Ltd, South Queensferry, United Kingdom) at the beginning of each grazing season using a plastic strap on the metatarsophalangeal joint on a rear leg of 30 steers ($n = 2$ per TRM paddock, total of 20; $n = 10$ in the CARM treatment). The USDA Central Plains Experimental Range Institutional Animal Care and Use Committee granted animal welfare approval (IACUC; Protocol CPER-4, approved 6 November 2015). Data were recorded at 1-s intervals. We removed pedometers approximately every 60 d during each grazing season ($n = 2$ times) to download data and then reaffixed them to the same animals. Data were initially collated in IceManager 2014 software. Days involving pedometer removal and subsequent reaffixment, as well as the day cattle were initially taken to paddocks in the spring and the day cattle were withdrawn from the grazing treatments in the fall, were removed before subsequent analyses. Pedometers failed throughout the season. When a pedometer failed, it was removed from the animal and data were recovered up to the day before the failure. New pedometers were deployed when available to lessen gaps in data collection.

Statistical analysis

We summed movement dynamics variables of step count, percent standing time, and percent lying time to hourly and daily intervals using individual animals as the replication unit (Walker et al. 1985). Associated metadata included year, grazing treatment (CARM or TRM), time since rotation (days), day number of the grazing season, paddock, grazing season phase (early, first one-third; middle; and late, last one-third), and weather variables of daily precipitation (mm), maximum temperature (°C), and maximum vapor pressure deficit (VPD max; hPa). Weather variables were acquired from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) Climate Group, Oregon State University data explorer database using a 4-km grid cell resolution (PRISM Climate Group 2004).

We calculated energetic expenditures using step-energy relationships based on Test et al. (1984) for the number of cattle steps and distance equivalents (2 222 steps leg^{-1} km^{-1} while grazing). Caloric output estimates of 9 kcal km^{-1} 100 kg body weight^{-1} (0% slope was assumed, as these paddocks were gently undulating in topography) from Di Marco and Aello (1998) were used to estimate energetic expenditure of steps above basal metabolism. Basal metabolism for an animal lying down was calculated using the Di Marco and Aello (1998) value of 1 983.6 kcal day^{-1} 100 kg^{-1} (82.65 kcal h^{-1} 100 kg^{-1}). Additionally, we estimated increased energy from standing using values derived from Aharoni et al. (2013) of 11.824 kJ kg metabolic body weight^{-1}, with metabolic body weight defined as body weight$^{0.75}$. Mid-grazing-season weight of steers each year was approximately 385 kg; this value was used in energy expenditure calculations.

We checked residuals of measured steer movement and behavior variables for normality. We applied transformations to response variables when normality assumptions were not met. Step count data were square root transformed. Both standing and lying data (percentages) were divided by 100 and then transformed using arcsine square root transformations (McDonald 2014).

One-way analysis of variance assuming unequal variances was used to assess differences in daily steps across the grazing season (both with and without rotation days included for CARM and TRM) and seasonal trends by phase. When rotation days were removed from CARM, those same days were also removed from the TRM treatment to prevent confounding results from altered animal behavior as the CARM herd moved past or through TRM paddocks. Sampling intensity was equal in both treatments with pedometers on approximately 20% of the animals within each treatment. Significant differences were determined at the 95% confidence level ($\alpha = 0.05$). Linear regressions were also conducted by treatment for steps by day across the grazing season both including and excluding rotation days from both treatments to assess trends in steps across the entire grazing season. An analysis of variance type III test was performed to assess model relevance.

For standing and step count response variables, we conducted separate model selection analyses by treatment using Akaike's Information Criterion (AIC) to differentiate the drivers of these variables in the separate treatments. Because standing and lying are dichotomous and autocorrelated variables, at least in the context of how the pedometers log one or the other, we only analyzed standing and it could be considered that the lying response would be the inverse. In each analysis, the 2 yr of data were combined and candidate predictor variables included treatment variables (phase [early, middle, and late as a categorical variable], numeric day, days within paddock, and ecological site by paddock [loamy, mixed, and sandy as a categorical variable]) and weather variables (precipitation, maximum temperature, and VPD). Ecological sites were grazed in different sequences each year depending on the stakeholder-determined grazing sequence. Before modeling, we used Pearson's correlation to evaluate collinearity among candidate variables. On the basis of a cutoff value of $r > 0.6$, we retained only one variable from any pairs of correlated variables (Coppedge et al. 2008; Hovick et al. 2015). For example, maximum temperature and VPD had issues of collinearity ($r = 0.94$) and we therefore only retained maximum temperature for AIC model selection. In all models, we included year as a random effect to account for differences in yearly grazing sequences and individual animal ID was included to account for repeated measurements on the same animals.

For each response variable and each grazing treatment, our initial model set included a separate model for each predictor variable and a null model that only included random effects. We conducted univariate models separately in two categorical steps, first for treatment models (using time since rotation, phase, and ecological site) and second for weather models (using maximum temperature and precipitation). Within each categorical step, the model with a ΔAIC value of zero was designated the "top model," while models with $\Delta\text{AIC} \leq 2$ points away from the top model were designated as "best models" (Burnham and Anderson 2002). We then examined additive and interactive combinations of the top models from each categorical step and used AIC to compare these more

Table 1

Mean (± 1 SE) pedometer measured response variables for yearling steers in contrasting grazing treatments. CARM indicates collaborative adaptive rangeland management, which employed rotational grazing among ten 130-ha paddocks, and TRM is traditional rangeland management with season-long (mid-May to October) grazing in each of ten 130-ha paddocks at the USDA-ARS Central Plains Experimental Range, Nunn, Colorado, 2016 and 2017. Values for rows "without rotation days" exclude data obtained on days for both CARM and TRM treatments when steers rotated between paddocks in CARM. Values with different superscripts represent a significant difference between grazing treatments ($P \leq 0.05$).

	Yr	Treatment	Mean daily number of steps	Daily standing time (%)	Daily lying time (%)
With rotation days	2016	CARM	6010 ± 64	55.4 ± 0.2a	44.6 ± 0.2b
		TRM	6074 ± 42	54.8 ± 0.1b	45.2 ± 0.1a
	2017	CARM	6308 ± 86a	56.1 ± 0.3a	43.9 ± 0.3b
		TRM	5984 ± 47b	54.1 ± 0.2b	45.9 ± 0.2a
Without rotation days	2016	CARM	5894 ± 62b	55.3 ± 0.2a	44.7 ± 0.2b
		TRM	6071 ± 42a	54.7 ± 0.1b	45.3 ± 0.1a
	2017	CARM	6225 ± 80a	56.1 ± 0.3a	43.9 ± 0.3b
		TRM	5772 ± 57b	54.1 ± 0.2b	45.9 ± 0.2a

Table 2

Mean energy expenditures per steer derived from pedometer step counts in contrasting grazing treatments. CARM indicates collaborative adaptive rangeland management, which employed rotational grazing among ten 130-ha paddocks, and TRM is traditional rangeland management with season-long (mid-May to October) grazing in each of ten 130-ha paddocks at the US Department of Agriculture−Agricultural Research Services Central Plains Experimental Range, Nunn, Colorado, 2016 and 2017. Assumptions include a 0% slope in paddocks, 385 kg body weight, and test (1984) distance values (2 222 steps leg^{-1} km^{-1}) and Di Marco and Aello (1998) energetic values (9 kcal km^{-1} 100 kg body weight^{-1}). Basal energy values for all steers were calculated using Di Marco and Aello (1998) values of 82.65 kcal h^{-1} 100 kg body weight^{-1}, was 7 636.9 kcal. Standing energy values were calculated using values derived from Aharoni et al. (2013, 11.824 kJ kg metabolic body weight^{-1}; with metabolic weight = body $\text{weight}^{0.75}$). Values for rows "without rotation days" exclude data obtained on days for both CARM and TRM treatments when steers rotated between paddocks in CARM.

	Yr	Treatment	Step energy	Standing energy	Total energy expenditure
			kcal d^{-1} 385 kg steer^{-1}		
with rotation days	2016	CARM	93.7	247.1	7977.6
		TRM	94.7	245.6	7977.2
	2017	CARM	98.4	250.5	7985.8
		TRM	93.3	245.6	7975.8
without rotation days	2016	CARM	91.9	247.1	7975.8
		TRM	94.7	245.6	7977.2
	2017	CARM	97.1	250.5	7984.5
		TRM	90.0	245.6	7972.5

complex models to the univariate and null models. The top model from this second step was designated as the "final model." We generated 95% confidence intervals for covariates in our final models (Bates et al. 2015).

Results

Step count and energy expenditure

For the entire grazing season, mean daily number of steps per steer did not differ between treatments in 2016 ($t = 0.837$, $P = 0.403$) but was 5.4% greater for CARM in 2017 ($t = 3.308$, $P < 0.001$; Table 1). Removing the days when yearlings rotated between paddocks in CARM resulted in mean daily step numbers being 3% lower for CARM in 2016 ($t = 2.364$, $P = 0.018$) but 7.8% greater for CARM in 2017 ($t = 4.617$, $P < 0.001$). Similar total energetic expenditures occurred between treatments for each year, however (Table 2). Energy expenditures were primarily associated with basal maintenance; energy expenditures on steps represents only about 1% of the total energy expenditures for yearling steers.

As the grazing season progressed in both years, steers in the TRM treatment exhibited a linear decrease in daily step count (2016: −28/d, $r^2 = 0.37$, $P < 0.001$; 2017: −27/d, $r^2 = 0.39$, $P < 0.001$). Conversely, steers in the CARM treatment did not exhibit a similar pattern in either year (2016, $r^2 = 0.004$, $P = 0.03$; 2017; $r^2 = 0.080$, $P < 0.001$). Steers in the CARM treatment in 2016 exhibited a decrease in daily number of steps following introduction to each paddock until day 8 of the grazing duration, but this trend did not occur in 2017 (Fig. 1).

Within grazing season, dynamics of daily steps differed across the grazing season. Steers in CARM took fewer daily steps during the first third of each grazing season (2016: $t = -9.7946$, $P < 0.001$; 2017: $t = -4.0615$, $P < 0.001$; Fig. 2). Daily steps did not differ strongly between grazing treatments in the middle third of the growing season in either year, though steps were slightly higher in CARM than TRM in 2017 (2016: $t = -1.0188$, $P = 0.3088$; 2017: $t = 6.2619$, $P < 0.001$; see Fig. 2). In contrast to the first third of the grazing season, CARM steers took more steps than TRM steers in the last part of the grazing seasons (2016: $t = 12.947$, $P < 0.001$; 2017: $t = 3.976$; $P < 0.001$; see Fig. 2).

Temporal patterns in the hourly step rate revealed similar peaks in animal activity for both grazing treatments in 2016 (hours of 07:00−10:00 for CARM steers; 06:00−08:00 for TRM steers) and 2017 (hours of 07:00−09:00 for CARM steers; hours of 06:00−08:00 for TRM steers) (Fig. 3). Evening activity peak did not differ between grazing treatments in either year with steer steps peaking between the hours of 18:00 and 20:00.

For categorical models predicting steer step count, the top treatment models did not differ between the grazing treatments, with days within paddock as the top model for both treatments (Table 3, $\omega_i = 1.00$ or 100% of the total model weight for both). Weather models differed for the grazing treatments. Maximum temperature was the top model for TRM steer step counts ($\omega_i = 1.00$) but not for CARM. When categorical models were integrated, the univariate time since rotation (or time in paddock) model remained the final AIC model for steer step counts for both CARM and TRM ($\omega_i = 1.00$ and $\omega_i = 0.80$, respectively). As days within paddock increased, step counts in both treatments decreased, though this relationship was more negative for CARM than

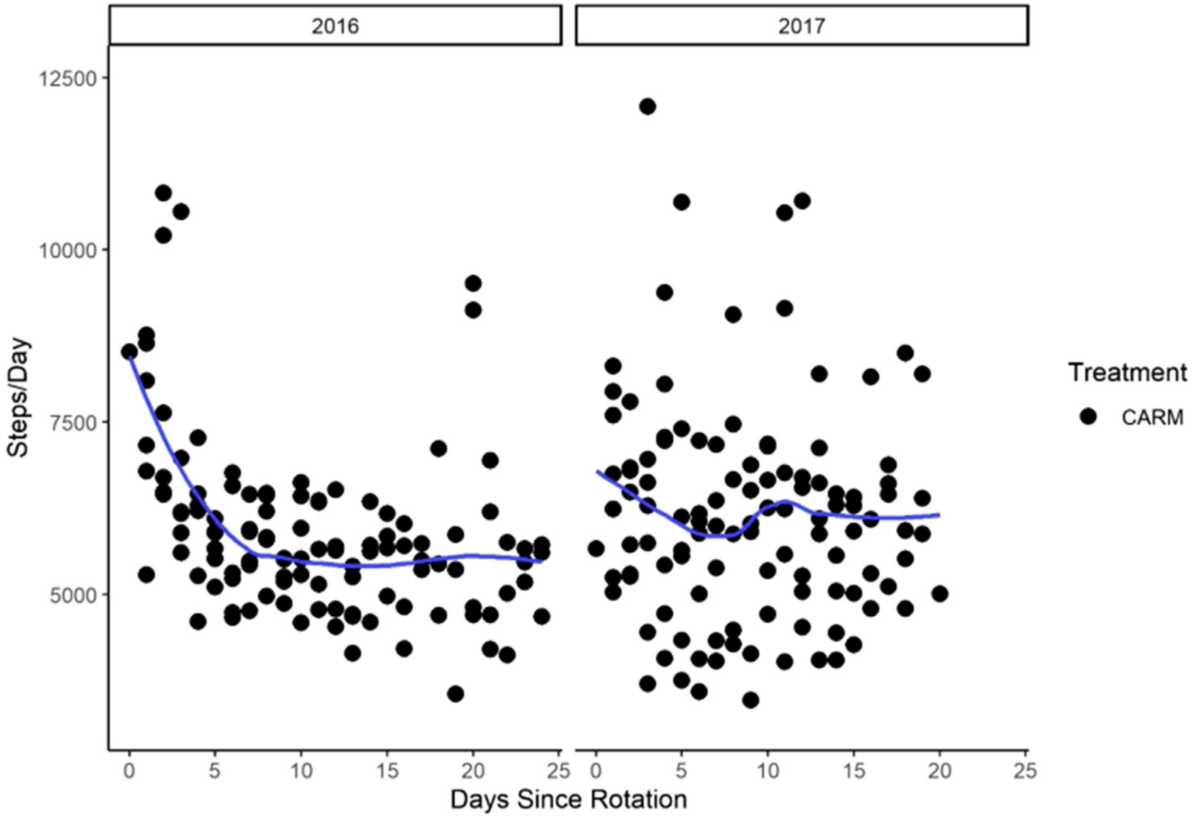

Figure 1. Mean daily step counts of yearling steers during the first 20–25 d within a paddock in the CARM (collaborative adaptive rangeland management) treatment, which employed rotational grazing among ten 130-ha paddocks at the US Department of Agriculture–Agricultural Research Services Central Plains Experimental Range, Nunn, Colorado, 2016 and 2017. Each point represents the average steps for all functioning pedometers on that each day of the rotation. Blue lines represent a smoothing curve of daily mean values, 2016 and 2017.

Table 3
Information-theoretic model selection using Akaike's information criterion (AIC) for yearling beef cattle step counts between years in contrasting grazing treatments. CARM indicates collaborative adaptive rangeland management, which employed rotational grazing among ten 130-ha paddocks, and TRM is traditional rangeland management with season-long (mid-May to October) grazing in each of ten 130-ha paddocks at the US Department of Agriculture–Agricultural Research Services Central Plains Experimental Range, Nunn, Colorado, 2016 and 2017. Model selection included year as a random effect and individual animal as a repeated effect.

	CARM			TRM		
Models	AIC	ΔAIC	ω_i	AIC	ΔAIC	ω_i
Treatment variables						
Days within paddock	13 614.9	0.00	1.00	30 921.8	0.00	1.00
Phase	13 629.0	14.10	0.00	30 983.5	61.70	0.00
Ecological site	13 673.6	58.70	0.00	32 095.2	1 173.40	0.00
Null	13 629.4	14.50	0.00	32 115.9	1 194.10	0.00
Weather variables						
Temperature (Tmax)	13 695.5	66.10	0.00	32 073.6	0.00	1.00
Precipitation	13 684.7	55.30	0.00	32 102.5	28.90	0.00
Null	13 629.4	0.00	1.00	32 115.9	42.30	0.00
Final model						
TSR	13 614.9	0.00	1.00	30 921.8	0.00	0.80
TSR + Tmax				30 924.6	2.80	0.20
TSR × Tmax				31 102.7	178.10	0.00
Tmax				32 073.6	1 151.80	0.00
Null	13 629.4	14.50	0.00	32 115.9	1 194.90	0.00

TRM (Table 4). Coefficient 95% confidence intervals did not overlap zero in either treatment (see Table 4).

Standing and lying time

Percentage of time steers spent standing was greater for CARM than TRM in 2016 ($t = 2.723$, $P < 0.05$) and 2017 ($t = 6.833$, $P < 0.001$) (see Table 1). Conversely, the percentage of time lying by steers was lower for CARM in 2016 ($t = -2.723$, $P < 0.05$) and 2017 ($t = -6.833$, $P < 0.001$). Inconsistent trends between treatments and years were observed for within-season dynamics regarding early, middle, and late thirds of the grazing season (Fig. 4).

For categorical models predicting standing time in CARM, phase was the best predictor, accounting for 99% of model weight (Table 5). Conversely for TRM, ecological site was the best predictor of standing time ($\omega_i = 1.00$ or 100%), with loamy plains having more standing time. The TRM model had a strong weather influence with maximum temperature (Tmax), whereas weather variables were not strong predictors for CARM. The final AIC

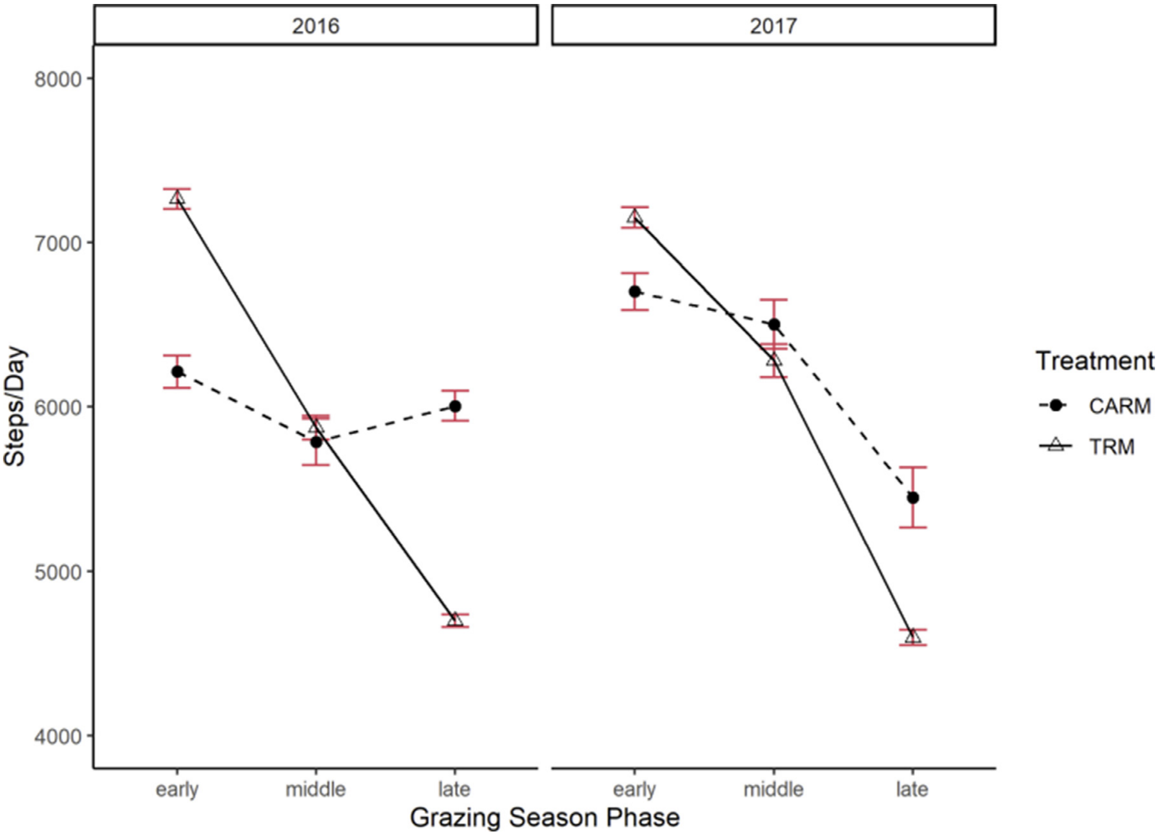

Figure 2. Mean (± 1 standard error) daily step counts of yearling steers for three phases (early, mid, and late) in contrasting grazing treatments. CARM indicates collaborative adaptive rangeland management, which employed rotational grazing among ten 130-ha paddocks, and TRM is traditional rangeland management with season-long (mid-May to October) grazing in each of ten 130-ha paddocks at the US Department of Agriculture–Agricultural Research Services Central Plains Experimental Range, Nunn, Colorado, 2016 and 2017.

Table 4
Coefficient estimates and 95% confidence intervals for weather variables selected using information-theoretic model selection influencing yearling beef cattle step counts between years in contrasting grazing treatments. CARM indicates collaborative adaptive rangeland management, which employed rotational grazing among ten 130-ha paddocks, and TRM is traditional rangeland management with season-long (mid-May to October) grazing in each of ten 130-ha paddocks at the US Department of Agriculture–Agricultural Research Services Central Plains Experimental Range, Nunn, Colorado, 2016 and 2017.

Best model	*P*	Estimate	95% CI
CARM			
Days within paddock	< 0.0001	−0.4391	−0.5330 to −0.3452
TRM			
Days within paddock	< 0.0001	−0.1820	−0.1915 to −0.1725

Table 5
Information-theoretic model selection using Akaike's information criterion (AIC) for yearling beef steer standing time between years as influenced by treatment and weather in contrasting grazing treatments. CARM indicates collaborative adaptive rangeland management, which employed rotational grazing among ten 130-ha paddocks, and TRM is traditional rangeland management with season-long (mid-May to October) grazing in each of ten 130-ha paddocks at the US Department of Agriculture–Agricultural Research Services Central Plains Experimental Range, Nunn, Colorado, 2016 and 2017. Model selection included year as a random effect and individual animal as a repeated effect.

	CARM			TRM		
Models	AIC	ΔAIC	ω_i	AIC	ΔAIC	ω_i
Treatment variables						
Phase	−4 871.6	0.00	0.99	−10 008.1	32.10	0.00
Null	−4 856.9	10.60	<0.01	−10 012.5	27.70	0.00
Days within paddock	−4 853.8	16.70	<0.01	−10 009.8	30.40	0.00
Ecological site	−4 848.9	18.60	0.00	−10 040.2	0.00	1.00
Weather variables						
Temperature (Tmax)	−4 841.9	15.00	0.00	−10 065.8	0.00	1.00
Precipitation	−4 857.6	0.70	0.41	−10 018.5	47.30	0.00
Null	−4 856.9	0.00	0.59	−10 012.5	53.30	0.00
Final model						
Phase	−4 871.6	0.00	1.00			
Ecological site + Tmax				−10 092.8	0.00	1.00
Ecological site × Tmax				−10 081.8	11.00	0.00
Tmax				−10 065.8	16.00	0.00
Ecological site				−10 040.2	52.60	0.00
Null	−4 856.9	14.70	0.00	−10 012.5	80.30	0.00

model for predicting standing time for CARM steers only included phase, whereas ecological site + Tmax was the final model for TRM (Table 6). For CARM, the phase coefficient estimates for standing time for both early and late phases were positive compared with midseason, and 95% confidence intervals did not overlap zero for either (see Table 6). For TRM, the coefficient estimates for ecological site (for both loamy and mixed) and Tmax were positive and 95% confidence intervals did not overlap zero, which suggests more standing time in loamier pastures and as temperature increased (see Table 6).

Discussion

Synthesis of scientific experiments comparing continuous, season-long, and rotational grazing have concluded that livestock performance is reduced with rotational grazing (Briske et al. 2008, 2011; Hawkins 2017; Augustine et al. 2020; Derner et al. 2021). Prior studies have hypothesized that a potential mechanism for lower weight gains was the additional energy expenditures of grazing animals incurred with rotation between paddocks (Walker

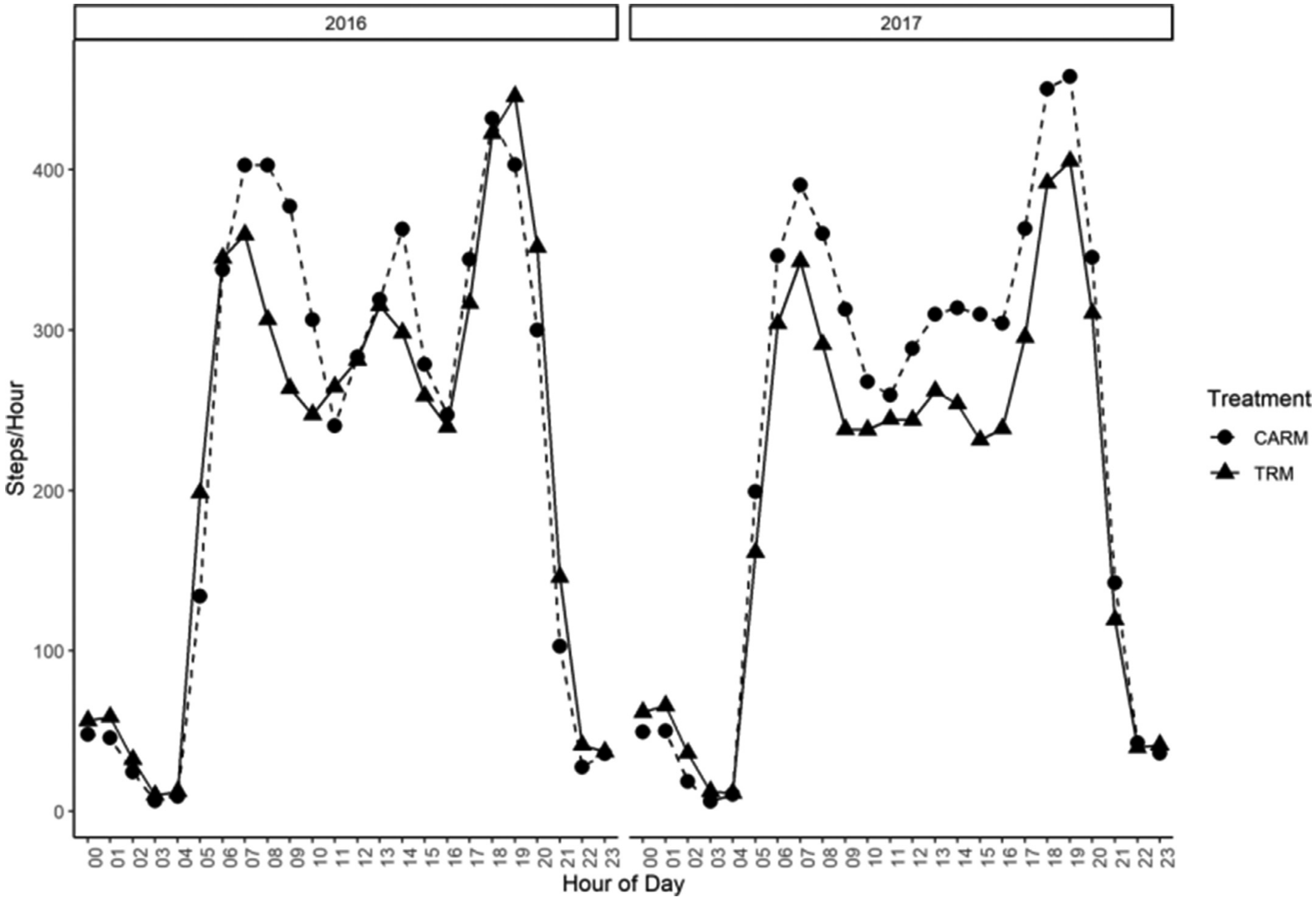

Figure 3. Mean diurnal cycle of step counts for yearling steers in contrasting grazing treatments. CARM indicates collaborative adaptive rangeland management, which employed rotational grazing among ten 130-ha paddocks, and TRM is traditional rangeland management with season-long (mid-May to October) grazing in each of ten 130-ha paddocks at the US Department of Agriculture–Agricultural Research Services Central Plains Experimental Range, Nunn, Colorado, 2016 and 2017.

Table 6

Coefficient estimates and 95% confidence intervals (CI) for top weather variables selected using information-theoretic model selection influencing yearling beef steer standing between study yr (2016 and 2017) in contrasting grazing treatments. CARM indicates collaborative adaptive rangeland management, which employed rotational grazing among ten 130-ha paddocks, and TRM is traditional rangeland management with season-long (mid-May to October) grazing in each of ten 130-ha paddocks at the US Department of Agriculture–Agricultural Research Services Central Plains Experimental Range, Nunn, Colorado.

Best model	*P*	Estimate	95% CI
CARM			
Phase—early	< 0.0001	0.0210	0.0136 to 0.0277
Phase—late	0.0142	0.0092	0.0018 to 0.0166
Phase—middle (set to 0)	—	—	—
TRM			
Ecological site—loamy	< 0.0001	0.0162	0.0108 to 0.0216
Ecological site—mixed	< 0.0001	0.0160	0.0107 to 0.0206
Ecological site—sandy (set to 0)	—	—	—
Maximum temperature (Tmax)	< 0.0001	0.0014	0.0011 to 0.0017

et al. 1985; Derner et al. 2008). Our results do not support this hypothesized mechanism. Differences in mean daily step numbers across the grazing season (from 3% lower in CARM in 2016 to 8% higher in 2017) did occur, but total energetic expenditures of steers in the treatments did not differ. Moreover, the total energy expenditures were predominantly due to basal metabolism, with little influences of standing or steps (about 4% of total energy expenditures). Thus, we conclude that season-long movement dynamics and energy expenditures of free-ranging steers in a semiarid, shortgrass steppe rangeland did not explain the observed weight gain differences between the two contrasting grazing management strategies, TRM versus CARM using adaptive, multipaddock rotational grazing (Augustine et al. 2020).

While we found little evidence that season-long step counts and energy expenditure patterns were related to weight gain differences between treatments, within-season dynamics of step counts suggest that forage quality was the primary driver for reduced weight gains in the CARM treatment (14% and 12% in 2016 and 2017, respectively) (Jorns et al. in prep). Steers in CARM took fewer steps early in the grazing season, suggesting more linear and less tortuous foraging efforts (Augustine et al. 2022). These patterns indicate that CARM steers at 10-fold greater stocking density were less selective in their foraging activities despite on-offer high-quality forage, and this depressed gain potential. In addition, CARM steers took more daily steps later in the grazing season when the animals were at a greater weight and therefore exerting additional energy, presumably in search of gut fill given the lower quality of reduced forage quantity, which further depressed gain potential. Incorporating additional precision livestock technologies, such as automated weight scales, could provide increased temporal resolution that would allow for more detailed assessments of animal energetic expenditures at both the individual animal and treatment levels. More standing, as well as less lying, time by the steers in CARM treatment could also contribute to lower weight gains.

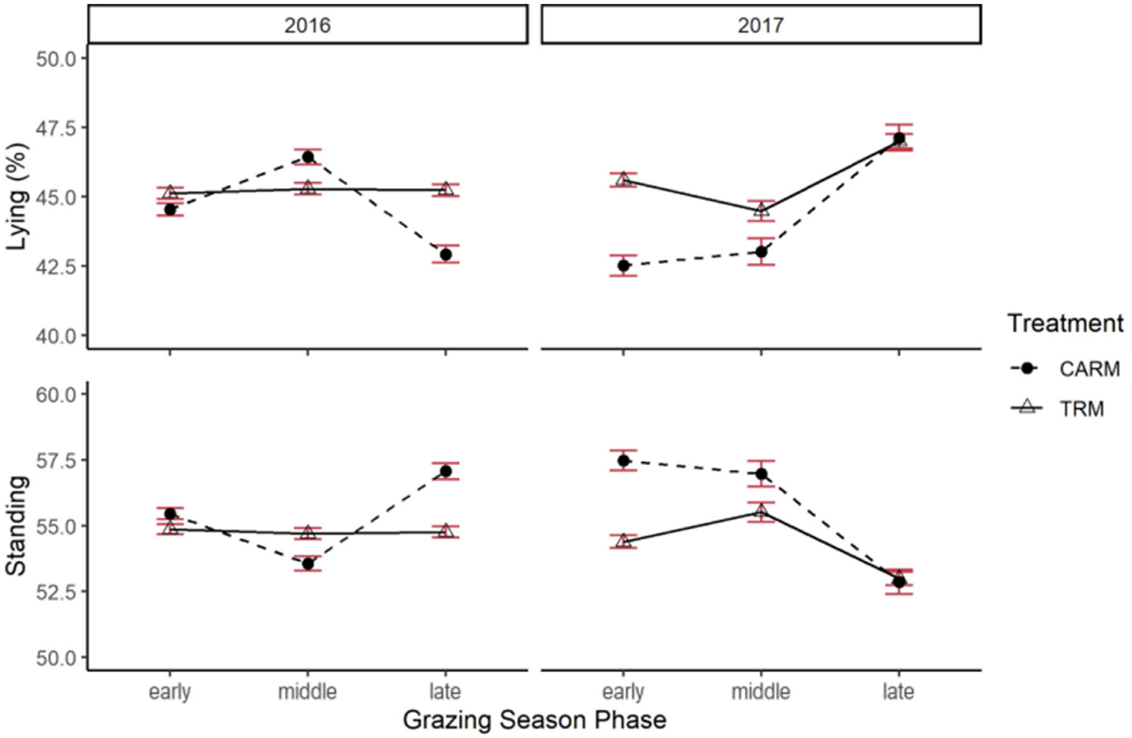

Figure 4. Seasonal yearling beef steer standing and lying percentages (mean ± 1 standard error) by early, middle, and late phase in contrasting grazing treatments. CARM indicates collaborative adaptive rangeland management, which employed rotational grazing among ten 130-ha paddocks, and TRM is traditional rangeland management with season-long (mid-May to October) grazing in each of ten 130-ha paddocks at the US Department of Agriculture–Agricultural Research Services Central Plains Experimental Range, Nunn, Colorado, 2016 and 2017.

Conversely, the decrease in step numbers for the TRM steers as the grazing season advanced suggests that the lower stocking density and familiarity with a single paddock for the entire grazing season resulted in spatial learning patterns, which may foster efficiency in intake of consistently higher quality of forage from nutrient-rich patches and increased patch residence time (Bailey et al. 1996). Prior studies have observed foraging strategies that enhance optimization of energy-time allocation results in positive effects on animal performance (Hixon 1982; Kacelnik and Houston 1984; Bergman et al. 2001).

Another speculation for lower animal performance per grazing animal with rotational grazing (Augustine et al. 2020) is the novelty of entry into "new" paddocks, especially if the animals are naïve (Walker et al. 1985; Launchbaugh and Howery 2005; Derner et al. 2008). We observed two different temporal patterns of naïve steers gaining familiarity with "new" paddocks: 1) steers in TRM exhibited a decline in number of daily steps as the grazing season progressed—possibly increasing patch residence time as the season progressed (Bailey et al. 1996) and 2) repeated, short-term (i.e., week) "familiarization periods" occurred for CARM steers following entry to new paddocks, particularly in 2016. For the latter, steers exhibited a greater number of steps upon entry to each "new" paddock with a plateau in step numbers reached around day 8 of the grazing duration (see Fig. 1). This plateauing after each "familiarization period" in paddocks suggests spatial memory patterns were achieved by CARM steers each time, though it is possible that differences in weather patterns cannot be completely ruled out (Launchbaugh and Howery 2005; Bailey and Brown 2011). We caution that results may be different on cow-calf operations where the cows are already familiar with paddocks.

Cumulatively, our results on within-season step count dynamics and our finding of a lack of difference in season-long energy expenditures between treatments suggest that diet quality is the primary cause of reduced weight gains for CARM (Jorns et al. in prep), rather than the marginal contributions of movement dynamics within the context of our assumptions about animal weights and energy calculations. Prior studies of rotational grazing management suggest that cattle grazing at higher stock densities forage less selectively and therefore consume lower-quality diets leading to reductions in weight gain (e.g., McCollum et al. 1999). Our results partially support hypothesis 1, that naïve free-ranging yearling steers would exhibit greater movements during the early versus later days in the grazing duration *within* a paddock in the CARM treatment (supported in 2016 but not 2017) but refute hypothesis 2 as steers in the CARM treatment did not exhibit consistent different cumulative animal movement dynamics across the grazing season due to both *within* paddock temporal aspects and the movement *between* paddocks over the grazing season.

In addition to human decision-making aspects of grazing management strategies (system of grazing, number of rotations in a grazing season, triggers to move animals between paddocks), steer movement dynamics were also affected by environmental variables. We observed that step counts increased with increasing maximum daily temperatures for steers in the TRM treatment, supporting previous work suggesting thermal environment can affect cattle distribution (Harris et al. 2002). One mechanism for this may be increased frequency returning to the water tank during days with increased temperatures to combat increased water intake requirements (Coimbra et al. 2010; Mannuthy 2017) and seeking better climatic conditions within pasture (Hoffman et al. 2020). Daily activity peak times of standing and lying were consistent for steers regardless of grazing treatment in both years supporting prior reports of diurnal patterns of behavior (DelCurto et al. 2005; Tomkins and O'Reagain 2007; Tomkins et al. 2009). Peak steer standing times were consistent with the hours that step counts were greatest. The total percentage of daily lying time (44–46%) with steers in our study was higher than prior findings (32–36%; Herbel and Nelson 1966; Gary et al. 1970) using mature cows.

Implications

Movement dynamics and energy expenditures did not explain differences in livestock weight gains between rotational and season-long grazing. Rather, high stocking densities employed in rotational grazing, such as the 10-fold higher values in this study, induced less selective foraging by animals (Augustine et al. 2022), leading to lower diet quality (Jorns et al. in prep), and this is likely the primary cause of reduced weight gains (Augustine et al. 2021). Adaptive aspects of the CARM grazing treatment do provide opportunities to mitigate some of the lower weight gains (Augustine et al. 2021) by matching forage availability and quality with animal demand through grazing sequences between paddocks (Derner et al. 2021). Managers could reduce stocking density in the early grazing season, by splitting into two or more herds, to provide greater opportunities for steers to select higher-quality forage through reduced intraherd competition. Combining cows with spatial memory of the paddocks and naïve steers in one herd could potentially benefit movement dynamics of yearling steers and enhance foraging selectivity. Another adaptive approach may be to rotate yearlings more quickly through the paddocks (i.e., shorter duration) early in the grazing season and then regraze the paddocks later in the season. This should result in a shorter "familiarization period" for yearlings the second time in paddocks as animals typically have a reference memory of at least 20 d (Bailey et al. 1996). The effectiveness of such an approach would depend in part on the capacity for cattle to remember paddock attributes and forage distribution and quality (or reference memory) (Bailey et al. 1996). It is also dependent on the capacity of vegetation to regrow following the first grazing period.

Declaration of Competing Interest

None.

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